Ecological Collapse in Mapped and Conserved Landscapes: The Architecture of Survival

Evidence from the Nepean Peninsula's Calcareous Dune Systems

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Executive Summary

Despite sustained investment in conservation and a growing extent of protected land, ecological collapse continues across many conserved landscapes. Vegetation may remain mapped and visually intact, yet critical processes—recruitment, ground-layer functioning, hydrological coherence, and biological connectivity—have already failed. This work argues that such outcomes are not the result of poor implementation or isolated local damage, but arise from a persistent conceptual error: the conflation of legal protection and structural retention with ecological function and persistence.

Using the Nepean Peninsula's calcareous dune systems as a fully resolved case, this study demonstrates that persistence depends on whether ecological routes for recruitment, movement, and renewal remain open under opposition. Where these routes are closed—by hydrological constraint, biological selection, or mis-sequenced disturbance—collapse proceeds inside protected land, even while canopy structure persists. Protection prevents further clearing, but it does not, on its own, reopen closed pathways or restore the conditions required for regeneration and continuity.

The work is structured in two Parts that operate at complementary scales. **Part I** establishes the diagnostic problem. It shows that area-based protection and condition-based assessments frequently mask functional collapse, allowing systems to persist structurally while failing ecologically. Drawing on the Nepean Peninsula as a diagnostic landscape, it reframes conservation outcomes in terms of functional thresholds and route availability rather than resilience, cover, or management intent. Persistence is treated not as a trait carried forward by protection, but as a conditional outcome disclosed when disturbance acts on a system whose internal pathways may already be exhausted.

Protection targets do not guarantee function.
A 30% protection target only has meaning if a sufficient proportion of that land is functioning ecologically. Where protection locks in systems that cannot recruit, cannot route movement,

and cannot renew under disturbance, the effort has not failed later—it failed at the point of designation. Protection preserves tenure; only function secures persistence.

Part II provides the mechanistic explanation for this diagnosis. Coastal Moonah Woodland occupies unconsolidated calcareous sands mantling calcarenite dune systems, where sand mantle thickness and soil profile development vary across dune crests, swales, and disturbed surfaces, yet a shared sand-over-calcarenite architecture governs surface hydrology and soil-water-repellency expression. Within this setting, dense thicket formation by *Gaudium laevigatum* (Coast Teatree) restructures microclimate, concentrates rabbit activity, and amplifies soil-water-repellency–driven preferential flow. These interacting processes produce a repeatable collapse sequence in which juvenile cohorts are truncated, ground-layer function fails, and recruitment routes close long before canopy loss becomes visible.

By tracing these mechanisms in detail, Part II explains why common management actions—blanket clearance, exposure-based weed control, or mis-sequenced thinning—frequently recreate the very disturbance conditions that sustain collapse. It shows that method choice and sequencing determine whether rainfall and disturbance function as recovery pathways or as invasion-facilitating pulses. Selective, in-situ suppression emerges not as a preference, but as a structural requirement under these substrate and hydrological conditions.

Taken together, Parts I and II demonstrate that increasing the extent of protected land is not equivalent to protecting ecological function. Persistence requires the restoration of functional architecture: open recruitment routes, coherent surface hydrology, suppression of cohort-truncating selectors, and connectivity operating **in use rather than appearance**. The Nepean Peninsula is presented not as a special case, but as a clear expression of processes likely operating wherever conserved landscapes retain structure while losing function.

The analysis is synthesised using an **Evolutionary Flexibility (EF) diagnostic framework**, in which persistence depends on the availability and use of ecological routes for recruitment, movement, and renewal under opposition. EF is employed here as an organising lens for interpreting observed collapse and recovery processes, rather than as an abstract model imposed on the system (**Brown, 2026, preprint**). *(See Brown, 2026, manuscript under review; Appendix A.5; and the companion volume Survival Is Conditional for the full EF–CT–FL framework and operational proxies)*

Scope clarification. *This analysis does not target any particular land-tenure category (public, private, conservation estate, roadside, or offset land). The mechanisms described operate wherever ecological function has been lost while structure and designation remain intact; tenure determines jurisdiction, not outcome. Findings are substrate-specific to calcareous dune systems and should not be transposed uncritically to siliceous sands, clays, or basaltic soils.*

Reader's guide ("*How to read this document*")

This work is structured in two Parts. Part I establishes why conservation outcomes fail when protection is mistaken for function, using the Nepean Peninsula as a diagnostic case. Part II provides the mechanistic and operational evidence for that diagnosis, detailing how hydrology, disturbance, and biological selection interact on calcareous dune systems to close and reopen ecological routes. Readers seeking policy implications may read Part I alone; readers seeking mechanism and management guidance should consult both Parts.

PART 1— PROTECTION WITHOUT FUNCTION

Conservation policy and practice have increasingly equated protection with persistence, assuming that formal designation, management intent, or area retained are sufficient to secure ecological futures. Yet across many protected landscapes, ecological function continues to decline despite intact canopy structure and long-standing tenure. Recruitment fails, ground-layers simplify, corridors cease to operate in use, and communities persist only as ageing structural remnants. This Part argues that such outcomes are not anomalous failures of implementation, but predictable consequences of conflating protection with function. Using the Nepean Peninsula as a diagnostic landscape, it shows that persistence depends not on designation or extent, but on whether ecological routes for recruitment, movement, and renewal remain open under opposition. Where these routes are closed—by hydrological constraint, biological selection, or disturbance sequencing—collapse proceeds inside protected land, even as vegetation remains mapped and visually present (Figures 1-4).

Figure 1. *Mapped Coastal Alkaline Scrub (CAS) on the Nepean Peninsula, originally Moonah Woodland. The mapping captures retained canopy structure but not ecological function; recruitment, ground-layer continuity, hydrological coherence, and movement pathways have already failed, illustrating the diagnostic problem that protection preserves appearance while function collapses.*

This reframes failure explicitly. A 30% protection target only has meaning if a sufficient proportion of that land is functioning ecologically. Where designation freezes systems that no longer recruit or connect, the failure does not emerge later through poor management—it occurs at the moment protection is conferred.

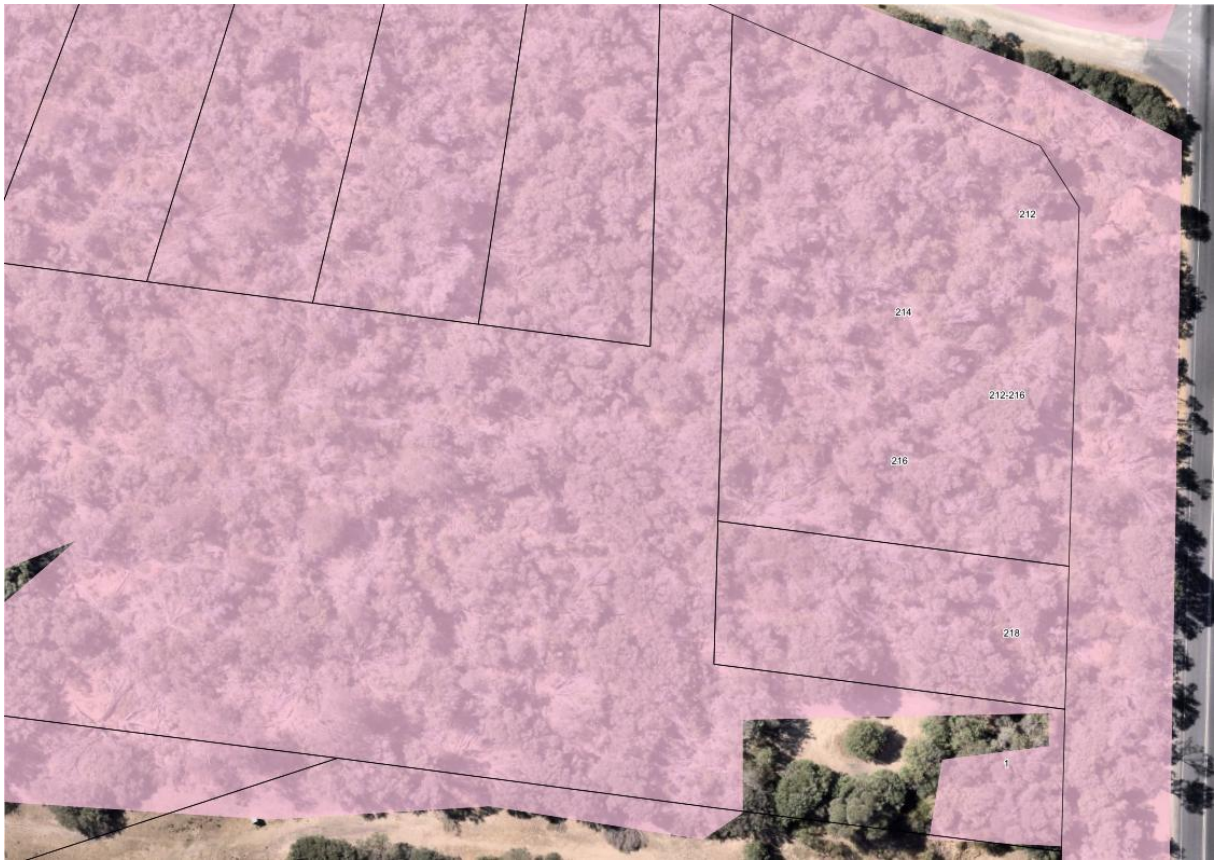

Figure 2. *Vegetation mapping of the Nepean Peninsula showing canopy-retained but functionally collapsed Coastal Moonah Woodland. Pink polygons indicate mapped vegetation extent; ground-layer collapse, hydrological incoherence, and recruitment failure occur within these mapped units.*

Figure 2.1. *On-ground condition within areas mapped as Coastal Alkaline Scrub (CAS). Dense* ***Gaudium laevigatum*** *thicket dominates the mid-storey, suppressing ground-layer architecture and driving hydrological bypass. The understorey is characterised by late-stage invasive species—including* ***Delairea odorata, Oxalis pes-caprae, Polygala myrtifolia, Rhamnus alaternus,*** *and scattered* ***Pittosporum undulatum****—indicating advanced functional collapse. Native species persist only as remnant survivors* ***(Leucopogon parviflorus, Poa labillardierei*** *[stressed/dying],* ***Tetragonia implexicoma, Rhagodia candolleana)****, with no evidence of recruitment or seed-safe microsites. Although still mapped as vegetation, the system has lost the functional processes—recruitment, ground-layer continuity, and hydrological coherence—required for persistence.*

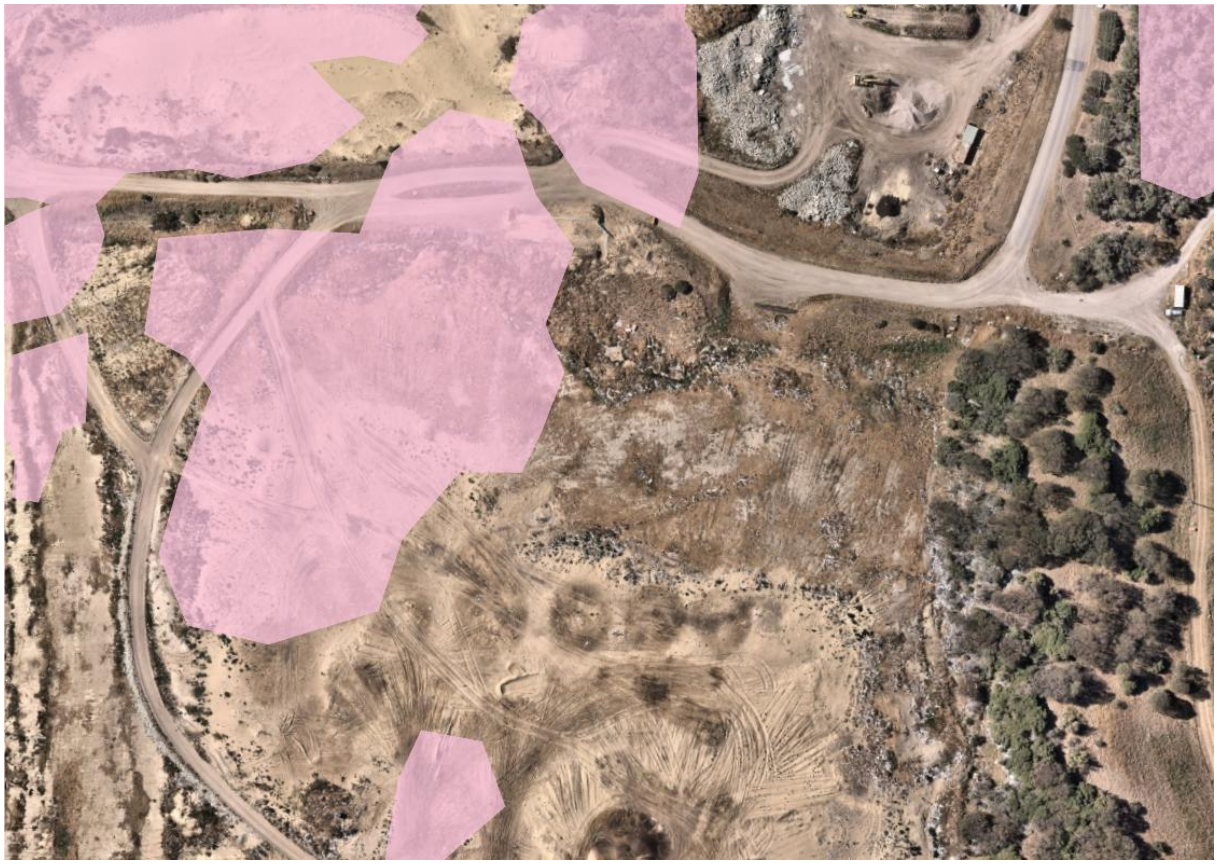

***Figure 3**. Mornington Peninsula Shire landfill disturbance mapped as vegetation. This site contains no remaining vegetation, no ground-layer architecture, and no recruitment potential, yet appears as mapped Coastal Moonah Woodland under current vegetation datasets. This illustrates the structural bias of mapping systems that record extent rather than ecological function.*

Figure 3.1. *On-ground condition of a former Coastal Alkaline Scrub (CAS) site within the Mornington Peninsula Shire landfill disturbance. Although mapped as native vegetation in current datasets, the site retains no vegetation, no ground-layer continuity, and no hydrological or recruitment function, illustrating the diagnostic gap between mapped extent and ecological reality.*

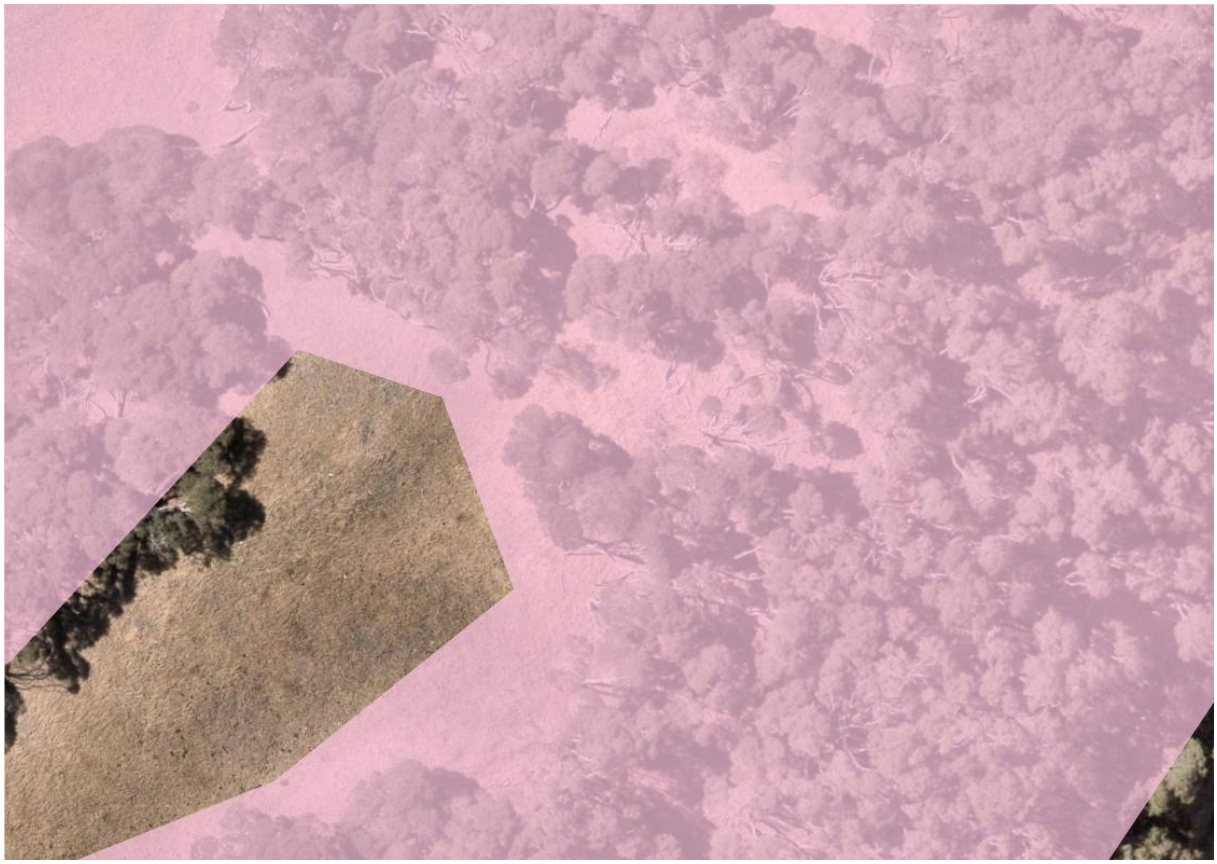

***Figure 4**. Close-up of mapped vegetation units showing structural retention with underlying degradation: exposure patches, weed-dominated surfaces, and early hydrological scarring.*

Figure 4.1. *The image shows a collapse-phase Moonah woodland within the pink-overlay zone: mature Moonah* ***(Melaleuca lanceolata subsp. Lanceolata)*** *stems persist, but African Boxthorn* ***(Lycium ferocissimum)*** *dominates the mid-storey and the ground-layer is effectively absent. Bare mineral sand, hydrophobic surface expression, and chronic rabbit and cattle pressure have closed recruitment routes, leaving only legacy adults and invasive structure. Although mapped as an EVC, the site no longer expresses the functional architecture, ground-layer continuity, or recruitment pathways required for that classification. It is structurally retained but functionally extinguished.*

The soft, easily eroded soil on slopes is the surface-process expression of the same collapse: loss of ground-layer architecture, SWR-driven bypass flow, thermal amplification, and chronic herbivore pressure have removed cohesion from the upper millimetres. Once these constraints fail, the surface mantle collapses into a friable, mobile skin that shears under foot pressure, reflecting route closure rather than competitive displacement. This surface instability is incompatible with the hydrological and microsite conditions that define the mapped EVC, further confirming that the polygon retains appearance but not ecological function.

PART 1.1 Moonah Woodland: When Protection Fails to Preserve Function

Selectors, Surface Processes, and the Loss of Evolutionary Pathways on Calcareous Dune Systems

Part I establishes the failure of protection-led conservation as a systemic problem rather than a site-specific exception, reframing conservation outcomes in terms of functional thresholds and lost routes rather than resilience or condition scores. The threshold discussed here does not refer to the proportion of land that is protected, mapped, or designated. It refers to the proportion of the landscape that is simultaneously functioning—actively recruiting, hydrologically coherent, and connected in use. It sets out the conceptual basis for diagnosing collapse in conserved systems and identifies the need for mechanistic explanation. That explanation—the processes by which routes are closed and, under specific conditions, reopened—is developed in Part II.

Moonah Woodland: When Protection Fails to Preserve Function

Selectors, Surface Processes, and the Loss of Evolutionary Pathways on Calcareous Dune Systems

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Scope and evidentiary basis.

The points set out below diagnose why increasing the extent of protected land does not, on its own, prevent ecological collapse. They are intended as a policy- and planning-level synthesis rather than a site report. The hydrological and ecological mechanisms underpinning these failures—particularly those involving soil-water-repellency, disturbance sequencing, seedbank activation, and route closure on calcareous dune systems—are examined in detail in *Hydrological and Structural Impacts of Gaudium laevigatum Thicket Formation in Coastal Woodlands* (Brown, 2026). That companion work provides the mechanistic and operational analysis supporting the diagnostic claims presented here.

1. Protected area expansion is desired, but functional habitat continues to collapse.

Across the Nepean Peninsula, increasing the amount of **protected land—private or public**—is often presented as the primary solution to biodiversity decline. Formal designation can prevent clearing and constrain new impacts, but it does not restore function. **Protected land ≠ functional habitat.** Protection lowers clearing risk and can reduce some pressures when well implemented, yet global assessments show **highly variable outcomes**; many sites still record biodiversity declines or unmanaged threats **inside** protected boundaries. Effectiveness depends on **sustained, threat-specific management rather than tenure alone** (Rodrigues & Rouyer, 2023; McNicol et al., 2023; Pulido-Chadid, Virtanen, & Geldmann, 2023; Pulido-Chadid, Rahbek, & Geldmann, 2025).

Moonah Woodland occupies unconsolidated calcareous sands mantling calcarenite dune systems—an architecture that varies locally in sand mantle thickness across dune crests, swales, and disturbed surfaces, yet consistently **produces soil-water-repellency (SWR)** as an **emergent surface condition once ground-layer processes degrade**, rather than as an inherent geological property.

On these Nepean dune systems, the active mechanisms of collapse—low-density rabbit browsing that truncates juvenile cohorts, and SWR-driven hydrology that diverts water via preferential flow—persist inside protected land unless directly treated; designation alone does not reopen recruitment routes or restore ground-layer function (Mutze, Cooke, & Jennings, 2016a; Mutze, Cooke, & Jennings, 2016b; Doerr, Shakesby, & Walsh, 2000). **Coastal Moonah Woodland (CMW)** remnants on Mornington/Nepean are frequently **degraded and weed-invaded,** underscoring the gap between protection and function (Moxham & Turner, 2009).

A hectare contributes nothing to persistence if it is:

- dominated by invasive species
- structurally blocked
- hydrologically or trophically incoherent
- losing redundancy in common species
- unable to support natural recruitment.
- **functioning as refuge supporting rabbit selection rather than native fauna**—a condition shown to truncate juvenile cohorts at **≤ 0.5–2 rabbits ha^{-1}** and depress native cover and richness (Mutze et al., 2016a; Mutze et al., 2016b).

Protection changes tenure. **Function changes only when evolutionary pathways reopen**: a porous, biologically active ground-layer, open dispersal corridors, and sustained juvenile cohorts. **Map colour does not deliver these outcomes.** Protected land can prevent loss; **only functioning land can produce future life.** Global syntheses consistently show that outcomes hinge on **threat-specific intervention**, not designation alone (Pulido-Chadid et al., 2023; Pulido-Chadid et al., 2025).

Functional thresholds and the case for restoration.

Persistence depends on how much **functional dune habitat remains at the local movement scale**, not merely how much land is protected. Empirical and theoretical work indicates that when the proportion of the landscape that is functioning *at the same time* falls well below roughly a quarter to a third, recovery becomes unlikely because recruitment and dispersal routes no longer overlap in space and time. This is a warning threshold, not a conservation or protection target, and **it cannot be achieved by designation alone**.

As an empirical guide, landscapes in which roughly a third of the landscape is *operationally functional* are far more likely to persist, whereas collapse risk escalates sharply once functioning habitat falls **below ~20–30%** (Fahrig, 2013; Estavillo et al., 2013; Zhang, Chase, & Liao, 2024). This does **not** justify inaction below the threshold; it establishes an **urgent**

restoration imperative. Where functional habitat sits below this range—as it does across much of the Nepean Peninsula—**active restoration is the only pathway** from **protected** land to **persistence**. A landscape may exceed a 30% protection target and still fall below the functional threshold; in such cases, protection has preserved space but not persistence.

Nepean Peninsula Coastal Moonah Woodland occupies relict aeolian calcareous dune systems—unconsolidated sands mantling partially lithified calcarenite (aeolianite) dune cores. On Nepean calcarenite dunes, ***"functional"*** means **recruitment across seasons**, **hydrology that wets beyond a thin surface skin (no soil-water-repellency crust or rilling)**, and **selectors suppressed** to cohort-keeping **levels (≤ 0.5–2 rabbits ha^{-1}). Protected colour on a map does not secure these conditions** (Doerr et al., 2000; Mutze et al., 2016a,b).

Function (mechanistic).

On Nepean calcarenite dunes, function means maintaining **infiltration continuity and surface moisture residence**, a **biologically active ground-layer** (moss–herb–litter–fine roots), **seed-safe microsites**, and **open dispersal routes**. Collapse follows a repeatable chain:

high canopy interception → hydrophobic litter / SWR → shallow pulse capture → preferential flow, with **rabbit selection** closing recruitment routes even inside protected land (Crockford & Richardson, 1990; Doerr et al., 2000; Miralles, Gash, Holmes, de Jeu, & Dolman, 2010; Mutze et al., 2016a).

Impact of weed invasion (Nepean calcarenite dunes).

- **Degraded CMW within protected estates**: Weed-dominated stands, including Polygala myrtifolia and Rhamnus alaternus, are frequently recorded **inside mapped CMW**—a direct demonstration that tenure ≠ function (Moxham & Turner, 2009).
- **Exposure-recruitment coupling**: Polygala myrtifolia shows **high germination (≈ 93–95%)** under autumn–spring regimes (light and dark) and **surface-biased emergence** (~48% at the surface; near-zero by **8 cm**); thus **fresh exposure pulses** on dunes rapidly convert to **weed recruitment surges** (Roberts, Moloney, Monie, & Florentine, 2023).
- **Hydrologic lock-in**: Weed-driven loss of the ground-layer (plus SWR) pushes systems toward **preferential flow and rilling**, further drying seed-safe microsites and **preventing native recruitment** (Doerr et al., 2000).

Seedbank dynamics (why inaction = ecological decay).

- **Native seedbank depletion**: Chronic cohort loss under **low-density rabbits** and repeated surface drying under **SWR** reduce the **native propagule pool** and the frequency of **seed-safe microsites**; each season without recruitment **draws down** the native seedbank (Mutze et al., 2016a,b; Doerr et al., 2000).
- **Invasive seedbank loading**: Polygala myrtifolia is **non-dormant** with **very high germination** under local temperature regimes; emergence is **strongly surface-weighted**, so disturbance and exposure **reload the surface layer** with invasive seedlings and seed inputs. In lab and cabinet trials, emergence fell to zero at **8 cm** burial, indicating that **surface exposure** is the critical risk layer (Roberts et al., 2023).
- **State shift inside protected tenure**: In degraded CMW, **very high weed cover** and altered structure are documented; stands can move into "***Potential/indeterminate CMW***" states where weeds dominate and natives persist mainly as residuals or seedbank traces (Moxham, Cheal, & Turner, 2009).

Protection without function is ecological decay—cohorts are lost, surfaces harden, and the seedbank is both depleted of natives and re-loaded with introduced species while maps stay green (Roberts et al., 2023; Doerr et al., 2000; Mutze et al., 2016a,b; Moxham & Turner, 2009).

Functional test for "*protected*" sites.

(Nepean calcarenite dunes; applies to protected land—private or public)

- **Recruitment present?** Juvenile classes of palatable natives visible across seasons → **Yes / No** (Low rabbit densities can remove whole juvenile cohorts; Mutze et al., 2016b).
- **Ground-layer continuous?** Moss–herb–litter continuity; low bare ground; fines retained → **Yes / No** (SWR/exposure increase runoff and erosion when the ground-layer is lost; Doerr et al., 2000).
- **Hydrology open?** No SWR crust at surface; wetting beyond a thin skin; no rilling/blowouts → **Yes / No** (Hydrophobic layers drive preferential flow and surface instability; Doerr et al., 2000).
- **Selectors reduced?** Rabbit sign low/absent within canopies and at pinch-points → **Yes / No** (Density–damage thresholds for vegetation condition and cohort survival; Mutze et al., 2016a; 2016b).

Fail any two: the site is **"*protected*" but not functional**; address **selectors** (e.g., rabbits) and **surface architecture** (avoid **bare-ground pulses** on SWR-prone sands) **before any structural opening** (Doerr et al., 2000; Roberts et al., 2023).**Principle:**
Protected land prevents loss. **Only restored, functioning land produces future life.**

Commitment Box: From Protection to Persistence (Nepean Calcarenite Dunes)

Commitment:
Protection without function is ecological decay—cohorts are lost, surfaces harden under **SWR**, and the **seedbank is simultaneously depleted of native propagules and re-loaded with introduced species** via exposure-triggered recruitment (Roberts et al., 2023; Doerr et al., 2000; Moxham & Turner, 2009). On the Nepean Peninsula, **restoration is not optional**—it is the only mechanism by which protected land can contribute to persistence.

We therefore commit to:

- Restore **landscape-level ecological function** to the point where a sufficient proportion of the landscape is operating simultaneously (empirically ~30%), recognising this as a persistence threshold—not an area target and not achievable through designation alone (Fahrig, 2013; Estavillo et al., 2013).

- **Suppress selectors to cohort-keeping levels (≤ 0.5–2 rabbits ha^{-1})** across public **and** private protected land (Mutze et al., 2016a,b).

- **Repair surface hydrology and ground-layer architecture** on calcarenite sands—eliminate **SWR crusts**, prevent **bare-ground pulses**, and retain/restore **moss–herb–litter** continuity so wetting extends beyond a thin skin and **seed-safe microsites** persist (Doerr et al., 2000).

- **Prevent invasive seedbank reload:** avoid scalping and maintain strict least-disturbance. The selective in-situ kill approach is **structurally symmetrical in constraint terms**: it preserves existing surface architecture so shade, litter continuity, and micro-roughness remain intact, **moderating surface temperatures** and **slowing** the **expression of soil-water-repellency (SWR).**
  By keeping the biologically active millimetres cooler and less hydrophobic, seed-safe microsites are not lost, and rainfall is less likely to bypass the surface entirely (Doerr et al., 2000). This **prevents** the **bare-soil exposure** and mineral disturbance that close recruitment routes and synchronise surface-biased weed germination (Roberts et al., 2023).
  In contrast, rough clearance is **structurally asymmetrical**, collapsing multiple surface constraints at once—destroying structure, exposing sand, increasing thermal load, accelerating SWR expression, and generating large disturbance-aligned pulses. Retaining killed plants in place also increases exposure for rabbits—reducing movement and digging—and removes the friable, open microsites favoured by blackbirds for foraging and seed deposition.
  Under least-disturbance, admissible routes are not further closed, and the residual invasive seedbank declines gradually through time and follow-up rather than being reactivated by disturbance.

- **Measure success by outcomes, not inputs**—report **recruitment across seasons**, **open hydrology (no SWR/rilling)**, **selector density below threshold**, and the **% of landscape that is functional** in each management unit (Fahrig, 2013; Doerr et al., 2000; Mutze et al., 2016a,b).

2. EF framing: selectors, routes, and collapse.

EF (Evolutionary Flexibility) = the **available, usable routes** a system has to persist under opposition **(formalised in Brown, 2026, manuscript under review)**. It is **observed through use**, not inferred from cover.

- **Routes** = coherent, open pathways that allow processes to continue (dispersal, recruitment, trophic transfer, hydrology, mutualisms).
- **Selectors** = **forces that remove routes** (e.g., chronic herbivory at cohort-truncating levels; hydrologic incoherence; pathogen spread; exposure pulses that synchronise weed recruitment).
- **Opposition** = the disturbance that **reveals** whether routes still exist and can be used (fire, drought, heatwaves, flooding, browsing pressure, pathogen pulses).
- **Function** = the **observable ability** to generate new individuals, to use routes (and link routes), and to carry processes forward (recruitment across seasons; movements through corridors; stable hydrology at the surface; trophic continuation).
- **Collapse** = **EF → 0** (the **loss of viable routes**) **even when the canopy remains** (i.e., the map still looks green).

EF is not an analogue for resilience, nor a synonym for adaptive capacity. It is the precondition for both: the set of admissible, usable routes that make persistence possible in the first place. **Resilience is a retrospective** verdict delivered after disturbance; **EF** is the forward-looking architecture that **determines whether resilience is even possible.** A system with no open routes cannot express resilience, no matter how intact its canopy or how favourable its condition score appears. EF therefore shifts the diagnostic focus from structural appearance to the **availability and use of functional pathways**—recruitment, hydrology, dispersal, trophic transfer—under real opposition.

Policy consequence: Either **routes exist and are used**, or **they do not**. **Tenure, policy language, or planting plans do not "*add resilience*."** At best, policy and works **remove selectors** and **re-open routes** so EF becomes **visible in use** (recruitment, movement, process carry-forward). *(See Brown, 2026, manuscript under review; Appendix A.5; and the companion volume Survival Is Conditional for the full EF–CT–FL framework and operational proxies).*

A common **misinterpretation** is **to treat retained structure**—canopy **cover**, mapped **extent**, or visual **greenness**—as **evidence that evolutionary pathways remain open.** This assumption is false on calcareous dune systems. Adults can persist for decades after recruitment routes have closed, hydrology has inverted, and selectors operate unchecked. In

such cases, disturbance does not test resilience; it merely exposes the absence of EF. Recognising this distinction is essential: **structural persistence is not functional persistence**, and the continued presence of adults does not imply that the system retains any capacity to generate future individuals under prevailing conditions.

One-line diagnostic: *If cohorts are not forming, routes are not open—regardless of cover or designation.*

3. What Actually Drives Outcomes: Constraints Admit Routes; Selectors Disclose Outcomes.

Competition is not a driver in this system. It is a *post hoc label* applied to outcomes that have already been determined by constraint architecture. Selection does not act from outside the system to generate winners; it merely discloses which of the routes left open by constraints were viable. Where constraints close, routes disappear **before** any competitive interaction can occur.

For example, when soil-water-repellency (SWR) on calcareous sandy or calcarenite-mantled surfaces causes rainfall to bead and bypass the biologically active surface millimetres, seed-safe microsites are removed and the recruitment route closes. Likewise, when rabbit densities truncate juvenile cohorts, entire recruitment classes are removed before establishment. In both cases, the route is lost irrespective of species identity, abundance, or putative competitive ability (Doerr, Shakesby, & Walsh, 2000; Mutze, Cooke, & Jennings, 2016a; Mutze, Cooke, & Jennings, 2016b). Under such conditions, invoking "*competition*" misdescribes the mechanism: there is nothing left to compete *for*.

EF terms (diagnostic).

- **Constraint Topology (CT)** defines which routes are admissible: thresholds, dependencies, bottlenecks, and timing rules that determine whether recruitment, movement, and renewal are even possible (Brown, 2026, preprint).
- **Selectors** (often mislabelled as "competition") operate *only* among the routes that CT leaves open. At cohort-truncating densities, rabbits do not suppress performance within an open pathway; they **eliminate the pathway itself** by removing entire juvenile classes (Mutze et al., 2016a; Mutze et al., 2016b).
- **Outcomes** are admitted by constraints and disclosed by selection. Systems collapse (EF → 0) when admissible routes are lost, even if canopy or visual structure persists (Brown, 2026, preprint; Doerr et al., 2000; Moxham & Turner, 2009).

Operational consequence.

Attempting to change "competition" without repairing constraints cannot reopen routes, because competition is not what closed them. Options return only when the constraint set itself shifts. Practically, this requires:

- **Re-establishing ground-layer continuity** so wetting extends beyond a thin hydrophobic skin on SWR-prone sands, recreating seed-safe microsites (Doerr et al., 2000);
- **Reopening corridor pinch-points in use**, so connectivity is functional rather than merely visual (Oehri, Wood, Touratier, Leung, & Gonzalez, 2024);
- **Maintaining rabbits ≤ 0.5–2 ha^{-1} during recruitment windows**, so juvenile routes are not closed at emergence (Mutze et al., 2016a; Mutze et al., 2016b).

Absent these shifts, selectors have nothing to select among.

Why "Building Resilience" Misdirects Management.

Resilience cannot be managed directly; **conditions can**. Framing management around resilience implicitly assumes that pathways remain open and merely need to be "*strengthened*". In systems where constraints have already closed routes, this assumption is false. Practical, testable conditions instead include: reducing chronic herbivore pressure to cohort-keeping levels (Mutze et al., 2016a, 2016b); restoring recruitment windows and ground-layer architecture that moderate SWR and recreate seed-safe microsites (Doerr et al., 2000); reopening dispersal and interaction pathways so connectivity is functional in use rather than appearance (Oehri et al., 2024; Neel, Tumas, & Marsden, 2014); and avoiding exposure pulses that synchronise *Polygala* flushes on opened sand (Roberts, Moloney, Monie, & Florentine, 2023).

Where these process conditions are not restored, systems do not "*become resilient*"; they continue to decay—adults persist while admissible routes collapse (Doerr et al., 2000; Mutze et al., 2016a).

Resilience Is a Retrospective Verdict, Not a Trait.

Policy language often promises to "*build resilience*," but resilience is a **post-disturbance verdict**—a description of whether persistence occurred—not a property carried forward in advance (Brown, 2026, manuscript under review). Field evidence repeatedly shows that appearance can persist while function fails: SWR blocks wetting; low-density herbivory removes cohorts; recruitment ceases despite canopy retention (Doerr et al., 2000; Mutze et al., 2016b).

Why Resilience Language Weakens Collapse Diagnosis.

Treating resilience as a property reframes architectural failure as a temporary deviation. Systems that have already lost recruitment, ground-layer function, dispersal pathways, or trophic routing can still be described as "*resilient*" so long as canopy or greenness remains—for example, degraded Coastal Moonah Woodland within protected tenure (Moxham & Turner, 2009). Management effort then tracks appearance rather than process repair (Doerr et al., 2000; Mutze et al., 2016b).

The diagnostic bottom line is simple: **a system either generates future individuals under prevailing conditions, or it does not**. Language cannot substitute for routes in use (Brown, 2026, manuscript under review).

Corridors, Recruitment, and the Illusion of Resilience.

Connectivity is not visual continuity. Corridors blocked by invasive shrubs or degraded by herbivore pressure are not corridors *in use*. Functional connectivity requires movement, interaction, dispersal, and reproduction; corridors that do not pass these tests fail functionally (Oehri et al., 2024; Neel et al., 2014).

Where corridors fail, populations isolate, recruitment windows collapse, and evolutionary processes cease. Describing such systems as "*resilient*" is therefore a **category error**. Persistence emerges from functioning evolutionary pathways—open, usable routes—not from retained structure or retrospective labels (Brown, 2026, manuscript under review).

4. Most Moonah Woodland and Coastal Alkaline Scrub are already collapsed (Nepean).

Community, not tree. Coastal Moonah Woodland (CMW) is a plant community defined by **structure, ground-layer architecture, and functioning processes**, not by the mere presence of Moonah (*Melaleuca lanceolata*) stems. Sites with mature Moonah but without the characteristic ground-layer continuity and recruitment are **not functioning woodland**, even where canopy persists (Moxham & Turner, 2009; Moxham, Turner, Walker, & Douglas, 2010).

Mapping shows structure; it does not diagnose function. On the Mornington Peninsula, CMW has declined to **< 9%** of its pre-settlement extent, and most remaining stands are significantly degraded, with Moonah regeneration rarely observed (SAC/FFG Action Statement; Tonkinson et al.; ARI/DSE summaries) (DSE, 2003; Tonkinson, Taranto, & Kefford, 2002; Moxham et al., 2010). In this condition, mapping commonly captures **adult structure** while **processes have already failed** (Moxham & Turner, 2009).

Mechanism of collapse — why adults persist while the community fails

- **On unconsolidated calcareous sands mantling calcarenite dune systems**, soil-water-repellency (SWR) forms a hydrophobic surface layer, causing rainfall to bead and bypass the biologically active seed layer via preferential flow. Seed-safe microsites are removed and recruitment windows close (Doerr, Shakesby, & Walsh, 2000).
- **Low-density rabbits**—even around **≤ 0.5–2 ha^{-1}**—truncate juvenile cohorts, so adults persist while recruitment classes are repeatedly erased (Mutze, Cooke, & Jennings, 2016a; Mutze, Cooke, & Jennings, 2016b).
- **Weed pressure** (e.g., *Polygala myrtifolia*, *Rhamnus alaternus*, *Ehrharta* spp.) and recreational disturbance further simplify understorey structure and block recruitment pathways across CMW and Coastal Alkaline Scrub (CAS) (DSE, 2003; Moxham et al., 2010).
- **What is typically observed on the ground:** ground-layer loss or discontinuity with clear SWR symptoms—water beading, fingered wetting, rilling, and fines loss (Doerr et al., 2000). Moonah juveniles are rare, spatially isolated, and commonly removed by rabbits or suppressed by invasive shrubs; pollination and dispersal pathways are broken. The community is **visually present but functionally absent** (Moxham & Turner, 2009; DSE, 2003).

Corollary (Nepean): Adults ≠ function. In many mapped CMW/CAS parcels, adults persist while **processes have collapsed**. Without recruitment, ground-layer architecture, and usable pathways, the system is already collapsed, irrespective of map colour, tenure, or canopy retention (Moxham & Turner, 2009; Doerr et al., 2000; DSE, 2003).

Operational Test for Any Mapped CMW/CAS Parcel

- **Recruitment present?** Palatable native juveniles visible across seasons (not one-offs) → Yes / No. Low-density rabbits can erase entire cohorts (Mutze et al., 2016b).
- **Ground-layer continuous?** Moss–herb–litter continuity; fines retained; no broad bare patches → Yes / No. Exposure on calcareous sands removes seed-safe microsites and drives runoff and erosion (Doerr et al., 2000).
- **Hydrology open?** No SWR crust; wetting extends beyond a thin hydrophobic skin; no active rilling or blowouts → Yes / No. Hydrophobic surface layers force preferential flow and surface instability (Doerr et al., 2000).
- **Selectors reduced?** Rabbit sign low or absent in canopies and corridor pinch-points (**≤ 0.5–2 ha^{-1}**) → Yes / No. Cohort truncation documented at low densities (Mutze et al., 2016a; Mutze et al., 2016b).

Fail any two: the site may be mapped as CMW/CAS, but it is **functionally collapsed**. First reduce selectors and **protect or repair the surface architecture** (no bare-ground pulses on SWR-prone calcareous sands) **before** any structural opening (Moxham et al., 2010; Doerr et al., 2000).

5. Why Moonah Woodland Is Listed as a "*Component*" of Coastal Alkaline Scrub (Nepean).

This classification reads a collapse gradient, not a nested hierarchy

In formal mapping and vegetation descriptions, Coastal Moonah Woodland (CMW) occurs predominantly within the Ecological Vegetation Class **Coastal Alkaline Scrub (CAS, EVC 858)**. On the Nepean Peninsula, listing "*Moonah Woodland*" as a component of CAS reflects the **current, degraded expression of remnants**, not an intact or hierarchically nested system (Moxham et al., 2010). The classification records **what remains structurally detectable along a collapse gradient**, rather than the persistence of a fully functioning woodland community.

Why CMW shows up as a "*component*"

Mapping frequently detects the **last remaining architectural element—Moonah (*Melaleuca lanceolata*)—after the ground-layer, mid-storey, dispersal pathways, and recruitment routes have already failed** (Moxham & Turner, 2009). On the Mornington Peninsula, regeneration of Moonah is rarely observed; age structures are strongly skewed toward mature individuals, and most remnants are significantly degraded. Adults persist while community-level processes are lost (DSE, 2003).

This persistence is **not incidental**. Moonah remains visible because it possesses architectural traits that allow survival after surface processes have collapsed.

Moonah as an architectural keystone

Moonah (*Melaleuca lanceolata*) functions as an **architectural keystone** in Coastal Moonah Woodland on the Nepean Peninsula. Its persistence reflects **physical structure and rooting architecture**, not ongoing community function.

Moonah is **deeply rooted into calcareous dune systems**, penetrating through **unconsolidated calcareous sands and palaeosols that mantle calcarenite (aeolianite) dune cores**. Its root system extends below the soil-water-repellent (SWR) surface layer into more stable moisture regimes, allowing individuals to remain physiologically functional even when surface wetting fails.

Moonah also forms extensive **vertical and lateral root networks** that physically bind unconsolidated calcareous sands. These roots act as **anchoring and pinning structures** within dune profiles, reducing sand mobility, resisting rilling and blowouts, and stabilising substrate even after ground-layer continuity has been lost. Unlike ground-layer stabilisers, Moonah does not depend on intact surface cover to maintain this anchoring function.

In addition, Moonah exhibits exceptional **reshooting capacity**. It possesses protected basal and epicormic buds embedded within woody tissue, supported by substantial stored

carbohydrate reserves. As a result, individuals can reshoot following cutting, stem breakage, wind-throw, or partial burial by sand. Moonah can therefore persist for centuries through prolonged periods of recruitment failure, disturbance, and surface instability.

These traits allow Moonah to remain **structurally present after collapse**, even while recruitment, ground-layer processes, and dispersal pathways have ceased. Moonah's persistence therefore reflects **architectural decoupling from failed surface processes**, not the continued functioning of the woodland community.

Architectural keystone does not imply redundancy

Although Moonah functions as an architectural keystone, it must be understood as **finite and conditionally fragile**, not an inexhaustible stabiliser. Historical and contemporary evidence indicates that Coastal Moonah Woodland on the Nepean Peninsula has lost much of its former **deep-rooted canopy redundancy**, particularly through the widespread removal and failure of species such as **Drooping Sheoak (*Allocasuarina verticillata*)** and other long-lived structural trees (Moxham et al., 2009; DSE, 2003).

The loss of multiple deep-rooted canopy species represents a **collapse of architectural redundancy**, leaving Moonah as a single remaining load-bearing element rather than one component of a distributed stabilising network. Under these conditions, persistence becomes contingent on the survival of individual Moonah trees rather than buffered by overlapping structural roles. This produces a **single-point-of-failure architecture**, in which disturbance, senescence, disease, fire, or hydrological stress acting on Moonah individuals can precipitate rapid structural and functional collapse.

Moonah's longevity and reshooting capacity therefore **delay collapse**, but do not prevent it. Where recruitment has ceased and no replacement deep-rooted cohorts exist, Moonah stands function as **ageing structural relics** rather than self-renewing systems. The woodland persists visually, but its **architectural and evolutionary future has already been foreclosed**.

Mechanistic origin of SWR on Nepean calcareous sands

On the Nepean Peninsula, soil-water-repellency (SWR) expressed in unconsolidated calcareous sands is **not an inherent or static substrate property**, but an **emergent surface condition generated and intensified by structural and biological collapse**.

As synthesised in *Hydrological and Structural Impacts of Gaudium laevigatum* Thicket Formation in Coastal Woodlands (V5), SWR develops and persists where ground-layer continuity is lost and replaced by dense shrub or tea-tree canopies. Hydrophobic waxes and oils from Myrtaceae litter accumulate on sand grains, while reduced decomposition, bioturbation, and microbial processing prevent their removal. Under these conditions, rainfall produces **shallow, discontinuous wetting fronts**, and infiltration is diverted into **preferential flow paths** that bypass the biologically active surface layer.

SWR on Nepean therefore reflects a **process-driven reconfiguration of the soil surface**, not a geological inevitability of calcareous sands. Once established, this hydrophobic surface state becomes **self-reinforcing**, eliminating seed-safe microsites, shortening wetting pulses, and closing recruitment windows across the community.

Mechanistic basis for the CAS–CMW gradient (Nepean)

On the Nepean Peninsula, Moonah Woodland occupies **unconsolidated calcareous sands mantling calcarenite dune systems**. Following ground-layer collapse, SWR expressed in these surface sands causes rainfall to bead and bypass the seed layer via preferential flow, eliminating seed-safe microsites and closing recruitment windows (Doerr et al., 2000; Brown, *Hydrological and Structural Impacts…*, V5).

Low-density rabbits—documented even at **≤ 0.5–2 ha^{-1}**—then truncate juvenile cohorts. Entire recruitment classes are repeatedly removed before establishment, while long-lived Moonah adults persist via deep rooting and reshooting. The result is **adult-only stands** that mapping still recognises structurally as CMW/CAS, despite functional collapse (Mutze et al., 2016a; Mutze et al., 2016b).

What "*CAS*" denotes here

In the Nepean context, **CAS commonly represents the post-collapse expression of Moonah Woodland**: a structural remainder dominated by Moonah stems, often with weed-simplified understorey, rather than a separate, fully functioning ecological system. EVC labels therefore track **structure**, while **function must be diagnosed independently** through evidence of recruitment, surface hydrology in use, and suppression of cohort-truncating selectors (Moxham et al., 2010; DSE, 2003).

Policy line (ready to quote)

Moonah appears as a component within Coastal Alkaline Scrub because it is an architectural keystone: deeply rooted into calcareous dune systems, extremely long-lived, capable of reshooting after damage or breakage, and able to anchor unconsolidated sands below a failed, SWR-affected surface layer. Its persistence indicates residual structural stability, not a functioning woodland community. With the loss of other deep-rooted canopy species, this stability is finite and fragile. CAS/CMW labels therefore record structure, not ecological function, unless recruitment, surface hydrology, and architectural redundancy are demonstrably operating now.
(Moxham et al., 2010; DSE, 2003; Brown, *Hydrological and Structural Impacts…*, V5)

Field cues that the "*component*" reading reflects collapse

- **Ground-layer patchy or absent**; water beading, fingered wetting, rilling, or fines loss after rain (SWR symptoms on calcareous sands) → recruitment windows closed (Doerr et al., 2000).
- **Juveniles rare or isolated** beneath Moonah canopies; browsing sign present; edges and pinch-points repeatedly cleared of palatable recruits at low rabbit densities (Mutze et al., 2016b).
- **Weed-dominated understorey** (e.g. *Polygala myrtifolia*, *Rhamnus alaternus*, *Ehrharta* spp.) replacing the native matrix across mapped CMW patches (DSE, 2003; Moxham et al., 2010).

Evidence box — Nepean CMW/CAS

- **Extent / condition:** CMW < 9 % of original extent on the Mornington Peninsula; most remnants degraded; Moonah regeneration rare (DSE/FFG Action Statement; Tonkinson et al.).
- **Community definition & EVC link:** CMW is a plant community that occurs predominantly within CAS (EVC 858); management guidance emphasises disturbance minimisation and avoidance of seedbank synchronisation (Moxham et al., 2010).
- **Mechanism:** SWR expressed in calcareous surface sands arises from vegetation-driven surface reconfiguration following ground-layer collapse; low-density rabbits truncate cohorts, producing adult-only stands anchored by **architectural keystone Moonah individuals in a system that has lost deep-rooted redundancy** (Doerr et al., 2000; Mutze et al., 2016a,b; Brown, *Hydrological and Structural Impacts…*, V5).

One-line anchor

Moonah persists because its architecture bypasses the failed surface system; the woodland is fragile because that architecture now stands alone.

6. Tea-tree Already Encouraged Rabbits — *Polygala* and Buckthorn Then Reinforce Collapse

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Sequence (diagnostic): staged, enforced, then locked-in

On the Nepean Peninsula, collapse in Coastal Moonah Woodland (CMW) commonly follows a **repeatable sequence**. Dense Coast Tea-tree (*Gaudium laevigatum - syn. Leptospermum laevigatum*) thickets first restructure the system; rabbits then act as cohort-truncating selectors within that structure; and *Myrtle-leaf Milkwort* (*Polygala myrtifolia*) and *Italian Buckthorn* (*Rhamnus alaternus*) subsequently **reinforce and stabilise the failed state**.

Stage 1 — Structural staging by Coast Tea-tree

On calcareous dune systems, dense Coast Tea-tree thickets **simplify the understorey, alter sub-canopy conditions, and suppress recruitment of Moonah and other native species**. The Flora and Fauna Guarantee Action Statement for Coastal Moonah Woodland explicitly documents significant structural change and, in some cases, invasion by Coast Tea-tree in coastal communities, noting that within CMW these changes are *"likely to have significantly affected the diversity and structure of the understorey"* and can *"prevent seedling establishment of Moonah itself"* (DSE/FFG Action Statement No. 141).

Beyond light reduction, Tea-tree thickets alter **sub-canopy air movement, humidity, and fuel distribution**, producing dense, low-visibility shrublands with modified flammability and reduced fine-scale disturbance buffering. These conditions differ fundamentally from open woodland states described historically and recognised in intact CMW elsewhere (Moxham et al., 2010).

Critically, these dense, evergreen thickets create **persistent refuge habitat for rabbits** within reserves and coastal scrub.

Stage 2 — Cohort loss enforced by rabbits (selection)

Within structurally dense Tea-tree shrublands, rabbits function as the **primary selector**, even at low densities. The FFG Action Statement lists rabbits among the degrading pressures across coastal remnants, including CMW (DSE/FFG No. 141).

Independent experimental and field evidence demonstrates that rabbit densities at or below **≈ ≤ 0.5–2 ha^{-1}** are sufficient to **truncate entire juvenile cohorts**, not merely suppress growth (Mutze, Cooke & Jennings, 2016a; Mutze, Cooke & Jennings, 2016b). This matches Peninsula observations: when palatable native recruits appear in gaps,

edges, or post-disturbance pulses within Tea-tree shrublands, they are rapidly removed, resulting in **adult persistence without replacement**.

Failure at this stage is therefore **route-based** (cohort erasure), not a gradual decline in competitive performance.

Stage 3 — Lock-in by *Polygala* and Buckthorn

Myrtle-leaf Milkwort (*Polygala myrtifolia*) and *Italian Buckthorn* (*Rhamnus alaternus*) typically establish **after Tea-tree-driven simplification** has already occurred. Both species increase **evergreen cover, year-round shade, litter accumulation, and physical obstruction**, further reducing visibility, movement, and understorey recovery.

Both the FFG Action Statement and the *Field Guide to Coastal Moonah Woodland in Victoria* list *Polygala* and *Rhamnus* as major woody weeds associated with remnant degradation and **suppressed native regeneration** (DSE/FFG No. 141; Moxham et al., 2010). Recommended management explicitly emphasises **low-disturbance, in-situ suppression**, recognising that broad disturbance or clearing **activates seedbanks and worsens collapse**—confirming that these species **reinforce and stabilise** the degraded state once present, rather than initiating it.

Surface hydrology interaction: why thickets hold the failure state

On these calcareous sands, litter-rich and persistently shaded surfaces frequently express **soil-water-repellency (SWR)** following exposure or drying. Rainfall beads and is diverted into **preferential flow paths** that bypass the biologically active surface layer, eliminating seed-safe microsites and closing recruitment windows (Doerr, Shakesby & Walsh, 2000).

This hydrological failure further explains why dense, evergreen thickets maintain collapse conditions **even under formal protection**. Without direct repair of surface architecture, recruitment routes do not reopen.

Where protection is not enough

Protection alone does not restore function. In this sequence:

- **Coast Tea-tree** sets the structural stage and creates refuge conditions;
- **Rabbits** remove palatable juveniles and erase cohorts, even at low densities;
- ***Polygala* and Buckthorn** lock-in shade, litter, and obstruction, stabilising the failed state.

Without **selector suppression** (rabbit control to cohort-keeping levels) and **surface-layer repair** (maintained ground-layer continuity; no bare-ground pulses on SWR-prone sands), mapping will continue to record shrub **structure** while ecological **function remains absent** (Doerr et al., 2000; Mutze et al., 2016a,b; Moxham et al., 2010).

One-line policy read-out

Coast Tea-tree creates the refuge and simplifies the floor; rabbits keep cohorts down; *Polygala* and Buckthorn make the thicket permanent—so selector suppression and low-disturbance, in-situ control under intact cover are prerequisites for recovery, not add-ons (DSE/FFG No. 141; Moxham et al., 2010; Mutze et al., 2016a,b).

7. Invasive Shrubs Drive Finite Feedbacks That Protected-Area and *"Area Treated"* Metrics Cannot Detect

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Sequence (diagnostic)

On the Nepean Peninsula, **Moonah Woodland occupies unconsolidated calcareous sands mantling calcarenite dune systems**. Within this setting, collapse typically follows a **finite, ordered sequence**:

Coast Tea-tree thickets → rabbit harbour (primary selector) → cohort failure with exposed / SWR-prone microsites → secondary shrub establishment (*Polygala*, *Rhamnus*) → lock-in.

Dense Coast Tea-tree (*Gaudium laevigatum*) stands are widely reported in coastal remnants and are associated with **understorey simplification and prevention of Moonah seedling establishment**, setting the structural stage for recruitment failure and refuge conditions (DSE/FFG Action Statement No. 141).

Primary selector (rabbits)

In dense, low-visibility Tea-tree interiors, rabbits persist inside reserves and coastal scrub and act as the **primary selector**.

- The *FFG Action Statement* lists rabbits among the degrading pressures across Coastal Moonah Woodland remnants, including the Nepean Peninsula (DSE/FFG No. 141).
- Independent experimental and field studies demonstrate that **low rabbit densities (≈ ≤ 0.5–2 ha^{-1})** are sufficient to **truncate entire juvenile cohorts**, not merely suppress growth (Mutze, Cooke & Jennings 2016a; Mutze, Cooke & Jennings 2016b).

This matches Peninsula observations of **adult-only stands** across Tea-tree shrublands and CMW/CAS mosaics: palatable recruits may appear opportunistically at edges, gaps, or after disturbance, but are rapidly removed before establishment (DSE/FFG No. 141; Moxham et al. 2010).

Surface hydrology failure (SWR)

On the **unconsolidated calcareous sands** mantling Nepean's calcarenite dunes, **soil-water-repellency (SWR)** forms a hydrophobic surface layer following exposure or drying.

- Rainfall beads on the surface and is diverted into **preferential flow paths**, bypassing the seed–soil interface.
- Seed-safe microsites are removed and wetting pulses shortened, closing recruitment windows even when propagules are present (Doerr, Shakesby & Walsh 2000).

This surface-hydrology failure compounds rabbit-driven cohort truncation and explains why protection or disturbance reduction alone does not restore recruitment (Doerr et al. 2000; DSE/FFG No. 141).

Secondary shrubs reinforce the state (lock-in)

After Tea-tree simplification and rabbit-driven cohort failure, **Myrtle-leaf Milkwort (*Polygala myrtifolia*) and Italian Buckthorn (*Rhamnus alaternus*)** typically establish into the altered understorey:

- Both increase **evergreen cover, year-round shade, and litter accumulation**.
- Both block visibility and movement, stabilising rabbit refuge.
- Both are identified as **major woody weeds of Coastal Moonah Woodland**, directly associated with remnant degradation and suppressed native regeneration (DSE/FFG No. 141; Moxham, Turner, Walker & Douglas 2010).

Management guidance in the *Field Guide to Coastal Moonah Woodland in Victoria* explicitly recommends **low-disturbance, in-situ suppression** (e.g. cut-and-retain rootstock; careful paint-on techniques), precisely to avoid soil disturbance and seedbank activation—confirming that **broad clearance reinforces the degraded state once these shrubs are present** (Moxham et al. 2010; DSE/FFG No. 141).

***Polygala* as a reinforcement amplifier**

Polygala myrtifolia intensifies lock-in on SWR-prone calcareous sands through both propagule and surface-process effects:

- Very high germination rates under local autumn–spring regimes (**≈ 93–95%**).
- Strongly **surface-biased emergence** (≈ 48% at the surface; ≈ 0% by ~8 cm depth).
- Disturbance or exposure pulses therefore **synchronise invasive flushes** precisely where native recruitment is hydrologically constrained (Roberts, Moloney, Monie & Florentine 2023).

Functionally, *Polygala* shifts moisture from **usable at the seed–soil interface** to **intercepted or bypassed**, while monopolising the narrow recruitment windows disturbance creates (Roberts et al. 2023; Doerr et al. 2000).

Why area-based metrics miss the problem

Metrics based on **hectares protected, hectares treated, or aggregate habitat scores** primarily describe **structure and condition at a point in time**, not whether critical ecological routes remain open.

Although the Vegetation Quality / Habitat Hectares framework includes components for recruitment, understorey life-forms, and litter, these are captured as **static snapshots** and cannot detect **repeated cohort truncation, surface-hydrology failure, or selector-maintained feedback loops**.

The operative collapse sequence—

Tea-tree → rabbit cohort truncation → SWR-affected surface sands → *Polygala*/*Rhamnus* lock-in

—operates at the **ground-layer and surface-hydrology level of unconsolidated calcareous sands** and unfolds **over time**, rather than within a single assessment window.

As a result, protected-area coverage and treatment extent can increase **while collapse deepens**, because recruitment routes are closed, ground-layer function is lost, and corridors exist only **visually**, not **in use** (DSE/FFG No. 141; Moxham et al. 2010).

Only process diagnostics reveal the finite loop

Only **process-based diagnostics** expose whether routes persist:

- **Recruitment in use:** Palatable native juveniles present across seasons at stratified positions (e.g. swales and lee slopes). Absence indicates active cohort truncation (DSE/FFG No. 141; Mutze et al. 2016a,b).
- **Ground-layer integrity:** Moss–herb–litter continuity; fines retained; wetting beyond a thin hydrophobic skin; no rilling or blowouts (Doerr et al. 2000).
- **Corridor function in use:** Demonstrated movement, dispersal, and pollination, not merely mapped or visual continuity (Moxham et al. 2010).

Italian Buckthorn (*Rhamnus alaternus*): why it escalates lock-in

- **Bird-dispersed seed** enables rapid spread into remnants, including partially intact patches (DSE/FFG No. 141).
- **Shade tolerance** allows persistence beneath Tea-tree, Moonah, and *Polygala* canopies, maintaining year-round shade and suppressing native ground-layers (Moxham et al. 2010).

- **Disturbance exploitation:** Combined with SWR, littered calcareous sands hold moisture unevenly, favouring shrub establishment while native seed-safe microsites disappear (Doerr et al. 2000).
- **Rabbit avoidance:** Minimal browsing pressure relative to native species creates a strong selector advantage (Mutze et al. 2016a,b; DSE/FFG No. 141).

Ranking for Nepean: After *Polygala*, *Rhamnus* is the next most serious structural invader of CMW/CAS because it **extends and hardens a collapse state already made admissible by Tea-tree, rabbits, and SWR**, and is difficult to reverse without direct process repair (DSE/FFG No. 141; Moxham et al. 2010; Doerr et al. 2000).

Policy line (ready to quote)

Invasive shrubs accelerate a finite feedback loop operating on unconsolidated calcareous sands that area-based metrics cannot detect; only process diagnostics—recruitment, ground-layer integrity, and corridor function—reveal whether collapse is deepening or routes are reopening
(DSE/FFG No. 141; Moxham et al. 2010; Doerr et al. 2000; Mutze et al. 2016a,b; Roberts et al. 2023).

8. Structural Occlusion by Polygala myrtifolia and Rhamnus alaternus.

Dense, evergreen thickets of *Myrtle-leaf Milkwort* (*Polygala myrtifolia*) and *Italian Buckthorn* (*Rhamnus alaternus*) produce **structural occlusion** in degraded Coastal Moonah Woodland (CMW) remnants. These shrubs exclude light at the ground-layer, suppress native shrubs, herbs, and sedges, and impede fauna movement. The *Field Guide to Coastal Moonah Woodland in Victoria* identifies both species as **major woody weeds** of CMW and emphasises **low-disturbance, in-situ control** to avoid further soil and seedbank disruption (Moxham, Turner, Walker, & Douglas, 2010).

Moisture mechanism.

Polygala in particular shifts moisture from **"*usable at the seed–soil interface*"** to **"*intercepted or bypassed*."** Its evergreen canopy and persistent litter layer maintain a **hydrophobic surface boundary**, causing rainfall to bead and finger past the biologically active surface millimetres. Where openings do form, rapid surface-flush recruitment recloses them, restoring evergreen shade and litter and re-establishing an SWR-prone boundary layer (Doerr, Shakesby, & Walsh, 2000; Roberts, Moloney, Monie, & Florentine, 2023; Moxham et al., 2010).

On the Nepean Peninsula, Moonah Woodland occupies **unconsolidated calcareous sands mantling calcarenite dune systems**. On these substrates, soil-water-repellency (SWR) produces a hydrophobic surface skin so rainfall beads and bypasses the seed layer via preferential flow, eliminating seed-safe microsites and shortening the wetting pulses required for imbibition and native germination (Doerr et al., 2000).

Depth-constrained seedbank expression (*Polygala*).

Data from Roberts et al. (2023) show that *Polygala myrtifolia* recruitment is **strongly depth-constrained**, which is decisive on SWR-prone sands:

- **Very high germination rates** under local autumn–spring regimes (≈ 93–95%);
- **Peak emergence at or extremely near the surface** (≈ 45–50% at the surface);
- **Sharp decline within the upper centimetres**;
- **Near-zero emergence by ~6–8 cm depth**.

This profile means *Polygala* is not advantaged by burial, but is **exquisitely tuned to surface exposure pulses**. Any disturbance that removes litter, reduces roughness, or exposes mineral sand synchronises emergence across the surface layer, producing dense flushes that rapidly restore evergreen shade and litter (Roberts et al., 2023).

How selective chemical control alters seedbank behaviour.

(mechanism, not just technique)

Modern **selective, in-situ chemical control**—including **drill-and-fill**, **basal bark application**, **precision cut-stem treatment**, **and selective foliar spraying applied only to target shrubs**—operates by **decoupling germination cues**, rather than resetting the system through exposure.

The critical distinction is that **selective foliar spraying here is structural-retentive**, not clearance-oriented. When foliar spray is applied narrowly to individual target plants (using low-volume, directed application that avoids off-target contact), it **neutralises canopy function without removing canopy structure**.

Across all selective methods, including **targeted foliar spray**, control is achieved while deliberately retaining:

- standing biomass (dead or senescing stems left upright),
- litter continuity,
- surface roughness,
- partial shade at the ground-layer.

By preserving these features, selective chemical control avoids the primary triggers of mass seedbank expression on unconsolidated calcareous sands.

Under these retained conditions, selective chemical control (including **selective foliar spraying that does not open the ground**) functions by:

1. **preventing uniform light shock** at the soil surface;
2. **buffering soil temperature oscillations** that cue synchronous germination;
3. **intercepting and attenuating rainfall pulses** before they contact bare mineral sand;
4. **maintaining microbial activity and litter processing**, promoting seed decay rather than recruitment.

Because the surface is not reset, seedbank expression becomes **asynchronous rather than pulsed**. Emergence occurs sporadically and at low density, allowing follow-up control to track recruits over time **without reopening recruitment routes** or triggering a system-wide reset.

This mechanism explains why in-situ, structurally conservative **selective chemical control** outperforms both mechanical broad clearance and broad-spectrum foliar knock-down on **SWR-prone calcareous sands**: it suppresses *Polygala* and *Rhamnus* **while withholding the surface-exposure cues that drive synchronous emergence from a shallow, depth-limited seedbank.**

Exploit, not create, the hydrophobic layer.

Importantly, *Polygala* and *Rhamnus* do **not** induce soil hydrophobicity de novo. Hydrophobic surface layers in these systems are typically **legacies of Myrtaceae-dominated phases** (e.g. Coast Tea-tree) combined with disturbance on calcareous dune sands. *Polygala* and *Rhamnus* **exploit and stabilise these SWR-prone microsites**, rather than chemically generating repellency themselves (Doerr et al., 2000; Moxham et al., 2010).

Sequence context (cross-reference to §7).

On Nepean dune systems, the recurring pattern is:

Tea-tree thickets → rabbit harbour (primary selection) → cohort failure with exposed / SWR-prone microsites → *Polygala*/*Rhamnus* occupation and lock-in.

Tea-tree phases simplify understorey structure and are associated with **rare Moonah regeneration**, while rabbits truncate cohorts even at low densities—creating the precise surface and selection conditions that secondary woody weeds then **reinforce and stabilise** (DSE/FFG Action Statement No. 141; Mutze, Cooke, & Jennings, 2016a, 2016b; Moxham et al., 2010).

Interpretation.

Structural occlusion by *Polygala* and *Rhamnus* is therefore **not merely competitive shading**. It is the **mechanism by which an already admissible collapse state becomes persistent**, combining:

- light exclusion,
- movement blockage,
- rabbit refuge maintenance,
- SWR-mediated loss of seed-safe microsites, and
- rapid re-closure following disturbance.

Modern **selective chemical control — including targeted foliar spraying — works because it interrupts this mechanism**, not because it maximises biomass removal.

9. Pollination and Dispersal Are Rerouted Against Natives. *(Feral Honeybees Amplify the Collapse)*

Pollination rerouting by *Polygala*

Myrtle-leaf Milkwort (*Polygala myrtifolia*) flowers for much of the year, with a strong late winter–spring peak. This produces a **near-continuous floral signal** that contrasts with the **short, seasonal flowering pulses** typical of many native Coastal Moonah Woodland (CMW) species (Eyre Peninsula Landscape Board, 2026).

In degraded CMW/CAS on the Nepean Peninsula—where the ground-layer is simplified and native cohorts are already suppressed by low-density rabbits—this extended bloom **re-routes pollinator movement through the shrub layer**. Rather than moving across the landscape to track brief, spatially dispersed native flowering peaks, foragers concentrate on a persistent exotic resource embedded within dense shrubs. This reduces effective visitation and seed set in native plants whose reproduction depends on synchronised pollination windows, even where adult plants remain present (Moxham, Turner, Walker, & Douglas, 2010; Mutze, Cooke, & Jennings, 2016b).

Critically, this represents a **change in movement pathways**, not merely reduced visitation rates.

Feral honeybees as collapse amplifiers

Persistent *Polygala* flowering provides a stable nectar source that favours **feral European honeybees (*Apis mellifera*)**, which are widely documented in Australia to:

- compete with native pollinators,
- dominate floral visitation where long-flowering exotic resources are present, and
- disrupt native pollination systems by monopolising reward pathways (The Conversation / national ecologists' brief, 2023; University of Adelaide, 2023).

Recent Australian studies further show that **higher honeybee densities reduce native bee fitness**, including fewer female offspring, higher mortality, and smaller male size—patterns consistent with **sustained resource monopolisation** rather than short-term competitive displacement (University of Southern Queensland, 2025; Curtin University, 2025).

In the Nepean context, feral honeybees do not initiate collapse; they **amplify and stabilise pollination rerouting** already driven by flowering phenology and shrub structure.

Evidence for routing[1]

Here, *routing* refers to a **persistent reorganisation of pollinator pathways through space and time**, inferred from the convergence of multiple independent lines of evidence rather than from direct tracking data alone. First, *Polygala* replaces pulsed native flowering with a **continuous temporal resource**, a known mechanism for collapsing seasonally expansive foraging into localised circuits (Eyre Peninsula Landscape Board, 2026). Second, dense evergreen shrub layers **physically channel movement through the shrub matrix**, bypassing ground-layer and open-canopy native species even where they persist (Moxham et al., 2010). Third, feral honeybees preferentially exploit these stable resources and are repeatedly documented to dominate visitation and suppress native pollinator performance, reinforcing repeated use of the same foraging paths (The Conversation, 2023; University of Adelaide, 2023; University of Southern Queensland, 2025; Curtin University, 2025). Finally, native reproductive failure and lack of recruitment persist **despite the continued presence of adult native plants**, indicating that pathways—not species presence—have been altered (Moxham et al., 2010; Mutze et al., 2016b). Taken together, these patterns support inference of **pollination rerouting**, not simple preference or transient competition.

How the feedback operates here

As honeybees key on *Polygala*, they:

1. **increase *Polygala* reproductive success**, strengthening its dominance in the shrub layer;
2. **stabilise evergreen shade, litter accumulation, and soil-water-repellent microsites**, maintaining conditions hostile to native recruitment;
3. indirectly **favour secondary invaders**, particularly bird-dispersed shrubs such as *Rhamnus alaternus*, which establish readily beneath shaded, low-competition canopies (Moxham et al., 2010; Glenelg Hopkins CMA, 2025).

This pollination feedback persists because earlier stages of collapse have already reshaped the system: Coast Tea-tree phases simplify understorey structure, rabbits truncate cohorts at ≤ 0.5–2 ha^{-1}, and soil-water-repellency on unconsolidated calcareous sands bypasses the

[1] **Routing evidence footnote.**
In this context, *routing* refers to a persistent reorganisation of pollinator and disperser movement pathways across space and time, inferred from convergent ecological evidence rather than from direct tracking alone. Pollination routing is supported where (i) a long-flowering exotic replaces pulsed native phenology, collapsing seasonally expansive foraging into localised circuits; (ii) shrub-layer structure physically channels movement through evergreen matrices; (iii) reproductive failure in native plants persists despite adult presence, indicating pathway disruption rather than competitive exclusion; and (iv) pollination and dispersal converge into the same shrub-dominated patches. This inferential framework is standard in landscape and network ecology, where movement pathways are diagnosed from phenology, structure, visitation dominance, and demographic outcomes rather than from telemetry data in isolation.

seed–soil interface—closing native recruitment windows irrespective of propagule availability (Mutze et al., 2016a; Doerr, Shakesby, & Walsh, 2000).

Pollination rerouting therefore **locks into**, rather than causes, an already constrained recruitment architecture.

Dispersal is rerouted as well

Italian Buckthorn (*Rhamnus alaternus*) produces abundant bird-dispersed berries, generating **perch-centred invasion nodes** that:

- redirect seed dispersal into degraded shrub patches,
- concentrate seed rain beneath existing thickets, and
- extend *Polygala–Rhamnus* matrices laterally and internally across mapped CMW/CAS (Florabase, 1996; Glenelg Hopkins CMA, 2025).

In this system, **pollination routing establishes the corridor; dispersal routing fills it**, reinforcing the same collapse pathways through successive life-history stages.

Why area-based metrics do not detect this

Area-treated and protected-area metrics record **structure**, not **routing**. They do not capture:

- reorganisation of pollinator movement pathways,
- redirection of dispersal flows, or
- feedbacks driven by long-flowering exotics and perch-based seed rain.

Only **process diagnostics**—recruitment in use, ground-layer integrity (absence of SWR crusting and rilling), and **corridor function in use**—can reveal whether pollination and dispersal routes are returning to native species (Moxham et al., 2010).

Policy line (ready to quote)

Feral honeybees and bird-dispersed woody weeds convert *Polygala*'s long flowering and *Rhamnus* fruiting into a routing system for collapse, overprinting native pollination and dispersal on top of cohort failure driven by rabbits and soil-water-repellency—processes invisible to area-based metrics but decisive for recovery.

10. Rabbits as Primary Selectors in Calcareous Dune Systems (EF view).

On the Nepean Peninsula's **calcareous dune systems**, rabbits act as **primary selectors**: they remove viable recovery routes faster than those routes can be regenerated. By selectively removing palatable seedlings, resprouts, and native ground-layer species, rabbits:

- reduce **diversity (D)** by eliminating recruitment of palatable taxa;
- collapse **redundancy (R)** by thinning or eliminating alternative recruitment pathways;
- constrain **contingency (C)** by closing recovery windows following disturbance; and
- degrade **coherence (K)** by dismantling the surface architecture that links soil, moisture, and biota.

This selection pressure operates even at low rabbit densities and precedes, rather than follows, visible vegetation collapse (Mutze, Cooke, & Jennings, 2016a; Mutze, Cooke, & Jennings, 2016b).

Evidence line *(field synthesis)*

Multiple, independent lines of evidence show that **low rabbit densities (≈ ≤ 0.5–2 rabbits ha^{-1})** are sufficient to **truncate entire seedling cohorts**, maintaining an open or repeatedly reset ground-layer. This sustains a **hydrological lock-in** characterised by soil-water-repellency (SWR), preferential flow, and loss of seed-safe microsites—conditions under which recruitment cannot restart even when propagules are present (Mutze et al., 2016a; Mutze et al., 2016b; Doerr, Shakesby, & Walsh, 2000).

EF verdict: A site with adult plants but no juveniles is **evolutionarily exhausted**. Protection, fencing, or tenure status cannot compensate for the loss of routes under active selection pressure (Moxham, Turner, Walker, & Douglas, 2010).

Rabbit selection and erosion are the same failure expressed two ways

By suppressing the ground-layer, rabbits expose **unconsolidated calcareous sands**, concentrate flow along tracks and scrapes, and deny litter, cryptogams, and surface roots the opportunity to reform. On calcareous dunes, this expresses as:

- increased runoff and **rilling**,
- **blowouts** and loss of fines,
- reduced infiltration and moisture residence.

These are classic outcomes when SWR forms a hydrophobic surface skin and rainfall beads and bypasses the seed layer via preferential flow (Doerr et al., 2000).

Erosion as an indicator *(not a secondary impact)*

On calcareous dune systems, visible erosion is not a late-stage or cosmetic issue; it is the **geomorphic expression of lost surface coherence (K)**—that is, removal of the ground-layer, litter, and cryptogamic cover that normally couple rainfall to the soil profile.

Erosion therefore signals that **functional processes have already failed**, not that failure is imminent or avoidable through later intervention (Doerr et al., 2000; Moxham et al., 2010).

EF reading: Once coherence (K) is lost, each rainfall or wind event becomes an **opposition** that closes additional routes. Collapse accelerates autonomously.

Rabbit behaviour collapses native recruitment windows

In CMW/CAS mosaics on calcareous dunes, rabbits:

- remove native seedlings and resprouts and keep the ground-layer functionally open at **low densities**, blocking cohort formation (Mutze et al., 2016b);
- leave many woody invaders relatively untouched, enabling exotics to persist while palatable natives are selectively removed (Moxham et al., 2010; Mutze et al., 2016b);
- maintain early-successional surface conditions that interact with SWR to shorten wetting pulses at the seed–soil interface (Doerr et al., 2000).

Outcome *(finite feedback)*

Under continued rabbit selection:

- native recruitment collapses,
- redundancy (R) thins to zero,
- coherence (K) fails at the surface, and
- functional pathways (*routes*) close.

This cohort failure **precedes** the establishment of secondary woody invaders (e.g. *Polygala myrtifolia*, *Rhamnus alaternus*) and prepares the surface for their successful occupation (Moxham et al., 2010; Mutze et al., 2016a; Doerr et al., 2000).

One-line operational rule ***(for site sheets and permits)***

Maintain rabbit densities ≤ 0.5–2 ha^{-1} and prevent bare-ground pulses on SWR-prone calcareous sands; otherwise, every rainfall event becomes an opposition that closes routes faster than they can be reopened (Mutze et al., 2016a,b; Doerr et al., 2000).

11. Disturbance Under Low EF (Evolutionary Flexibility) .

Principle

Disturbance is constructive only where **Evolutionary Flexibility (EF)** is sufficient to supply **redundant, coherent routes** that can be used when opposition acts. On the Nepean Peninsula's **calcareous dune systems**, EF is already depleted under chronic rabbit selection. Seedling cohorts are removed at low rabbit densities (≈ ≤ 0.5–2 rabbits ha^{-1}), the ground-layer remains open, and recruitment routes do not regenerate (cohort truncation) (Mutze, Cooke, & Jennings, 2016b).

In this state, disturbance **does not open options**; it closes the remaining ones. Exposure on **soil-water-repellent (SWR) sands** causes rainfall to bead and bypass the seed layer, preventing imbibition. Each disturbance shock converts more surface into preferential flow pathways, erasing seed-safe microsites and further constraining recovery (Doerr, Shakesby, & Walsh, 2000).

Observed sequence *(lock-in under low EF)*

Where EF is low, the pathway repeatedly observed on Nepean dunes is:

Coast Tea-tree thickets → rabbit harbour (primary selection) → cohort failure with SWR-exposed microsites → secondary shrubs establish → lock-in.

Tea-tree phases in Coastal Moonah Woodland are associated with **understorey simplification and rare Moonah regeneration** (DSE / ARI, 2003). Rabbits then truncate cohorts even at low densities (Mutze et al., 2016a; 2016b). The altered surface is subsequently colonised by woody invaders widely recorded in degraded CMW/CAS, for which **low-disturbance, in-situ control** is explicitly recommended to avoid seedbank activation (Moxham, Turner, Walker, & Douglas, 2010).

As a result, *"Tea-tree → rabbits → secondary shrubs"* becomes a **self-stabilising lock-in**, while vegetation mapping continues to report *"shrub cover"*—a clear instance where **structure ≠ function** (Moxham et al., 2010).

Secondary selectors reinforce the low-EF state

Polygala myrtifolia and *Rhamnus alaternus* function as **secondary selectors** once EF is depleted. Their evergreen architecture favours:

- year-round shade,
- litter accumulation, and

- movement pinch-points that suppress native understorey regeneration.

Both species are listed as **major woody weeds** in CMW, with guidance to use **low-disturbance, in-situ control** to avoid further seedbank activation (Moxham et al., 2010).

Why they exploit openings *(mechanism)*

Polygala and *Rhamnus* reliably establish following thinning, fire, or exposure because their life histories match the same **surface-dominated state that disturbance creates on SWR-prone sands**:

- **SWR hydrophobic skin** causes rainfall to bead and finger past the top millimetres, eliminating seed-safe microsites (Doerr et al., 2000).
- *Polygala* then **flushes rapidly from the surface**, with very high germination (~93–95%) under local autumn–spring regimes, strongly surface-biased emergence (~48% at the surface; ≈ 0% by ~8 cm), quickly reclosing openings with evergreen shade and litter that maintain SWR-prone boundaries (Roberts, Moloney, Monie, & Florentine, 2023).
- *Rhamnus* is **bird-dispersed**, so disturbance edges and perches create invasion nodes that extend thickets into collapse patches and shade out native species (Glenelg Hopkins CMA, 2025).

Rabbit selection and erosion express the same failure

By suppressing the ground-layer, rabbits expose **unconsolidated calcareous sands**, concentrate flow along tracks and scrapes, and deny litter and cryptogams the opportunity to reform. On calcareous dunes this expresses as:

- increased runoff and rilling,
- blowouts and loss of fines,
- reduced infiltration and moisture residence.

On these systems, **visible erosion is not a secondary impact**. It is the **geomorphic indicator of lost surface coherence (K)**—signalling that functional processes have already failed, not that recovery can be achieved later through revegetation alone (Doerr et al., 2000; Moxham et al., 2010).

EF reading: Once coherence (K) is lost, each rainfall or wind event becomes an **opposition** that closes additional routes. Collapse accelerates autonomously.

Management implications

- **Under low EF, disturbance closes routes.** Expect increased SWR expression, shorter wetting pulses, weed flushes, and further cohort loss—not recovery (Doerr et al., 2000; Roberts et al., 2023).
- **Do not treat hectares as success metrics** in CMW/CAS. Only **process diagnostics**—recruitment across seasons, ground-layer continuity without SWR crusting or rilling, and corridors functioning in use—indicate EF recovery (Moxham et al., 2010).
- **Precondition any disturbance with EF repair:** maintain rabbits ≤ 0.5–2 ha^{-1} throughout recruitment windows and avoid bare-ground pulses on SWR-prone calcareous sands; otherwise each rainfall event is an opposition that closes more routes (Mutze et al., 2016b; Doerr et al., 2000).

Bottom line *(EF reading)*

Disturbance is constructive only where EF is sufficient. On Nepean's calcareous dunes under chronic rabbit selection, **EF is too low**: disturbance does not open options—it **eliminates the last remaining routes**, while *Polygala* and *Rhamnus* rapidly stabilise the low-EF state whenever bare, hydrophobic surfaces are exposed (Mutze et al., 2016b; Doerr et al., 2000; Roberts et al., 2023; Glenelg Hopkins CMA, 2025).

12. Rabbits → Blackbirds → Secondary Weeds *(Operational Link)* .

Mechanism *(sequence)*

On Nepean's **calcareous dune systems**, rabbit activity creates and maintains **seed-receiving microsites** by removing palatable seedlings and ground-layer cover. Even at low densities (≈ ≤ 0.5–2 rabbits ha^{-1}), rabbits truncate cohorts and keep floors open, sustaining a surface state characterised by **soil-water-repellency (SWR)**, preferential flow, and bypassing of the seed–soil interface (Mutze, Cooke, & Jennings, 2016b; Doerr, Shakesby, & Walsh, 2000).

In this condition, native recruitment windows are closed irrespective of propagule availability, while **exotic propagules delivered to the surface can establish** if they tolerate shallow emergence and shade.

Role of Common Blackbirds (*Turdus merula*) as vectors

Common Blackbirds (*Turdus merula*) are abundant, ground-foraging birds across south-eastern Australia, frequenting **leaf-litter, bare soil, and low shrub cover** in bushland and peri-urban mosaics (BirdLife Australia; NSW DPI). As generalist frugivores, blackbirds are well-documented vectors of **fleshy-fruited invasive plants**, delivering seeds to ground-level microsites and beneath cover—particularly along edges, runways, and shrub margins (Gosper, Stansbury, & Vivian-Smith, 2005).

This behaviour aligns spatially with **rabbit-maintained bare patches and runways**, increasing the likelihood that bird-delivered seeds are deposited precisely where native recruitment routes have been closed by SWR and herbivory.

Operational read-out *(linking selectors)*

The operational sequence observed in degraded CMW/CAS landscapes is therefore:

Rabbit harbour forms first → open, SWR-prone microsites persist → blackbirds deliver fleshy-fruited seeds to those microsites → secondary woody weeds establish and stabilise shade.

In this sequence, rabbits act as **primary selectors** shaping the surface state (Mutze et al., 2016b), while blackbirds function as **propagule delivery vectors** that exploit that state (Gosper et al., 2005).

Blackbirds amplify secondary weed invasion

Blackbirds are recognised dispersers of several priority woody invaders in south-eastern Australia, including:

- **Privets (*Ligustrum* spp.)** — bird-dispersed fruits; widespread naturalisation (Victorian WRA; Weeds Australia).
- **Cotoneasters (*Cotoneaster* spp.)** — berries readily taken by birds; frequent establishment beneath perches and shrubs (RBG Victoria HortFlora; NSW WeedWise).
- **Sweet Pittosporum (*Pittosporum undulatum*)** — *Turdus merula* identified as a principal dispersal vector; seedling clumping beneath canopy and edges (Gleadow, 1982).
- **Blackberry (*Rubus fruticosus* agg.)** — bird-dispersed; listed as a threatening process with avian vectors contributing to spread (Victorian SAC FFG).
- **Italian Buckthorn (*Rhamnus alaternus*)** — bird-dispersed berries; forms dense evergreen thickets that suppress native regeneration (Glenelg Hopkins CMA; Florabase; VRO WRA).

Across these species, a consistent pattern emerges: **bird dispersal concentrates seed rain into shaded or structurally buffered microsites**, reinforcing invasion where ground-layer recovery is already suppressed.

Where seeds are delivered

As ground-foraging birds, blackbirds commonly deposit seeds:

- under evergreen shrubs and dense cover,
- along edges and runways,
- within bare patches and disturbed litter—
  all of which correspond to **rabbit-maintained microsites on SWR-prone calcareous sands** (BirdLife Australia; NSW DPI; Gosper et al., 2005).

These are the same locations where native seedlings fail to establish due to truncated wetting pulses and exposure.

Net effect *(finite feedback)*

The combined effect of:

- **rabbit selection** (cohort truncation; surface exposure),

- **SWR** (seed–soil decoupling), and
- **blackbird-mediated propagule supply**,

is a **directed pathway for secondary woody weeds**. Evergreen invaders (e.g. *Polygala*, *Rhamnus*) then restore shade and litter, stabilising the low-EF state and reinforcing native recruitment failure (Mutze et al., 2016b; Doerr et al., 2000; Moxham, Turner, Walker, & Douglas, 2010; Glenelg Hopkins CMA, 2025).

Why this coupling persists

Blackbirds are **locally mobile and sedentary** at neighbourhood scales, persisting in bushland–urban mosaics and repeatedly foraging in the same disturbed microsites (BirdLife Australia; NSW DPI). Rabbit disturbance therefore **continually refreshes** the very substrates that blackbirds utilise for feeding and seed deposition, maintaining an ongoing **rabbit → bird → weed loop**.

One-line operational rule *(for site sheets)*

Suppress rabbits (≤ 0.5–2 ha^{-1}), avoid bare-ground pulses on SWR-prone calcareous sands, and remove or contain fruiting shrubs near runways and shrub margins—otherwise the rabbit → blackbird → secondary weed loop will continue to seed into collapse patches (Mutze et al., 2016b; Doerr et al., 2000; Gosper et al., 2005; Moxham et al., 2010).

13. Corridors Are Functional Obligations, Not Green Lines.

What a corridor is (and is not)

Connectivity is **not visual continuity**; it is the **successful routing of movement, dispersal, and interaction**. A corridor exists *in use* only when organisms can traverse **pinch-points** at the times, frequencies, and scales required for persistence (Neel, Tumas, & Marsden, 2014; Oehri et al., 2024).

Dense shrub walls, chronic herbivore pressure, or surface conditions that block routes at pinch-points cause **functional fragmentation**, regardless of how "*green*" a corridor appears on maps or in reports. Accordingly, corridor assessment and delivery must rely on **effects-based tests**—movement recorded, dispersal achieved, interaction occurring—as compliance criteria, not aspirational design intent (Neel et al., 2014; VicRoads, 2012).

Cumulative disruption of biological corridors is a systemic failure

Loss or impairment of corridor function:

- isolates fauna populations (Neel et al., 2014; VicRoads, 2012);
- collapses dispersal pathways and gene flow (Oehri et al., 2024; VicRoads, 2012);
- shrinks recruitment windows by reducing successful arrivals (Neel et al., 2014);
- breaks trophic and mutualistic networks, including pollination and foraging links (Oehri et al., 2024);
- accelerates invasive spread via edge and perch-centred seed deposition into gaps (Gosper, Stansbury, & Vivian-Smith, 2005);
- amplifies rabbit and blackbird impacts by coupling open floors with propagule delivery (Mutze, Cooke, & Jennings, 2016b; Victorian SAC—Blackberry PTP).

These effects are **additive and reinforcing**: once corridor routing is broken at pinch-points, recovery elsewhere in the corridor is irrelevant.

Italian Buckthorn as a major corridor disruptor

Italian Buckthorn (*Rhamnus alaternus*) is a disproportionately effective **corridor disruptor** because it:

- forms dense, evergreen walls that **block small-fauna passage and shade out native understorey** (Glenelg Hopkins CMA; Florabase);

- invades **shaded, late-stage collapse zones**, tolerating low light and establishing within existing vegetation rather than only at edges (VRO Weed Risk Assessment);
- spreads rapidly via birds into **corridor pinch-points**, creating perch-centred invasion nodes that harden fragmentation (Glenelg Hopkins CMA; Florabase).

Where *Rhamnus* occupies pinch-points, corridors may remain mapped but are **functionally severed**.

Corridors accelerate every other feedback loop in this manuscript

Once movement corridors stop functioning:

- rabbit impacts intensify (pressure concentrates at blocked gates),
- blackbird seed delivery becomes more spatially focused,
- secondary woody weeds establish precisely where routes fail, and
- pollination and dispersal routing (see §§ 9–12) collapses into shrub-dominated sinks.

Accordingly, **pinch-points must be treated first**, with concurrent rabbit suppression and evergreen shrub suppression in situ, or the landscape graph remains broken regardless of restoration elsewhere (Mutze et al., 2016b; Glenelg Hopkins CMA).

Corridors as a planning obligation *(effects-based)*

Under Victoria's planning framework, **habitat connectivity is an effects-based obligation**, not a design aspiration.

- Environmental Significance Overlays (ESO) explicitly recognise **habitat connectivity and biolink corridors** and regulate impacts on movement and ecological function, not applicant intent (Victoria Planning Provisions, Clause 42.01).
- Examples of local ESO schedules reinforce this obligation:
    - **Yarra Ranges ESO1** identifies "*Highest Biodiversity Habitat Areas and Biolink Corridors"* and requires protection of functional connectivity.
    - **Mornington Peninsula ESO17 (Streamlines)** and **ESO28 (Bushland)** identify remnants and streamlines as **movement corridors**, with decision guidelines requiring retention of connectivity in use.

Therefore: where structural blockers—such as *Polygala*, *Rhamnus*, rabbit-maintained bare floors, or constructed barriers—prevent corridors from forming or functioning, the **effect is fragmentation and non-compliance**, irrespective of works intent or visual greenness (VPP Clause 42.01; MPSC ESO schedules).

Practical compliance test *(use in permits and works specs)*

A corridor complies **only when, after works**:

- **movement by target fauna is recorded** across the pinch-point (camera, track, scat, telemetry);
- **dispersal is evidenced** (propagule transfer observed); and
- **interaction occurs in use** (e.g. pollination or foraging linkage).

Visual continuity or mapped contiguity alone is **insufficient** (Neel et al., 2014; VicRoads, 2012; Oehri et al., 2024).

Field priority: fix the pinch-points *(method packet)*

- Suppress rabbits to **≤ 0.5–2 ha^{-1}** through recruitment windows to reopen gates (Mutze et al., 2016b).
- Remove or contain **evergreen barriers in situ** at pinch-points (e.g. *Rhamnus*, *Polygala*) to restore sightlines and passability, while **avoiding bare-ground pulses on SWR-prone sands** (Glenelg Hopkins CMA; Moxham et al., 2010; Doerr et al., 2000).
- **Verify function** (movement / dispersal / interaction) as the acceptance criterion; if absent, the corridor is **non-compliant and must be reworked** (Neel et al., 2014; VicRoads, 2012).

Bottom line

Corridors are **functional obligations**. If organisms cannot move, disperse, and interact across pinch-points, the corridor does not exist—ecologically or legally—regardless of how green it looks on a map.

14. Soil Protection on Calcarenite Dunes — *No Bare-Ground Pulses* (Highest Priority) .

"*Rip-and-tidy*" backfires on SWR-prone sands. Abrupt removal on Nepean calcarenites:

- **Synchronises invader seedbanks** — short wet pulses on exposed surfaces trigger mass *Polygala myrtifolia* flushes; *P. myrtifolia* germinates at ~93–95% under local autumn–spring temperatures and shows strong surface-biased emergence (~48% at the surface; ≈ 0% by 8 cm) (Roberts, Moloney, Monie, & Florentine, 2023).
- **Strengthens SWR, runoff, and erosion** by exposing a hydrophobic surface skin that makes rainfall bead and forces preferential flow, bypassing the seed layer and scouring fines (Doerr, Shakesby, & Walsh, 2000).
- **Breaks fungal and litter continuity**, collapsing the rough, organic boundary layer that moderates SWR and maintains seed-safe microsites for natives (Doerr et al., 2000).
- **Hands the surface to rabbits**; even ≤ 0.5–2 rabbits ha^{-1} can truncate juvenile cohorts along fresh edges and gaps (Mutze, Cooke, & Jennings, 2016a; 2016b).

Rule (operational)

No broad exposure.
Use selective in-situ shutdown of target shrubs that neutralises seed input **while retaining shade, litter, and roughness**—thereby decoupling germination cues (light, thermal spikes, shallow wetting) so *Polygala*-weighted seedbanks decline by **attrition**, rather than recruiting in synchronised waves (Roberts et al., 2023; Doerr et al., 2000).

Why this works *(mechanistic rationale)*

- **SWR blocks imbibition.** A hydrophobic skin repels liquid water; rainfall bypasses the top millimetres via preferential flow, so seeds fail to achieve continuous liquid water contact. Seed-safe microsites disappear and native cohorts stall (Doerr et al., 2000).
- **Exposure recruits weeds.** Brief wetting on opened sand flushes surface-queued invaders (very high *Polygala* germination; surface emergence), re-loading the top seedbank with exotics (Roberts et al., 2023).
- **Selectors finish the job.** Low-density rabbits remove palatable recruits and prevent cohort formation, locking in failure (Mutze et al., 2016a; 2016b).

Applies across boundaries

The same risks occur inside and outside reserves; degraded Coastal Moonah Woodland within protected tenure demonstrates that **designation ≠ function** (Moxham & Turner, 2009).

Field Protocol (Calcarenite Dunes)

- **Avoid scalping / blanket clearing.** Maintain strict least-disturbance, as any broad exposure of mineral soil accelerates surface heating, amplifies soil-water-repellency (SWR), and closes seed-safe microsites by causing rainfall to bypass the biologically active surface millimetres (Doerr et al., 2000). Exposed calcareous sands heat rapidly, increasing hydrophobicity, shortening moisture residence, and removing the fine-scale conditions required for recruitment. These are **constraint failures**, not competitive interactions: once microsites are lost, the recruitment route closes irrespective of species identity or abundance. Least-disturbance therefore remains essential to prevent disturbance-aligned pulses and to keep admissible routes open long enough for follow-up to exhaust the residual invasive seedbank rather than reactivating it.
- **Prefer contact-point treatments under intact cover.**
  Apply in-situ shutdown to target shrubs while canopies and litter remain in place, so seed input is neutralised while shade, litter, and roughness are retained, decoupling invader cues (Roberts et al., 2023).

Rationale: Polygala's high germination and surface-biased emergence mean opening the surface triggers synchronised recruitment; in-situ shutdown avoids exposure and preserves the boundary layer that blunts SWR and short wetting pulses (Roberts et al., 2023; Doerr et al., 2000).

- **Depth matters.**
  Where opening must occur, bury weed seed **> 6–8 cm equivalent**; *Polygala* emergence is ≈ 0% by ~8 cm, suppressing synchronised flushes (Roberts et al., 2023).
- **Hold rabbits below cohort-truncation thresholds.**
  Maintain rabbits at **≤ 0.5–2 ha^{-1}** across canopies, edges, and pinch-points during recruitment windows (Mutze et al., 2016a; 2016b).

One-line principle *(margins & site plans)*

Protect the surface; no bare-ground pulses.
Use in-situ shutdown to retire the seedbank by attrition and keep selectors below cohort-truncation thresholds—on all tenures (Roberts et al., 2023; Mutze et al., 2016a).

15. Structural Blockers Must Break Down *In Situ* (Sequence Matters).

To protect soils and prevent invader pulses, the **operational sequence must be followed**:

1. **Suppress rabbits (primary selectors).**
   Hold densities at or below ≈ ≤ 0.5–2 rabbits ha^{-1} to prevent cohort truncation at edges and gaps; otherwise every opening resets failure (Mutze, Cooke, & Jennings, 2016a; 2016b).
2. **Suppress *Polygala* / *Rhamnus in situ* (secondary selectors).**
   Kill in place under intact canopy and litter to neutralise seed input **without broad exposure**. This low-disturbance, *in-situ* approach is the recommended practice for woody weeds in Coastal Moonah Woodland (Moxham, Turner, Walker, & Douglas, 2010; Glenelg Hopkins CMA, 2025).
3. **Re-armour the surface / re-establish the ground-layer.**
   Retain or restore shade, litter, and surface roughness so soil-water-repellency (SWR) is moderated and seed-safe microsites return (Doerr, Shakesby, & Walsh, 2000; Moxham et al., 2010).
4. **Only then consider careful structural opening.**
   Any opening must be small, buffered, and sequenced, with corridor function verified **in use** at pinch-points rather than inferred from visual greenness (Neel, Tumas, & Marsden, 2014; VicRoads, 2012).

Reversing this order reliably recreates the degraded state:
opening first → exposure pulses → SWR beading and preferential flow → synchronised *Polygala* flush → rabbit cohort truncation (Doerr et al., 2000; Roberts, Moloney, Monie, & Florentine, 2023; Mutze et al., 2016b).

What "*break down in situ*" achieves

To protect soil integrity on calcarenite dunes, structural blockers must:

- be **killed in place** (Moxham et al., 2010);
- **remain standing temporarily** to buffer desiccation and wind/water shear (Doerr et al., 2000);
- **break down gradually**, retaining shade, litter, and roughness that blunt SWR (Doerr et al., 2000);
- **prevent seedbank activation** by avoiding bare-ground pulses that trigger surface-biased *Polygala* emergence (Roberts et al., 2023);

- **shield native seedlings from rabbits** while densities are held below truncation thresholds (Mutze et al., 2016b).

Selective chemical control is the only tool that enables this process.
It decouples germination cues by keeping shade, litter, and roughness in place while removing seed input, so invader seedbanks wind down by **attrition**, not by pulsed recruitment (Moxham et al., 2010; Roberts et al., 2023; Doerr et al., 2000).

Why *in situ* suppression is the enabling method on SWR sands

- *Polygala* has very high germination (~93–95%) with strong surface-biased emergence (~48% at the surface; ≈ 0% by ~8 cm), so broad clearing reliably synchronises flushes on opened sand (Roberts et al., 2023).
- SWR creates a hydrophobic skin; rainfall beads and bypasses the seed layer via preferential flow, stripping fines and removing seed-safe microsites required by natives (Doerr et al., 2000).
- Coastal Moonah Woodland guidance stresses **low-disturbance, *in-situ* control** for woody weeds because disturbance activates seedbanks and degrades the surface boundary layer (Moxham et al., 2010).
- *Italian Buckthorn* is bird-dispersed and shade-tolerant; exposure creates perch-rich nodes that rapidly infill pinch-points and re-establish structural walls (Glenelg Hopkins CMA, 2025; Florabase).

Effects-based formulation:
In-situ suppression is the method that decouples germination cues while removing seed input; when paired with rabbit suppression, it prevents reset of the degraded state (Roberts et al., 2023; Mutze et al., 2016b; Moxham et al., 2010).

One-screen checklist (crew brief)

1. Drive rabbits to **≤ 0.5–2 ha^{-1}** and hold through recruitment windows (Mutze et al., 2016a; 2016b).
2. Kill target shrubs **in place** under intact cover; **no broad exposure** (Moxham et al., 2010).
3. Retain shade + litter + roughness until native cover re-establishes; avoid scalping; (Doerr et al., 2000).
4. Watch for *Polygala* surface flush after any inadvertent exposure; bury seed **> 6–8 cm equivalent** and treat in place to retire seedbanks (Roberts et al., 2023).
5. Audit corridors by **effect** (movement, dispersal, interaction at pinch-points), not by greenness (Neel et al., 2014; VicRoads, 2012).

16. Plantings Are Not Ecological Function.

(with a defined reconstruction exception)

Plantings add individuals, not routes.
Connectivity, recruitment, and persistence depend on **functional pathways**—movement, dispersal, soil processes—not on the number of plants installed. Without reopened corridors, a porous ground-layer, and corrected surface hydrology, plantings remain **maintenance-dependent** and yield to selectors. Success is measured by **self-sustaining juvenile classes**, not by planting counts (Neel, Tumas, & Marsden, 2014; Moxham, Turner, Walker, & Douglas, 2010).

Plantings are not ecological function—and they are not a substitute for natural recruitment.

What plantings do—and do not—do

Plantings:

- add **individuals**, not processes;
- create **structure**, not function;
- do **not rebuild redundancy** (routes available under opposition);
- do **not restore trophic or hydrological coherence**;
- do **not re-establish pollination or dispersal networks**.

A planted landscape can look "*green*" while being **functionally hollow**. Where Tea-tree harbour and rabbit pressure persist, plantings enter an environment that still **selects for *Polygala* and *Italian Buckthorn*** over natives, regardless of planting density (Mutze, Cooke, & Jennings, 2016b; Moxham et al., 2010).

Plantings fail when structural blockers and invasive feedbacks remain

Plantings cannot succeed where:

- *Polygala* blocks light and queues surface-biased germination (Roberts, Moloney, Monie, & Florentine, 2023);
- *Italian Buckthorn* blocks movement and hardens corridor pinch-points (Glenelg Hopkins CMA, 2025);
- rabbits remove native seedlings at **low densities** (≤ 0.5–2 ha^{-1}) (Mutze et al., 2016b);
- blackbirds deliver secondary weed seed into disturbed microsites (Gosper, Stansbury, & Vivian-Smith, 2005);

- feral honeybees distort pollination routing and reduce native pollinator performance (The Conversation / University of Adelaide / UniSQ / Curtin, 2023–2025);

- soil is destabilised by **SWR and loss of the surface boundary layer** (Doerr, Shakesby, & Walsh, 2000).

Under these conditions, plantings die, stall, or are out-competed. They **cannot substitute for natural recruitment**, because the routes that permit recruitment remain closed (Neel et al., 2014).

Reconstruction exception: severely depleted species (e.g. Sheoak in Moonah Woodland)

A limited exception applies where **key native species have been reduced below viable propagule thresholds** and **cannot realistically recolonise even after routes are reopened**. Many Moonah Woodland remnants now fit this condition for **Sheoak (*Allocasuarina* spp.)**, where:

- adult trees are too sparse to supply effective local seed rain;

- dispersal is short-range and not mediated by mobile vectors; and

- seedlings are highly vulnerable to rabbits and surface instability.

In these cases, planting is **not supplementation** and does **not replace process repair**. It functions as **reconstruction of a missing recruitment node** and is justified **only after**:

1. rabbit densities are held below cohort-truncation thresholds;

2. surface coherence is restored (no bare-ground pulses; SWR buffered); and

3. corridors and pinch-points are functioning in use.

Operationally, reconstruction planting for Sheoak should:

- be **low-density and spatially strategic**, aimed at re-establishing seed sources, not creating stands;

- focus on sheltered microsites and corridor anchors; and

- cease once **self-sustaining juveniles appear without guards**, indicating that the species has transitioned back to natural recruitment.

Where juveniles recruit independently, reconstruction is complete and planting should stop.

This exception **does not weaken the general rule**: planting without repaired routes remains cosmetic. It clarifies where **EF repair alone is insufficient**, and biological absence—not blockage—has occurred.

Operational rule

Fix conditions first.
Break the **Tea-tree → rabbits → secondary shrubs** sequence; restore surface coherence and corridor function—**then, and only then**, consider targeted supplementation or reconstruction where propagule collapse has occurred (Moxham et al., 2010; Mutze et al., 2016b).

Diagnostic replacement for planting targets

Replace "*plants installed*" with **process diagnostics**:

- juveniles present across multiple seasons;
- recruitment occurring **without guards or irrigation**;
- movement observed through corridor pinch-points;
- seedling survival despite low-level disturbance;
- **declining invader seedbanks by attrition**.

If these are absent, planting has **not** produced ecological function, regardless of short-term survival at Year 1 (Neel et al., 2014; Doerr et al., 2000).

Bottom line

Planting is not restoration. Restoration restores **routes**; planting usually adds **units**. Where recruitment, movement, and renewal routes are closed, planting is cosmetic. In cases of true biological absence (e.g. Sheoak), planting may be **necessary as reconstruction**—but only **after routes are repaired**, and only until natural recruitment resumes.

Box 16.1 — Decision Test: When Is Planting *Cosmetic* vs *Reconstructive*?

Use this test **before any planting is proposed**.

Step 1 — Are recruitment routes open?

Ask: Is natural recruitment occurring *now*?

Look for evidence of:

- juveniles present across **multiple seasons** (not just germinants),
- seedlings establishing **without guards or irrigation**,
- survival despite low-level disturbance,
- dispersal occurring through corridors **in use**,
- declining invasive seedbanks by attrition.

If NO → recruitment routes are closed.
Planting here is cosmetic.

Step 2 — Are primary selectors still active?

Ask: Are selection pressures still removing recruits?

Indicators include:

- herbivores truncating cohorts at low density,
- invasive seed rain overwhelming native germination,
- soil processes (e.g. SWR, erosion) blocking establishment,
- pollination or dispersal routing distorted.

If YES → planting will fail or require indefinite maintenance.
Planting remains cosmetic.

Step 3 — Is the species propagule-limited?

Ask: Even if routes were repaired, could the species realistically recolonise?

Signals of **propagule collapse**:

- very low adult density,
- short-range dispersal only,
- no persistent soil seedbank,
- isolation from source populations.
- **If NO** → planting is unnecessary.
- **If YES** → proceed to Step 4.

Step 4 — Have routes been repaired *before* planting?

Planting qualifies as **RECONSTRUCTIVE** only if:

- herbivore pressure is below cohort-truncation thresholds,
- surface processes are stabilised (no bare-ground pulses),
- corridors and pinch-points function **in use**,
- invasive feedbacks are contained.

If YES → planting may be used **temporarily** to rebuild a missing recruitment node.
If NO → planting remains cosmetic.

Diagnostic summary

Condition	**Interpretation**
Routes closed, selectors active	X Cosmetic
Routes open, propagules present	X Unnecessary
Routes open, propagules absent	✓ Reconstructive
Planting precedes route repair	X Cosmetic
Planting follows route repair	✓ Conditional & temporary

Operational rule

Planting is cosmetic unless it follows route repair and compensates for genuine propagule absence.

Reconstruction planting ends when **self-sustaining recruitment resumes**.

17. Natural Recruitment Is the Mechanism of Persistence.

Recruitment is where persistence is actually built.
It is the point at which genetics, microclimate, soil biology, and biotic interactions recombine under site-specific filters, producing **locally adapted juveniles** and rebuilding redundancy. This is the only pathway that recreates persistence architecture and restores **Evolutionary Flexibility (EF)** (Neel, Tumas, & Marsden, 2014; Moxham, Turner, Walker, & Douglas, 2010).

What natural recruitment does

Natural recruitment:

- **selects for individuals adapted to microconditions** (soil moisture, shade, wind, chemistry);
- **maintains and sorts genetic diversity in place**, rather than importing genotypes;
- **rebuilds redundancy** (multiple viable routes through cohorts and seasons);
- **re-establishes soil–root–microbe relationships** disrupted by disturbance;
- **integrates with pollinator and disperser networks** already operating at the site.

Plantings bypass these filters. They insert individuals without passing through site constraints and therefore **do not rebuild architecture**. Accordingly, success is measured by **self-sustaining juvenile classes across seasons**, not by the number of plants installed (Neel et al., 2014; Moxham et al., 2010).

Natural recruitment only returns when constraints are removed

Natural recruitment does not need to be forced; it **emerges once constraints are lifted**.
On Nepean calcarenite dunes it returns only after:

- **structural blockers are killed in place** (no exposure pulses) (Moxham et al., 2010);
- **soil is protected** from SWR expression and erosion (Doerr, Shakesby, & Walsh, 2000);
- **microclimate stabilises** (shade, litter, roughness retained) (Doerr et al., 2000);
- **rabbits are suppressed below cohort-truncation thresholds** (Mutze, Cooke, & Jennings, 2016b);
- **pollinator networks re-orient back to natives** (see §9);
- **invasive feedbacks** (*Polygala*, *Rhamnus*, bird-mediated seed rain) are broken (Gosper, Stansbury, & Vivian-Smith, 2005; Glenelg Hopkins CMA, 2025).

Order matters on Nepean:
Suppress rabbits → suppress *Polygala* / *Buckthorn in situ* → re-armour the surface / ground-layer → **only then** consider careful structural opening.
Reversing this order reliably recreates the degraded state by synchronising invader

recruitment and resetting selection (Doerr et al., 2000; Roberts, Moloney, Monie, & Florentine, 2023; Mutze et al., 2016b).

Diagnostic standard *(replaces planting targets)*

Natural recruitment is present when:

- juveniles appear **without planting**;
- cohorts persist across **multiple seasons**;
- recruitment occurs despite **low-level disturbance**;
- invasive seedbanks **decline by attrition**;
- movement, dispersal, and pollination operate **through the site**.

If these conditions are absent, persistence has **not** returned—regardless of how green the site appears or how many individuals have been planted (Neel et al., 2014).

Bottom line

Natural recruitment is not an outcome—it is the mechanism.
If recruitment has not returned, persistence has not returned, no matter how much planting has occurred.

18. Functional Thresholds: When Habitat Stops Functioning.

Threshold principle

Ecosystems fail when **functional thresholds** are crossed—most critically those governing **recruitment**, **ground-layer continuity**, **corridor permeability**, and the availability of **coherent routes under opposition**. Beyond these limits, a system may retain adult structure yet **lose the capacity to generate future populations**. At that point, it appears intact but has ceased to function (Neel, Tumas, & Marsden, 2014).

The transition from functioning to non-functioning systems can occur without any visible loss of vegetation, as illustrated below

Figure 5. Functional threshold reached in structurally intact Coastal Banksia woodland. This site retains mature *Banksia integrifolia* and remnant native understorey species such as *Leucopogon parviflorus*, indicating that conditions previously supported natural recruitment and a functioning woodland community. Field observation confirms that juvenile cohorts established until a threshold structural condition was reached, after which recruitment ceased.

The mid-storey is now dense, including self-establishing introduced species (*Fraxinus* spp.), and the ground-layer is grass-dominated, with no evidence of ongoing regeneration.

This illustrates a functional threshold condition in which **native structural elements persist, but the capacity to generate future cohorts has been lost**, rendering the system no longer self-sustaining despite remaining mapped and protected.

On the Nepean Peninsula, **chronic rabbit selection pushes systems across functional thresholds before adults disappear**. Once this occurs, disturbance no longer opens recovery options; it removes remaining ones. Protecting land without reopening thresholds **delays loss but does not change the trajectory** under continued selection pressure (Mutze, Cooke, & Jennings, 2016b).

Why protection targets fail without function

Area-based targets create a false sense of progress when they are treated as substitutes for functional diagnostics. If protected land does not generate recruitment, does not route interactions through corridors in use, and does not renew under disturbance, then coverage statistics are irrelevant to persistence. Under these conditions, achieving a 30% protection target does not buy ecological time—it formalises decline under a conservation label.

The functional ratchet (synthetic framework)

A **functional ratchet** is used here as an **integrative framework** to describe a *directional degradation process* in which repeated disturbance or management activity **eliminates viable routes for persistence**, such that the system cannot return to prior function without **deliberate reopening of those routes**. In ratcheted systems, disturbance does not act as a reset—it **progressively tightens constraints**. Time alone does not reverse this process.

The ratchet concept is applied here as a **synthetic description of route loss**, drawing on functional connectivity diagnostics and recruitment theory, **not** as a new attractor-based state model (Neel et al., 2014).

How the ratchet differs from a tipping point

- **Architecture vs state.**
  A tipping point represents a transition between alternative system states when a driver crosses a critical threshold, often with hysteresis (e.g. lake eutrophication, coral reef phase shifts) (Scheffer et al., 2001; Scheffer et al., 2009).
  In contrast, the functional ratchet described here is **not a sudden attractor switch**. It is the **stepwise loss of functional routes**—recruitment pathways, surface coherence, and corridor permeability—under repeated disturbance and selection, as diagnosed using functional connectivity criteria (Neel et al., 2014).

- **Reversibility.**
  After a tipping point, reducing the driver may restore the prior state if hysteresis is limited (Scheffer et al., 2009).
  After a ratchet, reducing pressure alone is insufficient; **routes must be actively reconstructed** (e.g. restoring recruitment pathways, ground-layer continuity, and corridor permeability) before recovery is possible (Neel et al., 2014).
- **Field signals.**
  Tipping points are detected as **abrupt regime shifts**.
  Ratcheting presents as **adult persistence with chronic recruitment failure**, increasing invasive dominance, and blocked corridors **despite apparently "*green*" cover** (Neel et al., 2014).

Ratcheting processes on Nepean

On Nepean calcarenite dunes, multiple reinforcing ratchets operate simultaneously:

- **Hydrologic ratchet.**
  Disturbance exposes soil-water-repellency (SWR). Rainfall beads and bypasses the surface via preferential flow, removing seed-safe microsites, scouring fines, and expanding bare ground; each exposure lowers the probability of native recruitment at subsequent events (Doerr, Shakesby, & Walsh, 2000).

- **Seedbank ratchet.**
  Exposure synchronises invader recruitment. *Polygala myrtifolia* exhibits very high germination (~93–95%) and strong surface-biased emergence, so each opening produces a flush that rapidly reinstates evergreen shade and litter, re-loading the seedbank and resetting the SWR-prone boundary (Roberts, Moloney, Monie, & Florentine, 2023).

- **Selector ratchet.**
  Even at ≤ 0.5–2 rabbits ha^{-1}, rabbits truncate juvenile cohorts along edges and gaps, maintaining open floors that amplify SWR expression and invite further invasion. Each cycle tightens the ratchet (Mutze et al., 2016b).

- **Corridor ratchet.**
  Bird-dispersed, shade-tolerant shrubs such as Italian Buckthorn infill corridor pinch-points and form dense evergreen walls. Mapping may still show "*green corridors*," but **movement and dispersal fail**, increasing the cost and difficulty of later repair (Glenelg Hopkins CMA, 2025; Florabase).

Together, these processes ensure that **each disturbance leaves the system further below functional threshold**, even while adult plants persist.

Landscape implication: function, not protection, determines persistence

Species persistence depends on the **proportion of land that is functionally intact and connected**, not the proportion mapped or designated as protected. Labels do not reopen recruitment routes or restore interaction networks.

In fragmented systems of this type, a defensible **interim functional objective** is that approximately **20–30% of the landscape must be simultaneously functioning and connected**—that is, consistently generating recruitment and routing interactions. Below this range, loss continues because recruitment and dispersal remain below threshold; only above it does the system regain capacity to produce future populations and persistence become likely (Neel et al., 2014; Oehri et al., 2024).

Protected land that **cannot recruit, cannot route interactions, and cannot evolve** does not meet this threshold, regardless of area.

Roadside reserves: protection without threshold repair

Roadside reserves illustrate designation without functional recovery. They are frequently mapped as native vegetation remnants or wildlife corridors yet remain below functional thresholds decades after protection.

Common features include:

- rabbit pressure above cohort-truncation thresholds, preventing recruitment (Mutze et al., 2016b);
- recurrent disturbance (slashing, grading, firebreaks) re-exposing SWR-prone surfaces (Doerr et al., 2000);
- synchronised invader flushes, particularly *Polygala* (Roberts et al., 2023);
- blackbird delivery of fleshy-fruited weed seed into edge and bare microsites (Gosper, Stansbury, & Vivian-Smith, 2005);
- Italian Buckthorn infilling pinch-points, blocking movement despite mapped connectivity (Glenelg Hopkins CMA, 2025; Florabase).

In these cases, protection does not slow decline—it **allows the pre-existing trajectory to continue under a conservation label** (Neel et al., 2014).

Diagnostic shift: from intent to effect

A site is functioning **only if it demonstrates**:

- natural recruitment across multiple seasons;
- juvenile survival without protection;
- ground-layer continuity through dry and wet cycles;

- faunal movement through corridor pinch-points;
- declining invasive seedbanks by attrition.

If these are absent, the system remains **below functional threshold**, regardless of tenure, planting effort, or management intent (Neel et al., 2014).

Bottom line

Functional thresholds determine persistence.
Once crossed, decline becomes **directional**.
Protection without threshold repair does not restore function—it only **buys time**.

19. Rabbits as primary selectors: policy and practice.

Core principle

Rabbits must be recognised explicitly as **primary selectors**, not background stressors. Their effects operate **upstream of all other processes**—recruitment, disturbance response, invasion dynamics, and corridor function—and therefore determine whether **Evolutionary Flexibility (EF)** can recover at all (Mutze, Cooke, & Jennings, 2016b).

Where rabbits remain active:

- **EF cannot recover**, because viable recruitment routes are removed before cohorts can form (Mutze et al., 2016b).
- **Recruitment routes cannot reopen**, even where adults persist or planting is undertaken (Mutze et al., 2016a; Moxham et al., 2010).
- **Disturbance closes rather than opens options**, as exposed microsites are stripped of native recruits and handed to invaders (Doerr, Shakesby, & Walsh, 2000; Roberts, Moloney, Monie, & Florentine, 2023).
- **Invasive shrubs inherit and lock the state**, filling gaps created and maintained by rabbit selection and preventing corridor function (Glenelg Hopkins CMA, 2025).

Protected land without rabbit control is protected erosion.

Rabbits as selectors, not pressures

Treating rabbits as a diffuse "*pressure*" obscures their selector role. Rabbits do not merely reduce biomass; they **select against palatable juvenile cohorts**, truncating regeneration even at low densities. Empirical work shows that densities as low as **≤ 0.5–2 rabbits ha^{-1}** are sufficient to prevent tree and shrub recruitment, keeping systems below functional threshold despite adult persistence (Mutze et al., 2016b).

This selection occurs **before** other mechanisms can act:

- before soil processes stabilise,
- before corridors can function,
- before plantings can contribute, and
- before disturbance can be constructive.

As a consequence, rabbit control is **not one action among many**; it is the **precondition for all other works** (Cooke, 2012).

Interaction with the functional ratchet

Rabbit selection is a key **ratchet driver**. By truncating juvenile cohorts along edges, gaps, and beneath canopies, rabbits:

- maintain open floors, amplifying soil-water-repellency (SWR) and exposure (Doerr et al., 2000);
- enable invader pulses, particularly surface-biased species such as *Polygala myrtifolia* (Roberts et al., 2023);
- increase reliance on planting and repeated intervention, which further disturbs soils and **tightens the ratchet**.

Each disturbance removes additional routes, while rabbits ensure those routes **do not re-establish**. The system remains on the same trajectory—even under protection—until rabbit densities are reduced below cohort-truncation thresholds (Mutze et al., 2016b).

Policy failure: rabbits treated as secondary

Despite this evidence, rabbits are commonly treated in policy and planning as:

- a background stressor,
- a landholder responsibility external to conservation works, or
- a secondary issue addressed *after* vegetation actions.

This sequencing is **functionally incorrect**. Where rabbit control is delayed, partial, or spatially inconsistent:

- revegetation fails,
- soil protection measures are undermined,
- corridor investments do not function, and
- invasive shrubs gain structural dominance.

In effect, public investment subsidises the **rabbit-maintained state**.

Practice implication: rabbit control as a gating condition

Under a functional-threshold framework, rabbit control must be treated as a **gating condition**, not a parallel activity.

Minimum practice standard

1. **Rabbits must be suppressed and held below cohort-truncation thresholds (≤ 0.5–2 ha^{-1})** *before*:

1. structural shrub breakdown,
2. soil exposure or disturbance,
3. planting or seeding, or
4. corridor opening.

2. **Control must be landscape-coherent** (reserves, roadsides, private land), or reinvasion at edges maintains selection pressure and negates site-level work (Cooke, 2012; Mutze et al., 2016b).

Without this sequencing, subsequent actions **cannot reopen routes** and will instead accelerate the ratchet.

Diagnostic statement

If rabbits are present at cohort-truncation densities, the site is not functionally recoverable—regardless of protection status, planting effort, or investment.

This diagnostic replaces vague commitments to "*managing grazing pressure*" with a **testable, effects-based condition** tied directly to persistence.

Bottom line

Rabbits are **primary selectors**.
Unless they are controlled first, all other conservation actions—protection, planting, corridor work, disturbance management—will fail to restore function. **Until rabbits are treated as primary selectors in policy and practice, conservation action will continue to stabilise erosion rather than restore persistence.**

20. Compulsory Control of Invasive Species Under Climate Change *(EF-Aligned)*

Framing principle

Climate change intensifies **existing failures rather than creating new ones**. On Nepean calcarenite dunes, hotter and drier periods, sharper rainfall pulses, and longer recovery lags compress recruitment windows and magnify exposure costs, particularly where soils are water-repellent and functional routes are already constrained (Doerr, Shakesby, & Walsh, 2000; CSIRO, 2022).

Under these conditions, **invasive species control cannot remain optional**. Where routes for recruitment, movement, and interaction are already thinned, mis-sequenced or discretionary actions remove remaining options and lock systems into continued decay. Under climate change, failure to control invasive species becomes a **mechanism of loss**, not a management shortfall (Neel, Tumas, & Marsden, 2014).

Persistence therefore depends on **compulsory, effects-based standards** aligned with Evolutionary Flexibility (EF), not on aspirational targets or discretionary sequencing.

Human-maintained subsidies amplify selection against natives

Human-maintained subsidies—predictable food, water, shelter, and thermal refuge—**amplify selection in favour of introduced exploiters** while increasing opposition faced by native species. Concentrated subsidies (refuse, feeders, irrigated edges, watered lawns, mown verges, culverts, buildings as nest sites) inflate generalist populations, increase aggregation, and distort interaction networks (Galbraith et al., 2015; Becker et al., 2017).

In south-eastern Australia, and urbanising landscapes more broadly, such subsidies consistently benefit introduced species (e.g. blackbirds, starlings, rabbits) that forage along roadsides and anthropogenic edges, while native avoiders and specialists decline unless high-complexity habitat and intact routes are retained (D'Amico et al., 2013; Rogers et al., 2021). For pollination, feral European honeybees capitalise on human-dominated landscapes and often become the dominant visitors, distorting native pollination networks and reducing native bee fitness where densities are high (Prendergast, Dixon, & Bateman, 2022; Dorey, 2023).

The net effect is a **subsidy ratchet**: human provisioning sustains high, predictable resources for introduced species, while native species experience hotter microclimates, greater competition, altered disease dynamics, and shortened recruitment windows. Unless subsidies are redesigned or withdrawn **in parallel with invasive control**, functional thresholds remain closed and EF cannot recover (Becker et al., 2017; Neel et al., 2014).

Compulsory minimum standards *(Nepean calcarenite dunes)*

The following standards are **preconditions for ecological function**, not enhancements.
If they are not met, persistence cannot occur—regardless of investment or protection status.

1) Order of works — compulsory (sequence is a precondition)

Rabbits → in-situ shrub suppression → surface re-armouring → only then structural opening

- **Rabbits first.**
  Rabbits must be suppressed and held below cohort-truncation thresholds (**≤ 0.5–2 rabbits ha^{-1}**). Where rabbits remain active, recruitment routes cannot reopen and all subsequent actions fail (Mutze, Cooke, & Jennings, 2016b).
- **Secondary shrubs next.**
  Polygala and *Rhamnus* must be killed in place, neutralising seed input **without exposing soil** and preserving shade, litter, and roughness (Moxham, Turner, Walker, & Douglas, 2010; Roberts, Moloney, Monie, & Florentine, 2023).
- **Surface re-armouring / ground-layer restoration.**
  Retain or restore micro-roughness and organic cover to blunt soil-water-repellency (SWR) and recreate seed-safe microsites under pulsed rainfall (Doerr et al., 2000).
- **Structural opening last.**
  Opening before routes reopen re-engages the ratchet and reliably recreates the degraded state (Neel et al., 2014).

This sequence is non-negotiable. Reversing it guarantees failure.

2) No exposure methods clause — compulsory

On calcarenite dunes, **broad clearing, scalping, and blanket disturbance are prohibited**. Methods must be selective and in situ, retaining shade, litter, and roughness.

Under warming climates, exposure pulses synchronise invasive recruitment and collapse native recruitment windows; if a method exposes bare ground, it is **non-compliant** (Doerr et al., 2000; Roberts et al., 2023).

3) Effects-based corridor test — compulsory

Corridors are assessed by **function in use**, not mapped greenness.

If a **pinch-point blocks movement or interaction**, the corridor is non-compliant regardless of vegetation cover or tenure (Neel et al., 2014). Bird-dispersed, shade-tolerant shrubs (e.g.

Italian Buckthorn) that block routing must be treated until passage and interaction are restored.

A green corridor that cannot be traversed is not a corridor.

4) KPIs — replace hectare tallies

Area treated and plants installed do not measure function. Replace with **process diagnostics**:

1. Sustained juvenile cohorts of palatable natives across seasons (reopened recruitment routes) (Mutze et al., 2016b).
2. Ground-layer continuity (declining bare ground; stable litter and roughness) through dry–wet cycles (Doerr et al., 2000).
3. Pinch-points reopened, demonstrated by movement or interaction (Neel et al., 2014).
4. Downward trends in SWR depth and expression at representative sites (Doerr et al., 2000).

Failure on **any** KPI indicates the system remains **below threshold**, irrespective of expenditure.

5) Across tenures — compulsory

These standards must apply **across all tenures** within biolink corridors (public land, roadsides, and private land). Corridors must function as routes, not exist as mapped lines; otherwise subsidies and reinvasion at edges hold routes closed (Neel et al., 2014).

Why compulsion is unavoidable under climate change

Climate change compresses recovery time and amplifies penalties for error. Where human subsidies persist, introduced exploiters gain and native species face increased opposition; mis-sequenced or optional actions **burn routes faster than they can be rebuilt**. Compulsory sequencing, no-exposure methods, effects-based corridor tests, functional KPIs, and **subsidy redesign or withdrawal** are therefore **risk controls**, not preferences (CSIRO, 2022; Becker et al., 2017).

Policy conclusion

Under climate change, invasive species control must be **compulsory, sequenced, effects-based, and subsidy-aware**.
Anything less institutionalises the ratchet and stabilises decay under a conservation label.

1.2 — Core Principle *(EF-aligned)*

More land may be protected, mapped, and managed—yet **functional habitat can continue to collapse**.

Under Evolutionary Flexibility (EF), this occurs when **persistence routes are closed and route redundancy is exhausted**, even if vegetation structure and tenure remain intact. Persistence is conditional, not guaranteed by designation.

On the Nepean Peninsula, selectors dominate and **conditional routes are progressively removed**:

- **Rabbits act as primary selectors**, truncating juvenile cohorts and closing recruitment routes at the gateway.
- **Secondary shrubs** (e.g. *Polygala*, Italian Buckthorn) act as secondary selectors, inheriting disturbance and locking the system into **low-route (low-EF) architectures**.
- **Recruitment pathways remain closed**, so renewal cannot occur.
- **Corridors are blocked at pinch-points**, eliminating movement and dispersal despite apparent greenness.
- **Ground-layer coherence is absent**, removing soil-mediated routes for germination and establishment.
- **Disturbance closes routes rather than opening them**, accelerating route loss instead of generating options.
- **Plantings substitute for routes**, adding individuals without rebuilding conditional pathways.
- **Human-maintained subsidies** amplify introduced selectors, increasing opposition faced by autochthonous species.

In EF terms, **designation without route restoration does not prevent collapse**.
It leaves the system **persisting structurally while failing conditionally**, and may not alter the trajectory or rate of decline.

Functional habitat must be restored as architecture, not designated as area.

Reading ecological state on the Nepean Peninsula therefore requires reading **process and sequence**, not cover or protection status:

Tea-tree (gateway opening) → Rabbits (primary route-closing selectors) → Secondary shrubs (route lock-in)

Only where **redundancy of recruitment, movement, and renewal routes is restored**—that is, where evolutionary pathways resume under opposition—does **persistence become possible**.

EF corollary:
Protection preserves area; persistence requires routes. When selectors close recruitment, movement, and renewal pathways, collapse proceeds regardless of designation. Only restoration of route redundancy permits survival under opposition.

Under EF logic, collapse is indifferent to ownership. A system fails when routes are closed, not when tenure changes. Public, private, and offset lands exhibit the same failure signature where recruitment, movement, and renewal pathways are absent, and the same recovery requirements when they are restored.

EF makes the diagnostic boundary explicit: if routes are closed, protection cannot secure persistence. CAS and Moonah Woodland on the southern Peninsula now sit squarely on this boundary.

Part 1.3 — Conclusion: Protection Without Function on the Southern Peninsula.

Coastal Alkaline Scrub (CAS) and Moonah Woodland on the southern Mornington Peninsula now illustrate the central diagnostic problem established in Part I: protection has been mistaken for function. **The analysis that follows concerns the guidance embedded in the overlays, not the performance of the agencies or personnel tasked with applying them; management operates within the planning settings they are required to implement..** Across these calcareous dune systems, vegetation remains mapped and visually present, yet the processes that once sustained these communities—recruitment, hydrological coherence, trophic routing, and wildlife movement—have already failed. Adults persist while the evolutionary pathways that generate future individuals have been lost. This is not a temporary deviation or a management gap; it is the predictable outcome of protecting structural appearance rather than the functional architecture required for persistence.

The planning framework reinforces this collapse by safeguarding the wrong attributes. ESO23, the primary overlay applied across semi-stabilised dunes, is designed to maintain landform stability, prevent erosion, and regulate building placement. Its objectives are geomorphic rather than ecological. It contains no provisions for recruitment, hydrology, ground-layer architecture, seedbank dynamics, or wildlife movement—processes that determine whether these systems can continue to function. The overlay protects the dune surface but not the ecological system that depends on it. It regulates slope, wind turbulence, and siting, yet remains silent on the conditions that underpin ecological continuity.

This misalignment is compounded by the fact that the overlay does not cover the full ecological footprint of the EVC. Moonah Woodland and CAS occupy unconsolidated calcareous sands across dune crests, swales, slopes, and disturbed surfaces, yet ESO23 is mapped only over selected semi-stabilised dunes. Large areas of the same ecological system

fall outside the overlay entirely, receiving no protection despite being part of the same hydrological and biological architecture. The result is a fragmented regulatory landscape that protects patches of landform while leaving the ecological system unprotected, unconnected, and unable to function. Mapping captures structure; it does not diagnose whether the system is still capable of generating future life.

A similar misalignment occurs within the National Park under ESO24. Although this overlay is intended to protect sites of scientific significance, its operational logic centres on avoiding modification rather than maintaining or restoring ecological function. ESO24 recognises botanical and zoological significance, yet defines protection through the prevention of change—"to avoid any modification to sites of scientific significance"—even when the system is already functionally collapsed. On calcareous dune systems, disturbance-sequenced repair is often the only pathway to restoring hydrological coherence, seed-safe microsites, and recruitment routes. By prohibiting modification, ESO24 freezes ecological collapse in place. It protects significance as a static attribute rather than as a dynamic system dependent on open routes for recruitment, hydrology, and movement. As with ESO23, the overlay does not align with the ecological footprint of the EVCs it contains, nor does it address the processes required for regeneration. The National Park is therefore protected in tenure but not in function.

Where protection does apply, it often inhibits the actions required to restore ecological function. Recovery on calcareous dune systems requires disturbance-sequenced hydrological repair, selective in-situ suppression of Gaudium laevigatum, restoration of ground-layer continuity, and the reopening of recruitment and dispersal routes. Yet both ESO23 and ESO24 discourage or prohibit surface disturbance, ground-layer manipulation, and works on slopes—precisely the interventions needed to break soil-water-repellency crusts, restore infiltration, and recreate seed-safe microsites. By prioritising the avoidance of disturbance, the overlays lock the system into its collapsed state. Protection prevents clearing, but it does not reopen closed pathways or restore the conditions required for regeneration and continuity.

The absence of wildlife-movement protection further accelerates collapse. Functional connectivity requires corridors that operate in use, not merely in appearance. Yet the planning framework contains no mechanism to protect fauna movement, corridor pinch-points, or trophic routing. CAS and Moonah Woodland remnants are isolated by fencing, roads, weeds, and recreational pressure, with no regulatory recognition that movement pathways are essential to persistence. Corridors blocked by invasive shrubs or degraded by herbivore pressure are not corridors in use; without movement, recruitment windows collapse and evolutionary processes cease.

Taken together, these failures produce a system that is both unprotected and over-protected: unprotected in ecological terms, over-protected in ways that prevent restoration. CAS and Moonah Woodland are unprotected where it matters—recruitment, hydrology, seedbank dynamics, wildlife movement, and corridor function—and over-protected where it harms function, through restrictions that prevent the disturbance-sequenced interventions required

for recovery. Collapse proceeds inside protected tenure, and the appearance of protection masks the loss of ecological pathways. Persistence requires the restoration of functional architecture—open recruitment routes, coherent hydrology, biologically active ground-layers, and corridors that operate in use. Until planning frameworks recognise and protect these processes, CAS and Moonah Woodland will remain protected in name but collapsing in fact.

Summary of Part I — Protection Without Function

Part I established that ecological collapse on the Nepean Peninsula is not a failure of management effort, nor a consequence of inadequate protection targets, but the predictable outcome of conflating structural retention with ecological function. Across Coastal Alkaline Scrub and Moonah Woodland, vegetation remains mapped and visually present while the underlying processes that sustain these systems—recruitment, hydrological coherence, trophic routing, and wildlife movement—have already failed. Adults persist, but the evolutionary pathways that generate future individuals have been lost.

The diagnostic boundary is therefore functional, not structural. Persistence depends on whether ecological routes remain open under opposition. Where hydrology has inverted, where soil-water-repellency prevents wetting, where ground-layer architecture has collapsed, and where selectors such as low-density rabbits truncate juvenile cohorts, the system no longer possesses the routes required to carry life forward. In such conditions, protection preserves tenure but not persistence.

The planning framework on the southern Peninsula reinforces this collapse by protecting the wrong attributes. Overlays such as ESO23 and ESO24 safeguard landform stability and scientific significance but do not protect recruitment processes, hydrological function, seedbank dynamics, wildlife movement, or the full ecological footprint of the EVC. Large areas of CAS and Moonah Woodland fall outside any meaningful ecological protection, while areas that are protected are constrained by regulations that inhibit the disturbance-sequenced interventions required for recovery. The result is a landscape that is simultaneously unprotected where it matters and over-protected where it harms function.

Part I therefore concludes that collapse proceeds inside protected tenure because protection has been defined in structural rather than functional terms. Persistence requires the restoration of functional architecture—open recruitment routes, coherent hydrology, biologically active ground-layers, and corridors that operate in use. Until these conditions are restored, protection will continue to mask ecological decay rather than prevent it.

Transition Into Part II

Part II now develops the mechanistic basis for this diagnosis, tracing how hydrology, disturbance, and biological selection interact on calcareous dune systems to close and, under specific conditions, reopen ecological routes.

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PART 2 — MECHANISMS OF COLLAPSE

Opening paragraph (Part II):

Part II provides the mechanistic grounding for the diagnostic claims advanced in Part I. Focusing on Coastal Moonah Woodland on the Nepean Peninsula, it examines how substrate architecture, hydrology, disturbance, and biological selection interact to close recruitment pathways despite formal protection. Moonah Woodland occupies unconsolidated calcareous sands mantling calcarenite dune systems, where sand mantle thickness and soil profile development vary across dune crests, swales, and disturbed surfaces, yet a shared sand-over-calcarenite architecture governs surface hydrology and soil-water-repellency expression. Within this setting, dense thicket formation by *Gaudium laevigatum* restructures surface conditions, concentrates rabbit activity, and amplifies soil-water-repellency–driven preferential flow, producing a repeatable collapse sequence in which juvenile cohorts are truncated, and ground-layer function fails before canopy loss becomes visible.

By tracing these mechanisms in detail, Part II demonstrates why commonly recommended interventions—including blanket clearance, poorly sequenced thinning, or exposure-based weed control—frequently recreate the very disturbance conditions that maintain collapse. It shows that method choice and sequencing determine whether rainfall, disturbance, and recruitment cues function as recovery pathways or as invasion-facilitating pulses. This mechanistic framework explains why protection alone does not restore function, why non-disturbance is often misapplied, and why selective, in-situ suppression is a structural requirement rather than a management convenience. Read together, Parts I and II link policy-level diagnosis to field-scale causation and operational constraint.

PART 2.2 Mechanisms of Functional Collapse

Hydrological and Structural Impacts of *Gaudium laevigatum* Thicket Formation in Coastal Woodlands: A Mechanistic Synthesis.

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Abstract.

Coastal woodlands dominated by *Gaudium laevigatum*[2] (coastal tea-tree)—hereafter *Gaudium*; syn. *Leptospermum laevigatum*—arise primarily from **European-driven disturbance**, with sustained rabbit-grazing then perpetuating and intensifying the shift by preventing native recruitment and structural recovery. Although coastal tea-tree is native to parts of south-eastern Australia, its proliferation into **dense, closed thickets** represents a marked departure from the **open, multilayered architecture** characteristic of healthy Moonah (*Melaleuca lanceolata*) woodlands (Moxham & Turner, 2011; Moxham, Turner, Walker, & Douglas, 2010).

This paper synthesises hydrology, soil science, fire ecology, and vegetation dynamics to explain how tea-tree thicket formation alters **infiltration**, **soil-moisture availability**, and **ground-layer function**. Five interacting hydrological–structural mechanisms are identified:

1. **High canopy interception** reducing throughfall (Crockford & Richardson, 2000; Keim, Skaugset, & Weiler, 2006);
2. **Hydrophobic litter layers** characteristic of Myrtaceae that generate soil-water-repellency and inhibit infiltration (Doerr, Shakesby, & Walsh, 2000; Siteur et al., 2016);
3. **Shallow, near-surface pulse capture** by root systems concentrated in the upper soil profile, rapidly pre-empting near-surface moisture inputs (Lam, 2002; Groom, 2000);
4. **Suppression and collapse of the ground-layer**, removing its moisture-holding, soil-aerating architecture (Lin, Jung, Hsiao, & Hamburg, 2006; Nilsen et al., 1999); and
5. **Rabbit-driven selector pressure**, which accelerates thicket consolidation and locks the system into a **low-diversity, low-infiltration** state (Mutze, Cooke, & Jennings, 2016; Moulton, Hesp, Miot da Silva, Keane, & Fernandez, 2020).

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[2] **Taxonomic note.**
Leptospermum laevigatum has been transferred to *Gaudium laevigatum* (Wilson, 2023; Australian Native Plants Society [ANPSA], 2025).

Although no single study traces the entire causal chain, the convergent evidence shows that tea-tree thickets create **functionally drier, less aerated, and less biologically open soils**, with reduced capacity for infiltration and regeneration (Doerr et al., 2000; Siteur et al., 2016). The synthesis provides a **mechanistic foundation for restoration** in threatened coastal woodlands and clarifies the operational sequence required for recovery: **reduce rabbit pressure → protect and rebuild the ground-layer → stage structural change** so interventions **reopen, rather than reset, recruitment corridors** (Roper et al., 2015; Lam & van Etten, 2002).

Key Terms for clarity.

Aesthetic reset.
Management actions that prioritise visual tidiness (e.g., clearing, "*tidy-ups*," ornamental planting) at the expense of ecological function. On calcareous dunes, aesthetic resets typically remove stabilisers, expose hydrophobic sand, synchronise seedbanks, and recreate foreshore-template conditions **inland**.

Actinorhizal nitrogen boundary.
A functional nutrient constraint created by actinorhizal trees (e.g., *Allocasuarina* spp.) hosting *Frankia* symbionts. On nutrient-poor calcareous sands, this boundary stabilises nitrogen availability, supports microbial processes, and constrains disturbance-aligned shrub dominance.

Bare-ground pulse.
A transient but ecologically consequential exposure of mineral soil caused by clearing, grubbing, scraping, fire, or heavy grazing. On hydrophobic sands, bare-ground pulses intensify soil-water-repellency (SWR), promote runoff and erosion, and synchronise recruitment of disturbance-aligned species.

Biologically active surface layer.
The upper soil zone (typically the top few centimetres) comprising litter, mosses, fine roots, organic fines, microbes, and invertebrates. This layer governs moisture residence, infiltration buffering, seed-safe microsites, and trophic support. Its loss marks structural collapse.

Constraint architecture.
The configuration of structural, hydrological, and biological constraints that determine which ecological pathways remain admissible under disturbance. In this study, constraint

architecture includes ground-layer continuity, canopy layering, rooting depth complementarity, nutrient boundaries, and grazing pressure.

Constraint-first sequencing.
A restoration principle requiring that dominant pressures and missing functions (e.g., rabbits, ground-layer loss, disturbance-aligned shrubs) be addressed **before** major structural removal. Reversing this order reliably recreates collapse conditions.

Disturbance-aligned shrubs.
Woody species whose recruitment, persistence, and dominance are favoured by exposed surfaces, high light, shallow wetting, and simplified structure. In this study, *Polygala myrtifolia* and *Rhamnus alaternus* are primary examples.

Drought/Dry-phase rabbit subsidy.
A feedback mechanism in which rabbits sustain themselves during dry periods by accessing moisture and soluble carbohydrates from woody plant tissues (e.g., cambium chewing on *Polygala*/*Rhamnus*), allowing grazing pressure to persist through drought and continue suppressing ground-layer recovery.

Evolutionary Flexibility (EF).
A framework formalising persistence as a property of system architecture rather than a trait. EF is expressed as **EF = (D + R) + C + K**, where **D** (diversity) and **R** (redundancy) provide latent options; **C** (contingency) determines admissible pathways under disturbance; and **K** (coherence, signed $\in \{-1, 0, +1\}$) captures whether internal couplings buffer or amplify fragility. In this study, EF is used as an interpretive framework to organise mechanisms and restoration sequencing, not as an alternative to established ecological processes.

Foreshore template.
A structural–hydrological state characterised by low vegetation cover, disrupted litter and moss, exposed hydrophobic sand, shallow wetting, high runoff, and disturbance-aligned recruitment. Inland reproduction of this template drives shrub dominance and geomorphic degradation.

Fragility gate.
A threshold or bottleneck within the fragility landscape where small disturbances produce disproportionate effects (e.g., exposure of hydrophobic sand converting rainfall into runoff). Fragility gates concentrate risk and determine collapse points.

Ground-layer / ground-layer continuity.
The assemblage of grasses, herbs, sedges, mosses, litter, and fine roots forming the surface architecture. Continuity refers to spatially connected cover that buffers evaporation, suppresses SWR expression, supports invertebrates, and maintains seed-safe microsites.

Hydrological closure.
A condition in which rainfall inputs are largely intercepted, repelled, or diverted into preferential flow, resulting in shallow wetting, reduced infiltration, and low moisture residence within the biologically active layer.

Microsite / seed-safe microsite.
A small-scale surface feature (e.g., litter island, moss patch, shaded depression) that buffers temperature and moisture, enabling germination and early survival. Loss of microsite redundancy signals collapse.

Opposition (Ω)
A sustained pressure that tests system architecture, such as chronic rabbit-grazing, repeated disturbance, or fire. Opposition is not a mechanism; it is the condition that discloses whether admissible routes remain **once mechanisms act**.

Preferential flow.
The channelling of water through discrete pathways that bypass the surrounding soil matrix. In water-repellent sands, preferential flow reduces effective soil wetting and accelerates runoff and erosion.

Replacement state.
A persistent vegetation configuration that arises after collapse of historical constraints and does not naturally transition back without intervention. Inland tea-tree thickets are treated here as replacement states, not successional phases and does not naturally transition back without intervention **even under extended timeframes**.

Selective suppression.
Low-disturbance, **in situ** treatment (typically targeted herbicide) that neutralises a plant while retaining standing biomass, shade, litter, and surface roughness. Selective suppression prevents bare-ground pulses and seedbank synchrony and is distinct from physical removal.

Selective suppression vs removal (distinction).
Selective suppression: Kills the target *in situ* while retaining shade, litter, surface roughness, and ground-layer continuity.
Removal: Physical extraction (pulling, grubbing, scraping) that exposes hydrophobic sand, synchronises seedbanks, and resets recruitment filters.
On calcareous dunes, suppression is required until late, localised phases.

Soil-Water-Repellency (SWR).
A condition where soil particles resist wetting due to hydrophobic coatings, causing shallow wetting fronts, runoff, and preferential flow. SWR is intensified by litter loss, heat, drought, and exposure on sandy substrates.

Stabilisers (native stabilisers).
Native ground-layer or low-shrub species (notably *Rhagodia candolleana* and *Tetragonia implexicoma*) that trap fines, retain litter, buffer microclimate, and stabilise calcareous sands. They are functional scaffolds and must not be removed.

Structural diversity / layering.
The presence of multiple vegetation strata (ground-layer, shrubs, mid-storey, canopy) with complementary rooting depths and resource use. Structural diversity widens recruitment corridors and buffers hydrological extremes.

Tea-tree spot-work.
Highly localised, low-disturbance reduction of *Gaudium laevigatum* undertaken **only after** constraints are repaired and **only where** tea-tree directly obstructs ground-layer recovery. It is not a primary intervention. Undertaken **only after constraints are repaired** and only where tea-tree directly obstructs ground-layer recovery

Transition state (legacy usage).
A term used in some vegetation classifications to denote degraded conditions presumed to recover over time. In this study, such states are reinterpreted as **conditionally recoverable or replacement states**, depending on whether opposition persists.

Water–energy subsidy.
Combined provision of moisture and soluble carbohydrates from plant tissues that sustains herbivores during dry periods. In this system, water–energy subsidies prolong rabbit pressure and maintain collapse feedbacks.

1. Introduction.

Coastal woodlands and alkaline scrub systems of south-eastern Australia—including Moonah (*Melaleuca lanceolata*) woodlands—are among the continent's most **structurally distinctive and ecologically fragile** vegetation communities. Their persistence depends on a mosaic of canopy species, a diverse mid-storey, and a **grass–herb–sedge ground-layer** that collectively maintain **soil porosity, infiltration, and nutrient cycling** (Moxham, Turner, Walker, & Douglas, 2010). Historically, these systems included a substantial **sheoak** (*Allocasuarina*) **component** arranged in open, grassy mosaics with Moonah and Banksia on calcareous dunes, providing **functional redundancy** in rooting depth, nutrient inputs, and soil stability (Moxham, Sinclair, Walker, & Douglas, 2009).

Across many regions, however, these systems have undergone a **marked structural collapse** driven by long-term rabbit-grazing, the proliferation of *Gaudium laevigatum* (coastal tea-tree) and altered fire regimes acting as amplifiers (Weber, 2003; Lam & van Etten, 2002). In Australia, invasive alien species are the **leading cause** of biodiversity loss and species extinction (CSIRO, 2023).

Although tea-tree is native to parts of Victoria, its behaviour under sustained grazing pressure resembles that of an invasive shrub: it forms **monospecific stands**, suppresses recruitment of other species, and **alters soil and hydrological processes** (Lam, 2002; Lam & van Etten, 2002).

Land managers frequently describe these thickets as *"dry," "impenetrable,"* or *"hydrologically closed,"* yet the **mechanisms underlying these observations have not been synthesised.** Rabbits are a key threat to **more than 300 at-risk native species** nationally, and even low rabbit densities can eliminate seedling cohorts of long-lived woody plants, preventing structural recovery (Bush Heritage Australia, 2021).

Statutory conservation assessments already recognise these structural effects within Coastal Moonah Woodland. The Victorian Flora and Fauna Guarantee (FFG) Action Statement for Coastal Moonah Woodland documents significant change, and in some cases effective

invasion, by Coast Tea-tree within coastal vegetation communities. Within CMW specifically, these changes are described as having "*likely significantly affected the diversity and structure of the understorey"* and as *"preventing seedling establishment of Moonah itself,"* indicating that dense Coast Tea-tree thickets maintain site conditions that suppress native recruitment and cohort replacement (DSE, Action Statement No. 141). Importantly, this diagnosis is demographic and structural rather than taxonomic: Moonah may persist as mature individuals, but regeneration pathways are blocked. This study builds on that statutory recognition by identifying the hydrological and structural mechanisms through which these thickets maintain recruitment failure and inhibit recovery.

The aim of this study is to assemble a **mechanistic, evidence-based explanation** of how tea-tree thicket formation alters hydrological pathways and soil-moisture availability in coastal woodlands. Rather than treating "*dryness*" as a qualitative descriptor, the paper identifies the **structural and functional mechanisms**—canopy interception, hydrophobic litter, near-surface pulse capture and pre-emption, ground-layer collapse, and rabbit-driven selector pressure—that collectively produce a **functionally drier soil** environment (Crockford & Richardson, 2000; Keim et al., 2006; Doerr et al., 2000; Siteur et al., 2016; Lam, 2002; Groom, 2000; Lin et al., 2006; Nilsen et al., 1999; Mutze et al., 2016; Moulton et al., 2020).

This paper forms the mechanistic component of a broader diagnostic framework addressing why protected landscapes frequently lose ecological function despite intact structure. The policy and conceptual implications of these processes are developed separately in **Increasing protected land is not the same as protecting function** *(Brown, 2026), where loss of recruitment, hydrological incoherence, and route closure are framed as systemic conservation failures rather than site-specific anomalies*

Fire effects in Coastal Moonah Woodland on calcareous dunes are primarily structural—**with no consistent difference in total richness across fire histories despite strong shifts in structure and functional groups**—and tea-tree persists across the full fire gradient; therefore fire alone cannot adequately account for inland thicket dominance **in these systems** (Moxham & Turner, 2008, unpublished).

Scope statement: This report diagnoses **tea-tree thicket formation** as a disturbance-driven, hydrologically locked state on calcareous dunes, then specifies the **constraint-first** sequence required to reverse it; rabbits, fire, and disturbance-aligned shrubs are treated only as **mechanistic amplifiers** of this tea-tree mechanism.

Fire as a tested explanatory candidate. In keeping with established fire ecology in southern Australia, this study explicitly examines whether **fire history can explain inland dominance of *Gaudium* on calcareous dunes**. Evidence from calcareous dune systems at Point Nepean shows that **increasing fire frequency simplifies vegetation structure**, with reductions in canopy and mid-storey cover, litter and moss, and increases in perennial grasses (Moxham & Turner 2008). However, **overall species richness remains broadly unchanged**, and ***Gaudium laevigatum* persists across all fire histories** (Moxham & Turner 2008). **Fire alone therefore cannot account for inland tea-tree dominance.**

Consistent with regional vegetation classification, **closed inland tea-tree canopies are**

Box — What "*dense scrub*" meant historically

- **Structure:** Inland "*dense scrub*" = Moonah thickets in swales; dune crests = open Sheoak–Wattle–Banksia with grasses (Moxham, Sinclair, Walker, & Douglas, 2009).
- **Mechanism:** Closed inland tea-tree = Transition State (TS1–TS3), i.e., **post-disturbance**, not historical (Moxham, Cheal, & Turner, 2009).
- **Today:** Near infrastructure, late-stage *"replacement"* is biased toward bird-dispersed woody weeds (e.g., *Polygala*, *Rhamnus*), matching elevated exotic frequencies in infrastructure matrices (Moxham & Turner, 2011).

recognised as transition states arising under altered disturbance regimes since European settlement, rather than representing the historical inland reference condition (Moxham, Cheal & Turner 2009). **This indicates that an upstream process, operating prior to fire, is required** to explain the emergence and persistence of inland tea-tree dominance.

This synthesis supports ecological restoration, informs management of threatened Moonah woodlands, and provides a **conceptual framework** for understanding how structural change propagates through hydrological and soil systems (Moxham & Turner, 2011).

Historical descriptions and unburnt mosaics corroborate an inland baseline of **sheoak–Moonah–Acacia with grassy ground-layers** on calcareous dunes, consistent with the Nepean Peninsula synthesis and recent Coastal Moonah Woodland studies (Moxham et al.,

2009; Moxham et al., 2010).

Historical meaning of *"dense scrub."*

Historical references to "*dense scrub*" on inland calcareous dunes of the Nepean Peninsula are best interpreted as **Moonah (*Melaleuca lanceolata*) thickets** in sheltered swales and depressions, with **open, grassy sheoak–Banksia–Acacia** structure on dune crests. Tea-tree (*Gaudium laevigatum*) was present but **not inland dominant prior to European disturbance** (Moxham, Sinclair, Walker, & Douglas, 2009).

Contemporary classification formalises this pattern: Moonah is a **diagnostic canopy species** in sheltered dune positions, whereas **closed tea-tree canopies are classified as Transition States** that increase under altered regimes (e.g. clearance or changed fire), and therefore **post-date the historical inland baseline** (Moxham, Cheal, & Turner, 2009). Species that increase under recent disturbance—including coastal tea-tree—support the interpretation of **inland tea-tree dominance as a post-disturbance condition**, not the historical reference state.

Closed inland tea-tree canopies (TS1–TS3) were explicitly classified as **Transition States,** with Moxham et al. noting that such *sites "presumably once supported a higher density (to dominance) of M. lanceolata,"* with *L. laevigatum* becoming dominant after disturbance or altered fire regimes (Moxham, Cheal, & Turner, 2009).

Historical Structure of the Sandy Hillocks (1841–1925).

1841–1866 surveys.
Surveys of the dune-rise country on the western margin of Tootgarook Swamp (modern Fingal/Boneo) describe "***open, calcareous sandy hillocks*"** dominated by **"*She-oak*, *Banksia, Acacia**, and scattered Moonah"*—not dense tea-tree scrub** (Smythe, Surveyor-General's Office, 1841).

1841 survey baseline.
The 1841 **(Figure 6).** coastal survey labels this belt as ***"undulating grassy hills, timbered with She Oak and Wattle trees,"*** with dense scrub confined to lower sites. The absence of *Gaudium laevigatum* on dune rises is consistent with its role as a **later disturbance coloniser**.

Professional Board (1866).
The Board describes drift sand over white limestone, capped by 2–3 ft of shelly marl, with ***"She-oak, Banksia, Acacia, Exocarpus, eucalypts**, and scattered ti-tree"* **(Figure 7).** Water

accumulated only where thin clay lenses interrupted infiltration—matching the **fragility-gate mechanism** discussed in this study (Victorian Parliamentary Paper, 1866).

Geological context (1920's).
Memoirs of the Geological Survey document **dune limestone / clay-lens hydrology**, explaining perched wet hollows amid otherwise leaky dunes in the Nepean–Fingal/Boneo belt. Keble's geological mapping of the Nepean Peninsula was completed in **1927**, with the results later synthesised in his 1950 **Memoirs of the Geological Survey of Victoria** and the 1946 **Sunklands** paper. His survey documented calcareous dune formations overlying thin, discontinuous clay lenses, producing perched wet hollows amid otherwise rapidly percolating dune sands — the same hydrological architecture reflected in 1841–1925 accounts.

McCrae's (1840s).
Journals from Arthur's Seat's pastoral era describe **grassy "*She-oak–Wattle rises*"** and Moonah thickets in pockets—again matching the She-oak–Moonah mosaic. **McCrae, Georgiana (1840s). *Journals and drawings from Arthur's Seat*. McCrae Homestead Collection, National Trust of Australia (Victoria).**

1889 collapse signal.
An 1889 report describes widespread **eucalypt death** on the dune rises *"about 20 years"* earlier and notes ***"She-oak"* loss** from stock, fire, and cutting, with collapse attributed to "myriads of small insects." This pattern is consistent with **secondary insect attack** on drought- and fire-stressed trees (The Australasian, 22 June 1889).

1925 Boneo–Sorrento collapse record.
A 1925 account describes a shift from *"richly grassed lands"* with scattered She-oaks to ***"grassless wastes thickly covered with tall ti-tree",*** attributing the change to rabbits having *"consumed every other kind of vegetation."* This is **direct evidence** that inland tea-tree dominance is a **post-collapse, herbivore-driven condition**, not the historical baseline (The Advocate, 28 Feb 1925)

Interpretation.
The sandy hillocks were historically **open, infiltration-dominant woodlands**.
Dense tea-tree on crests is a **post-disturbance phenomenon** arising from:

- hydrological modification of a calcareous dune system (lens-bound perched wet hollows amid rapid percolation),
- repeated burning, and

- rabbit-driven recruitment failure of Sheoak, Banksia, and Acacia.

This interpretation is consistent with the hydrologic substrate logic described by Keble (1950) and the disturbance dynamics captured in the 1889 and 1925 accounts.

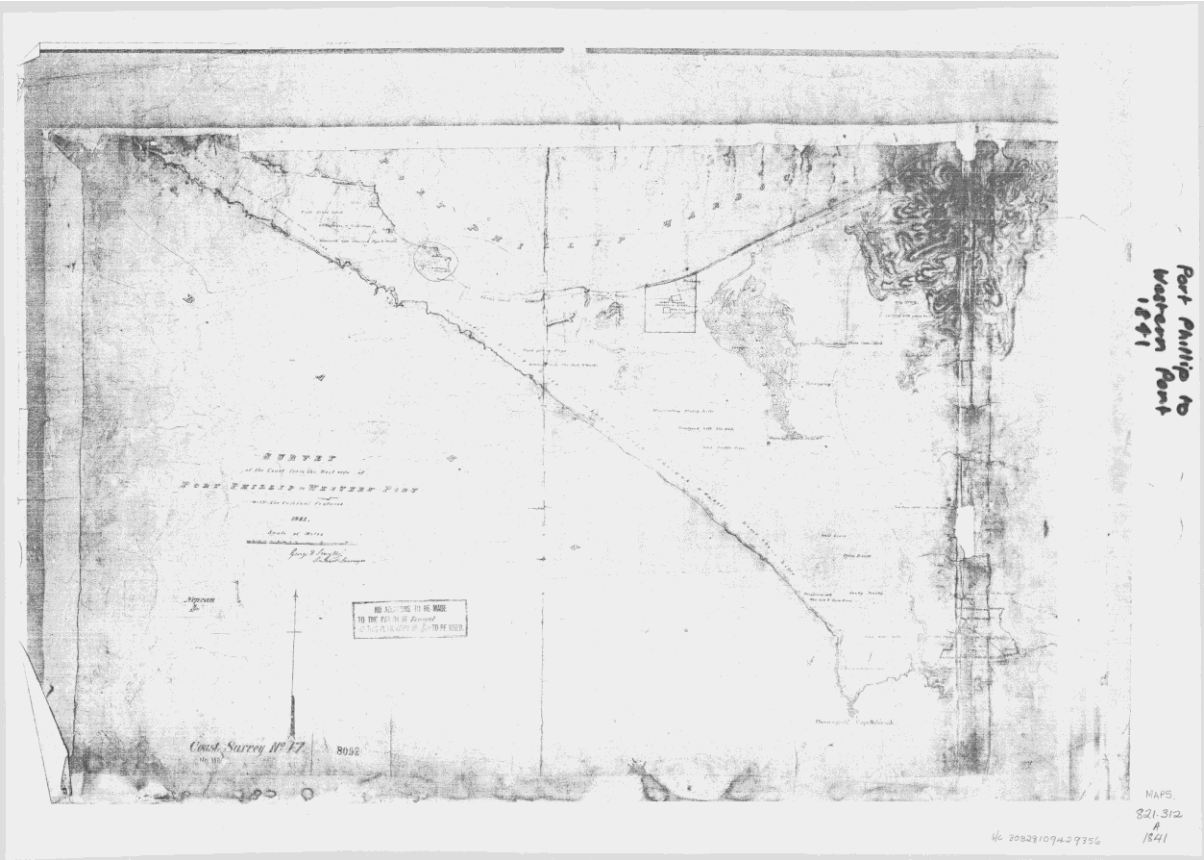

Figure 6. 1841 coastal survey *annotations on the western dune-rise belt (modern Fingal/Boneo). Labels read* ***"Undulating grassy hills"*** *and* ***"Timbered with She-Oak and Wattle trees,"*** *with a nearby note* ***"substratum of limestone"*** *(partly obscured), confirming open, calcareous hillocks timbered by She-oak and Wattle rather than dense scrub.*

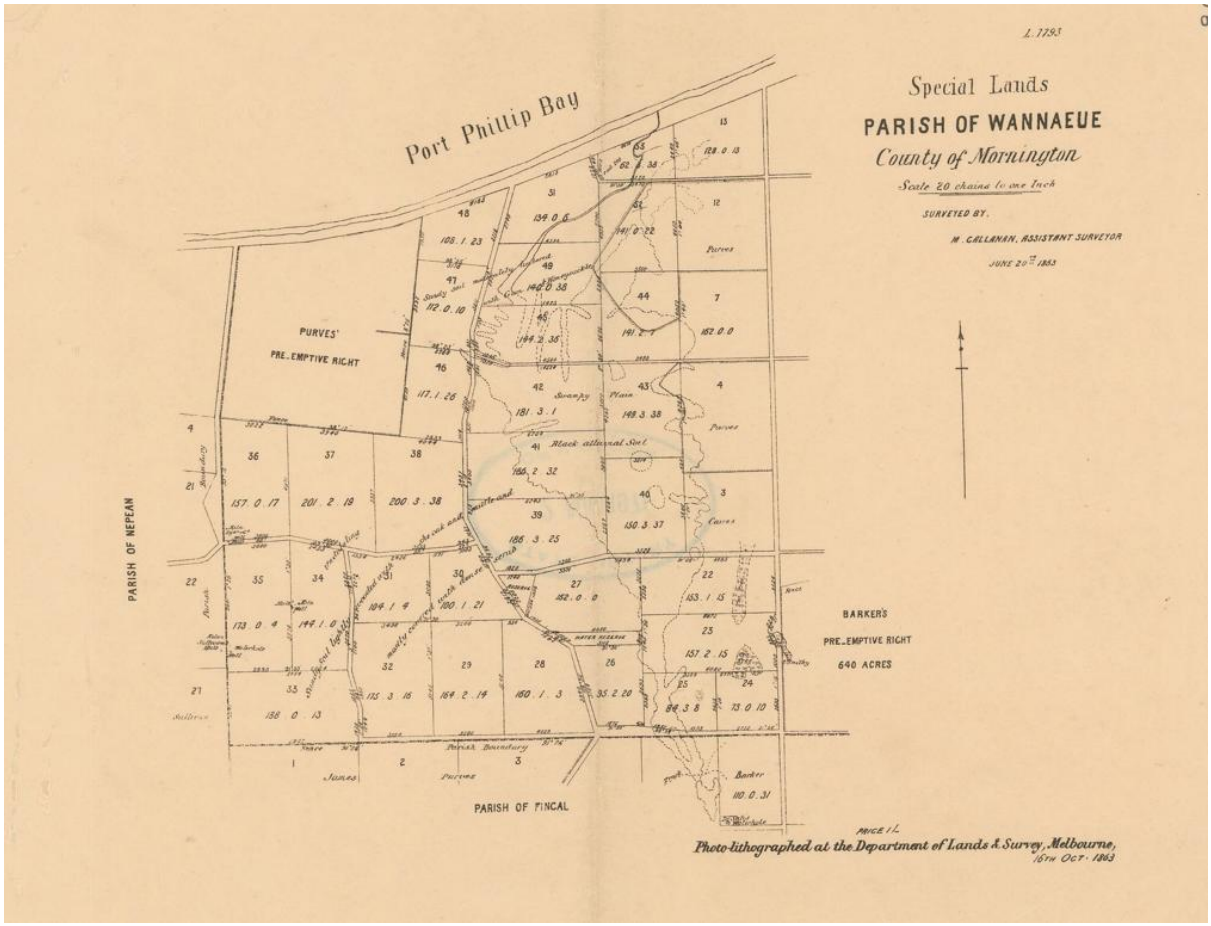

Figure 7*. *Parish of Wannaeue (County of Mornington), 26 June 1866. *Port Phillip Bay at north; Parish of Fingal to south. The Tootgarook Swamp is mapped centrally. The dune-rise belt associated with the 1866 lease area lies along the* ***western margin****, corresponding to modern* ***Fingal/Boneo****. Vegetation and substrate notes (Sheoak–Banksia mosaics on* ***drift sand over limestone/marl; perched water on thin clay lenses****) match the sandy-hillock diagnostics referenced in the main text (Professional Board map and report, 1866).*

1.1. Evolutionary and Historical Context: Foredune Origins and Inland Expansion.

Although *Gaudium laevigatum* is native to parts of south-eastern Australia, its ecological behaviour is best understood through the conditions that shaped its evolutionary niche. The species evolved primarily as a **foredune coloniser**, occupying exposed coastal margins characterised by salt spray, wind shear, mobile sand, low nutrient availability, and frequent disturbance—conditions that selected for shallow, rapidly deploying root systems, short-lived seedbanks, and **disturbance-responsive** seed release (Lam, 2002; Lam & van Etten, 2002; Florabase DBCA, 1995).

Orientation note.
The historical descriptions referenced in this section apply specifically to the **western margin of Tootgarook Swamp (modern Fingal/Boneo)**, not the eastern side.

Historically, inland coastal woodlands operated under **a very different constraint architecture.** Dense ground-layer vegetation, deep-rooted shrubs and trees — dominated by sheoak, with Moonah and Banksia as key associates — and a moisture-retentive, aerated litter layer collectively prevented tea-tree recruitment. Under these conditions, *Gaudium laevigatum* remained largely confined to foredunes, where periodic disturbance created the bare, sunlit microsites required for establishment (Moxham et al., 2010; Moxham & Turner, 2011).

Multiple historical reconstructions for the Nepean Peninsula indicate that inland systems were **sheoak-rich open grassy woodlands**, intergrading with Moonah and Banksia. Sheoaks contributed dune stabilisation and actinorhizal nitrogen inputs, supporting ground-layer diversity and function on nutrient-poor calcareous sands (Moxham et al., 2009; DAFF, 2019).

Keble's 1927 geological mapping of the Fingal/Boneo dune rise shows a **highly porous calcareous system**, with wet patches occurring only where thin clay–marl lenses perch water. Subsequent dune infill of tidal channels and sea-level/fault-controlled changes rerouted flow paths over late Quaternary to Holocene times, long before European disturbance, confirming a hydrological template dominated by **rapid percolation punctuated by localised perched lenses**.

Taken together, the inland expansion of tea-tree is **not** a natural broadening of its ecological niche. It is a **constraint-release phenomenon** driven by European land-use change. Clearing removed canopy and mid-storey filters, exposed bare soil, and simplified hydrological pathways, creating inland microsites and soil conditions that functionally resembled **foredune recruitment surfaces** (Weber, 2003; Lam & van Etten, 2002).

Rabbits then removed the remaining biological constraints, disproportionately clipping native seedlings and resprouts while leaving tea-tree largely untouched. This selective grazing indirectly favoured tea-tree recruitment and accelerated the shift toward tea-tree dominance, preventing re-establishment of the multilayered structure that historically excluded it (Mutze, Cooke, & Jennings, 2016; PestSmart, n.d.). Grazing acted as a **dominant selector force**, amplifying tea-tree's advantage under disturbed conditions.

This historical context clarifies why tea-tree behaves *"invasively"* under sustained disturbance and grazing despite being native. What appears as aggressive inland expansion is the expression of a **foredune-coloniser strategy** in a landscape where structural and

biological constraints have collapsed (Lam & van Etten, 2002). At continental scale, rabbits are among Australia's most destructive invasive species, linked to the decline of hundreds of native plants and animals and implicated in local extinctions (Bush Heritage Australia, 2021; DCCEEW, 2004/2021).

Unburnt quadrats and 19th-century descriptions of sheoak–Acacia on dune crests and Moonah ("*dense scrub*") in swales corroborate the existence of a multilayered inland mosaic prior to rabbit-driven collapse (Moxham et al., 2009; Moxham et al., 2010).

1.1.1 Swales as Hydrogeomorphic Mosaics Rather Than Vegetation Unit.

Keble's geological synthesis demonstrates that interdunal swales on the Nepean calcareous dune system were not uniform landforms, nor did they support a single vegetation type. Swale hydrology was governed by depth-dependent interception of thin clay or marl lenses embedded within otherwise freely draining calcareous sands. The presence, thickness, continuity, and lateral extent of these lenses varied spatially, generating highly localised moisture residence times (**Keble, 1946; Keble, 1950**).

As a result, individual swales could express distinct wetland–grassland–woodland outcomes. Many shallow swales retained moisture only briefly or seasonally, forming small marshy depressions or damp hollows within an otherwise leaky dune matrix. Where swales were deeper, or where clay lenses intersected with greater depth or continuity, moisture residence increased, wetness expanded laterally, and more persistent marshy flats developed. At landscape scale, this hydrological convergence expressed itself as a dominant regional wetland system, rather than a simple aggregation of small swales (**Keble, 1946; Keble, 1950**).

Within the coastal limestone belt between Sorrento and Cape Schanck, this hierarchy of wetness culminates in the Tootgarook Swamp system, the principal expression of sustained wetness in the broader dune–swale mosaic. Smaller marshy swales and damp flats occur throughout the landscape, but these features are hydrologically subordinate to, and spatially organised around, the larger swamp complex and its marginal wet–dry transitions. A contemporaneous nineteenth-century traverse across this corridor describes limestone rises punctuated by marshy flats, some "*of considerable extent*," consistent with a dominant swamp system rather than uniformly wet swales (**The Australasian, 1889**).

Vegetation followed hydrology, not topographic position alone.
Moonah (*Melaleuca lanceolata*) occurred selectively where swales or swale margins combined shelter with sufficient moisture residence and fire buffering; it was not a default or ubiquitous swale taxon. Many swales were historically woodland-free, supporting calcareous

grasslands, herbfields, sedge–herb mosaics, or ephemeral wetland assemblages, depending on moisture persistence. The early collapse of these ground-layer systems under grazing and repeated disturbance has obscured the former extent and diversity of both grassy and wetland swales (**The Australasian, 1889**; see also **Keble, 1946; Keble, 1950** for hydrological context).

This depth-controlled hydrogeomorphic variability explains why historical descriptions of "*dense scrub*," "*open grassy hills*," and "*wet hollows*" coexist without contradiction—they refer to different positions within the same nested hydrological system, rather than competing accounts of a single vegetation type. Sustained rabbit-grazing compounds this loss of differentiation by removing palatable recruits and ground-layer cover, a mechanism recognised in Australian government listings of rabbit impacts as a key threatening process (**DCCEEW, n.d.**).

Swales therefore cannot be treated as a single ecological unit: they were inherently heterogeneous, structured by hydrological hierarchy rather than vegetation identity. Their subsequent simplification represents a loss of hydrological and biological differentiation, not successional change—most notably the collapse of small marshy swales and grassy flats feeding into the Tootgarook system—rather than a shift from one stable vegetation type to another (**Keble, 1946**; **Keble, 1950**; **The Australasian, 1889**).

1.2. Evolutionary Origin of *Gaudium laevigatum* as a Coastal Foreshore and Foredune Coloniser.

The ecological behaviour of *Gaudium laevigatum* is best understood through its evolutionary origin as a coastal foreshore and foredune coloniser, rather than as an inland woodland species. Across southern Australia, tea-tree populations are historically concentrated on exposed coastal margins where substrates are unstable, nutrients are low, salt spray is frequent, and disturbance from wind and sand movement is recurrent (Lam, 2002; Lam & van Etten, 2002; Florabase DBCA, 1995).

These environments exerted selective pressure for a functional architecture adapted to surface exposure, shallow substrates, and frequent microsite renewal. As a result, *Gaudium laevigatum* expresses traits that are highly effective on the foredune but normally filtered out by intact inland woodland structure:

- **Characteristically shallow rooting**, optimised for rapid capture of near-surface moisture pulses on freely draining sands (Lam, 2002).

- **Disturbance-responsive recruitment**, with establishment favoured in open, sunlit microsites created by sand movement or canopy removal (Lam & van Etten, 2002).
- **High tolerance of exposure**—salt spray, wind shear, and high evaporative demand—consistent with survival where few woody taxa persist (Florabase DBCA, 1995).
- **Rapid canopy closure once established**, enabling early dominance in settings where persistence is limited more by substrate instability than by long-term structural buffering (Lam & van Etten, 2002).

In intact foreshore systems, these traits are advantageous yet **self-limiting under intact coastal disturbance regimes**: persistent sand movement, salt exposure, and shallow soils prevent long-term canopy closure and continually refresh open recruitment surfaces (Lam & van Etten, 2002). Inland coastal woodlands historically presented the **opposite constraint architecture**—stable substrates, dense ground-layers, deeper rooting profiles, and multilayered canopies—rendering tea-tree recruitment largely inadmissible away from the shoreline (Moxham, Turner, Walker, & Douglas, 2010; Moxham & Turner, 2011). Following European land-use change, **rabbits became a primary selector force**—formally listed as a key threatening process—driving recruitment failure of palatable natives and enabling tea-tree capture of inland microsites (NSW Department of Climate Change, Energy, the Environment and Water [DCCEEW], n.d.).

The inland expansion of *Gaudium laevigatum* therefore reflects **constraint release**, not adaptive range expansion. European land-use and rabbit-grazing **re-created inland conditions that functionally resemble the foredune**—exposed surfaces, high light availability, simplified hydrological routing, and weakened recruitment constraints—allowing a foredune-adapted lineage to express dominance in contexts where it was historically filtered out (Lam & van Etten, 2002; Weber, 2003; Mutze, Cooke, & Jennings, 2016).

This evolutionary framing clarifies why tea-tree dominance is **neither historical nor stable** in Coastal Moonah Woodland. It is the predictable expression of a **foreshore coloniser** operating in an inland system where structural and biological constraints have collapsed (Lam & van Etten, 2002; Moxham & Turner, 2011).

Restoration implication.
Restoration does not require opposing tea-tree's traits directly; it requires **reinstating the inland constraint architecture**—ground-layer continuity, depth-partitioned rooting, and selector gates—that historically rendered these foredune traits ineffective away from the shoreline (Roper, Carter, & Weaver, 2015; Lam & van Etten, 2002).

2. Methods: Literature Synthesis Approach.

This study employs a **structured, problem-focused literature synthesis** integrating hydrology, soil science, fire ecology, coastal dune ecology, and herbivore-driven vegetation dynamics. Searches targeted combinations of terms such as "***Gaudium laevigatum***," "*Myrtaceae* ***hydrophobicity***," "***canopy interception***," "***soil-water-repellency,"*** "***coastal dune hydrology***," "***rabbit-grazing*** *vegetation structure,"* and "***Moonah woodland*** *ecology."* Sources included **peer-reviewed articles**, **government reports**, and **ecological management documents**.

Because no single study traces the **full causal chain—rabbit-grazing → structural simplification → hydrological alteration**—in a single system evidence was synthesised **across disciplinary domains** to construct a **mechanistic explanation** of system behaviour. This cross-domain approach follows established **systems-ecology synthesis** practice (Pickett, Kolasa, & Jones, 2007) and draws on well-developed hydrological frameworks, including:

- **canopy-interception modelling** (Crockford & Richardson, 2000), and
- **soil-water-repellency diagnostics** in Myrtaceae-dominated systems (Doerr, Shakesby, & Walsh, 2000).

2.1 Search Scope and Source Selection.

- **Databases/venues.** Web of Science/Scopus equivalents for peer-reviewed literature; government/agency repositories for management and status documents; state/federal listings for key threatening processes relevant to rabbits.
- **Time window.** Classic foundations (e.g., 1990s–2000s hydrology/SWR) through the most recent applied management sources relevant to Coastal Moonah Woodland and southern Australian dune systems.
- **Inclusion criteria.** Studies that (i) quantify or infer **mechanisms** affecting infiltration, soil-moisture, or recruitment (e.g., interception, SWR, root-zone pulse capture), (ii) document **structural responses** to disturbance or grazing, or (iii) provide **regional context** for Moonah/tea-tree dynamics.
- **Exclusion criteria.** Sources limited to **distributional lists** without mechanistic content; **opinion-only** pieces without empirical or clearly referenced bases; highly site-specific reports lacking transferable mechanism.

2.2 Evidence Integration and Triangulation.

- **Mechanism mapping.** Findings were first coded to **structural**, **hydrological**, or **biological** mechanisms (e.g., "*interception*," "*SWR*," "*rabbit-selector effects*"), then linked to observed outcomes (**ground-layer collapse**, **drier soil profiles**, **recruitment failure**).

- **Cross-domain corroboration.** Where possible, hydrological claims (e.g., interception/SWR) were corroborated by **independent** lines of evidence (e.g., root-zone dynamics, recruitment patterns) rather than single-study inference (Crockford & Richardson, 2000; Doerr et al., 2000).
- **Consistency testing.** Causal links were accepted when **multiple independent sources** converged on the same mechanism →outcome relationship (e.g., grazing → recruitment loss → structural simplification), consistent with **mechanistic synthesis** standards in systems ecology (Pickett et al., 2007).

2.3 Boundaries and Rigor.

- **Not a meta-analysis.** Given heterogeneous designs and endpoints across hydrology, vegetation dynamics, and management literature, **statistical aggregation was not attempted**. Instead, inferences rest on **concordance of mechanisms** and **repeatability of patterns** across contexts (Pickett et al., 2007). The synthesis is qualitative and mechanistic rather than quantitative or predictive.
- **Transferability.** Preference was given to studies with **clear process logic** (e.g., interception physics, repellency diagnostics) that reasonably transfer to **calcareous, sandy coastal systems** typical of the Nepean–Mornington region (Crockford & Richardson, 2000; Doerr et al., 2000).
- **Documentation.** Key statements about **Coastal Moonah Woodland** structure and tea-tree behaviour in degraded inland settings are anchored in **regional syntheses and applied studies** (Moxham et al., 2010; Weber, 2003).

Outcome. This integrative method identifies how **interacting structural (canopy closure, root architecture), hydrological (interception, SWR, pulse capture), and biological (rabbit-selector)** mechanisms combine to produce the **functionally drier, less aerated soil environments** characteristic of *Gaudium laevigatum* thickets, supporting a **coherent** mechanistic account of system change in **Coastal Moonah Woodland** (Crockford & Richardson, 2000; Doerr et al., 2000; Moxham et al., 2010; Weber, 2003). Causal links are evaluated through **consistency across independent literatures**, not pooled effect sizes, in line with **mechanistic synthesis** approaches (Pickett et al., 2007).

Scope note on fire. Fire is treated here as a **candidate driver and potential conditional amplifier**, rather than a presumed primary cause. Fire responses are interpreted using existing datasets for Coastal Moonah Woodland on calcareous dunes, where **frequency-dependent structural simplification** has been documented (Moxham & Turner 2008). These patterns are incorporated into the **mechanistic synthesis**, rather than being used to prescribe optimal fire intervals or fire-management targets.

3. Results: Mechanisms of Hydrological and Structural Change.

3.1 Canopy Interception and Reduced Throughfall.

Gaudium laevigatum exhibits a dense, fine-textured canopy with a high leaf area index (LAI)—traits strongly associated with substantial rainfall interception in sclerophyll vegetation. In comparable canopy types, interception commonly ranges from **~20–50% of gross rainfall**, with a large proportion evaporating directly from leaf surfaces before reaching the soil (Crockford & Richardson, 2000; Keim, Skaugset, & Weiler, 2006). Although species-specific data for *Gaudium laevigatum* remain limited, its canopy morphology closely aligns with taxa known to exhibit high interception capacity.

Reduced throughfall lowers direct soil-moisture inputs, particularly beneath **closed thickets.** This alters infiltration dynamics and constraining the depth and continuity of wetting fronts (Crockford & Richardson, 2000; Keim et al., 2006). These changes reduce both the **frequency** and **magnitude** of moisture availability in near-surface horizons, reinforcing the **functionally dry (reduced effective infiltration**) conditions characteristic of **dense tea-tree stands.**

Limitation.
Species-specific interception measurements for *Gaudium laevigatum* are scarce; inferences here are drawn from canopy traits and analogous sclerophyll species.

3.2 Hydrophobic Litter and Soil-Water-Repellency.

Myrtaceae species produce **hydrophobic, oil- and wax-rich litter** that promotes **soil-water-repellency (SWR)**—a well-documented inhibitor of infiltration that increases surface runoff and promotes preferential flow paths bypassing the biologically active root zone (Doerr, Shakesby, & Walsh, 2000). SWR is ubiquitous in coastal dune systems dominated by sclerophyll shrubs; plant-derived hydrophobic compounds coat soil particles, inhibit wetting, and contribute to vegetation patterning and patch dynamics (Dekker & Ritsema, 1994; Siteur et al., 2016).

In *Gaudium* thickets, slowly decomposing litter accumulates due to low decomposition rates and high hydrophobic content. This **persistent litter layer (Figure 8.)** sustains water-repellent soil conditions, reducing effective infiltration **via shallow wetting and bypass flow** even under high-intensity rainfall. As a result, wetting fronts remain **shallow and discontinuous**, strengthening the shift toward **functionally drier surface horizons** and constraining moisture availability for ground-layer recruitment (Doerr et al., 2000; Siteur et al., 2016).

On **calcareous sands**, infiltration impediments are not random. **Thin clay/marl lenses** form via illuviation, silicate weathering, dust deposition, and carbonate–clay precipitation. These **lens-controlled fragility gates** locally impede infiltration, creating small **perched water patches** within an otherwise leaky matrix. This mechanism is consistent with Keble's mapping and bore syntheses for the Nepean–Mornington dune field (e.g., Sorrento and Wannaeue bores; lens-bound hollows on the Nepean Bay Bar) and with nineteenth-century survey descriptions of marshy flats amidst limestone rises (Professional Board, 1866, Professional Board, 1866, as collated by Keble; see also Keble, 1927).

Hydrophobic litter, interception, and ground-layer suppression act **synergistically**, producing **surface-dominated hydrological closure**—a defining attribute of tea-tree thicket expansion in Coastal Moonah Woodland.

3.3 Shallow Rooting and Near-Surface Pulse Capture Dynamics.

Gaudium laevigatum possesses a dense, fibrous root system concentrated within the upper 10–20 cm of sandy coastal soils, enabling rapid uptake of near-surface pulse **inputs** immediately after rainfall (Lam, 2002). Regional studies across myrtaceous shrubs show similar shallow rooting and rapid pulse capture, particularly under freely draining, low-retention substrates and where groundwater tables decline (Groom, 2000). These traits allow **pre-emption of shallow wetting events**, narrowing moisture access and reducing recruitment windows for other species.

This mechanism does not "*dry the soil*" in an absolute hydrological sense; it **re-partitions** available water toward rapid shallow capture, toward rapid shallow capture **within the biologically active surface layer** diminishing infiltration to deeper horizons and shortening moisture persistence (Lam, 2002). Over time, this contributes to ground-layer recruitment failure and reinforces the structural collapse typical of tea-tree thickets.

Keble's geological survey confirms that the Nepean "*Cups*" include **perched swamps** where discontinuous clay/marl lenses interrupt rapid percolation, producing peat over marl hollows inside the dune field, and that over late Quaternary to historic times, **tideway blockage, sea-level oscillation, and local faulting** progressively altered these hydrological pathways. The **failure patches** evident today are the same **lens-controlled hollows**, now operating under modern stress toward functional collapse **under contemporary disturbance regimes** (Keble, **1950**).

3.4 Suppression of Ground-Layer Vegetation.

Tea-tree thickets reduce understorey light to extremely low levels—often ≥ 80% attenuation, **a level typical of closed canopies**—thereby suppressing grasses, herbs, and sedges that maintain porosity, infiltration, and surface-moisture buffering in coastal woodlands (Lin, Jung, Hsiao, & Hamburg, 2006; Weber, 2003; Nilsen et al., 1999). Beneath these canopies, resource supply to seedlings declines; available water is ≈ 20% lower and survival drops accordingly (Nilsen et al., 1999).

Ground-layer collapse removes:

- organic-matter inputs, vital for aggregate stability and water-holding capacity (Weber, 2003);
- soil aeration, due to loss of fine-root turnover and biopore formation (Nilsen et al., 1999);
- **root-driven porosity**, facilitating infiltration and near-surface moisture redistribution;
- microbial diversity and activity, including moisture-dependent decomposers essential for nutrient cycling (Weber, 2003); and
- moisture-buffering architecture, such as fibrous roots and humic materials that slow evaporative loss.

Role of sheoaks prior to rabbit-grazing.
Before chronic browsing, sheoak (*Allocasuarina/Casuarina*) played a pivotal role in sustaining ground-layer function via **actinorhizal nitrogen fixation** (*Frankia* nodules). This contributed biologically fixed N to nutrient-poor calcareous sands, supported microbial communities, enhanced soil aggregation, and maintained the grass–herb–sedge matrix (Department of Agriculture, Fisheries and Forestry [DAFF], 2019).

Sheoak-linked microhydrological functions.
Beyond N inputs, sheoaks contribute **rooting-depth complementarity**, **biogenic porosity**, and **structural litter**, all critical on calcareous, water-repellent sands. Fine root mats and nodulated laterals create infiltration pathways and stabilise microaggregates. Sheoak litter—structurally persistent and low in labile N—helps maintain a fibrous, moisture-buffering forest floor. Together, these functions support microbial activity that can **moderate SWR expression** after rainfall pulses (DAFF, 2019; Nguyen & Pawlowski, 2017; Obertello et al., 2003/2004).

Where sheoaks are lost, these microhydrological functions disappear, tightening feedbacks—low porosity, elevated repellency expression, shallow pulse capture (**§3.3**)—that drive **structural dryness** and ground-layer collapse in tea-tree-dominated systems (Moxham, Sinclair, Walker, & Douglas, 2009; Sanginga, Danso, & Bowen, 1989).

Figure 8. *Hydrophobic litter accumulation and ground-layer exclusion beneath young tea-tree thickets. Dense juvenile Gaudium laevigatum stems generate heavy, slowly decomposing litter rich in hydrophobic compounds. The continuous litter carpet shown here prevents seed–soil*

Box 2 — Convergent shrub architectures under disturbance

Tea-tree (Gaudium laevigatum) and Polygala myrtifolia are taxonomically unrelated species, yet under sustained disturbance they converge on the same recruitment-suppressing shrub architecture. Both intercept rainfall before it reaches the soil, both maintain a dense, vertically continuous canopy that suppresses light and moisture at the ground-layer, and both rely on shallow, near-surface root systems that rapidly capture pulse rainfall before it can infiltrate to depth. Neither species carries a protected bud bank or deep reserve system, such that both typically collapse if cut below the last green node.

Together, these features define how the shrub form occupies space, controls resources, and maintains dominance: interception limits throughfall, shallow roots pre-empt surface moisture, and canopy closure suppresses ground-layer recovery and recruitment. Tea-tree expresses this architecture through small, rigid, chemically fortified leaves and dense fine branching; Polygala expresses it through broad, leathery, evergreen foliage. Different species, different mechanisms—but the same **canopy-locked, interception-driven, shallow-rooted, recruitment-suppressing shrub architecture**.

contact, inhibits infiltration, suppresses herbs, grasses, and mosses, and promotes shallow, discontinuous wetting—reinforcing soil-water-repellency and ground-layer collapse.

3.5 Rabbit-Driven Selector Pressure and Positive Feedback Dynamics.

Rabbits selectively graze palatable species, preventing recruitment of Moonah, Banksia, eucalypts, and diverse ground-layer plants. Even **low densities (≤ 5 rabbits ha^{-1})** well below visual abundance thresholds produce steep declines in native cover and species richness (Mutze, Cooke, & Jennings, 2016; Cooke, 2012). In coastal systems, this pressure restructures vegetation toward **shrub-dominant architecture**, frequently expressed as tea-tree thickets, which subsequently reinforce hydrological dysfunction (Moulton, Hesp, Miot da Silva, Keane, & Fernandez, 2020; Lam, 2002; Lam & van Etten, 2002).

Positive feedback sequence.

1. **Constraint removal.**
   Grazing suppresses seedlings and resprouts of palatable species, removing the biological filters that historically constrained shrub dominance (Mutze et al., 2016;

Cooke, 2012).

2. **Tea-tree expansion.**
   Relatively unpalatable tea-tree occupies newly opened recruitment space (Lam, 2002; Lam & van Etten, 2002).
3. **Canopy closure.**
   Increasing cover elevates interception and shading, reducing throughfall and understorey light (Crockford & Richardson, 2000; Keim, Skaugset, & Weiler, 2006).
4. **Ground-layer collapse.**
   Loss of grasses, herbs, and sedges removes porosity, organic inputs, and microbial support (Weber, 2003; Nilsen, Bao, Hultine, & others, 1999).
5. **Hydrological shift.**
   Reduced infiltration and heightened SWR concentrate preferential flow and diminish near-surface moisture (Doerr, Shakesby, & Walsh, 2000; Siteur et al., 2016).
6. **Recruitment failure and lock-in.**
   Native recruitment stalls under altered light and moisture regimes, maintaining a tea-tree-dominated, low-option **architectural** state (Mutze et al., 2016; PestSmart, n.d.).

Grazing pressure therefore does more than shift species composition. It drives a **system-level collapse of structural diversity**, (**Figure 9.)** re-partitioning water in favour of **shallow, rapid capture** and away from the ground-layer and palatable recruits. This rerouting of water reinforces surface-dominated hydrology, via interception, SWR, and shallow pulse capture accelerates ground-layer loss, and ultimately **locks the system into a tea-tree-dominated architecture** (Moulton et al., 2020; Doerr et al., 2000).

Figure 9. *Rabbit-driven microsite opening enables tea-tree recruitment.*
Native wallaby grass ***Austrodanthonia racemosa var. raceme*** *(foreground/left) shows active grazing and ground-layer depletion, with disturbed, friable patches adjacent to it. Juvenile* ***Gaudium laevigatum*** *individuals are emerging preferentially in the disturbed zone, illustrating the selector-pressure sequence: grazing removes palatable species → ground-layer collapses → bare, high-light microsites form → tea-tree recruits into the opened corridor.*

4. Discussion.

Alignment with prior fire studies. The mechanism sequence identified in this study—**canopy interception, development of soil-water-repellency, shallow pulse capture and ground-layer collapse under sustained rabbit pressure**—accords with documented fire responses on calcareous dunes (Moxham & Turner 2008). **Increased fire frequency simplifies dominance and vertical layering**, with canopy and moss declining and grasses increasing, while ***Gaudium laevigatum*** **persists across the fire gradient** (Moxham & Turner 2008). **Fire alone does not initiate inland tea-tree dominance**, but instead **expresses underlying system constraints**.

Interpretive frame (EF): why "*transition*" and waiting misdiagnose recovery.

Interpreting legacy "*transition state*" language under EF.
Regional syntheses describe degraded expressions of Coastal Moonah Woodland (CMW) as **"*transition states*"**, reflecting a resilience/state-and-transition framing in which these conditions are treated as non-final and expected to resolve toward higher-quality woodland if disturbance regimes subside (e.g., Moxham, Cheal, & Turner, 2009). In the same sources, these states are presented as **guides to condition and regeneration potential**, with recovery linked to seedbank presence and to sites where disturbance histories (grazing, fire, nutrient change, weed invasion) have altered composition and structure (Moxham et al., 2009).

EF diagnosis.
Under the **Evolutionary Flexibility (EF)** frame, recovery is **conditional**, not assumed. Where **opposition** (Ω)—notably chronic rabbit-grazing, repeated disturbance, and ground-layer suppression—**persists**, these states do **not** transition in practice, regardless of elapsed time. They are **disturbance-maintained, arrested configurations**: recruitment corridors remain closed, and latent options cannot be expressed. Recovery observed **after** management reflects **constraint removal**, not an intrinsic successional tendency. Accordingly, states elsewhere labelled "*transitional*" are interpreted here as **conditionally recoverable only if** opposition is reduced and constraint architecture is rebuilt. Empirical descriptions of disturbance-driven change and the presence/absence of faithful taxa in degraded stands are documented by Moxham et al., 2009. EF is used here to organise diagnosis and sequencing; it does not introduce new mechanisms beyond those demonstrated in the Results.

Time is not neutral when opposition persists.
Time does not heal ecological wounds under sustained opposition; instead it **depletes a finite reserve of latent potential**. In rabbit-affected coastal dune systems, seedbanks and regenerative capacity function as **finite components of conditional capital**, not an inexhaustible buffer. Under ongoing grazing and disturbance, recruits are repeatedly removed before contributing back to the system, and the **option set is progressively thinned**. (Disturbance-driven degradation, weed increase, and loss of faithful species in degraded CMW remnants are summarised in Moxham et al., 2009.)

Sequencing implication.
Pulse interventions that do not first alter constraints—for example, broad clearing or other disturbance applied without output control (rabbits)—**risk spending latent potential**,

exposing seedbanks and regenerating cohorts to the same suppressive forces. Under EF, recovery depends on **changing both inputs and outputs**: **rebuild structural and floristic scaffolds** (ground-layer continuity, layered canopy, depth-partitioned rooting, nutrient gating) **while removing the pressures that continually erase them**. Only then do "*transitions*" become **admissible outcomes** rather than assumptions.

What this reframing accomplishes (concise cross-walk to Results & Methods).

- **Maps cleanly onto the demonstrated mechanisms** (**§**3.1–3.4): interception + SWR + shallow pulse capture + ground-layer collapse together create a **surface-dominated hydrology** that **cannot unwind by waiting**; it requires **active constraint repair** and removing opposition.

- **Explains observed "*non-transitioning transitions*"**: degraded CMW stands remain static because **corridors stay closed**; EF names the condition (arrested under opposition) and the **unlock** (constraint removal + opposition reduction).

- **Translates into operational sequencing** (developed in **§**4.3–4.5): **Polygala/Rhamnus first**, **ground-layer stabilisation**, **tea-tree reduction last**, with **asset-protection exceptions** applied narrowly and **steep-slope caution** for warrens.

Bridge to §4.2. The hydrostructural diagnosis in §4.1 explains *how* tea-tree thickets make soils functionally drier by re-wiring canopy–litter–soil pathways; §4.2 identifies **what keeps those pathways locked over time**—chronic rabbit opposition (Ω) that prevents ground-layer re-establishment and maintains the very conditions under which hydrological rerouting persists.

4.1. Tea-tree Does Not "*Dry Soil*" — It Reconfigures Hydrological Architecture.

Continuity from §3. Given that tea-tree does not "*dry the soil*" metabolically but **reconfigures hydrology** (§3.1-3.4), we next ask: *what maintains that configuration over time?* The answer is **rabbit-driven selector pressure**, which closes recruitment corridors, suppresses ground-layer repair, and **keeps** the interception–SWR–preferential-flow–shallow-capture loop active.

Tea-tree thickets alter hydrological pathways without requiring elevated transpiration

through **multiple interacting mechanisms**. The soil becomes **functionally drier** not because tea-tree extracts more water than other species, but because **water movement is re-architected**. Less rainfall reaches the soil surface due to **high canopy interception**; less of

the water that does arrive actually infiltrates because of **hydrophobic litter layers** and **water-repellent surface horizons**; more water is diverted into **preferential flow paths** that **bypass the biologically active root zone**; **shallow root systems** rapidly capture **near-surface pulses** immediately after rainfall; and the **ground-layer can no longer retain moisture** because the vegetation, organic inputs, porosity, and microbial processes that maintain soil water-holding capacity have collapsed (Crockford & Richardson, 2000; Doerr, Shakesby, & Walsh, 2000; Keim, Skaugset, & Weiler, 2006; Nilsen et al., 1999).

This represents a **structural, not a metabolic, shift**. Tea-tree does **not** "*dry*" the soil through exceptional transpiration. Rather, the **collective alteration of hydrological architecture—reduced throughfall**, **reduced infiltration**, **increased repellency**, **shallow pulse capture**, and **loss of ground-layer retention**—produces a soil system that is **drier in functional terms**, even when rainfall inputs remain unchanged (Crockford & Richardson, 2000; Doerr et al., 2000; Keim et al., 2006; Nilsen et al., 1999).

Comparable dominance dynamics occur in other degraded coastal shrub systems. Long-term management of *Polygala myrtifolia* in Coastal Moonah Woodland shows that shrub dominance **emerges after ground-layer buffering collapses and disturbance-aligned recruitment corridors open**, and that it **reverses** when **surface constraints are preserved** and those corridors are **closed** using **low-disturbance intervention** (Brown, 2025).

Scope/limitation. The claim here concerns **hydrostructural reconfiguration** (interception → SWR/repellency → preferential flow → shallow pulse capture → loss of retention), **not** unusually high transpiration rates. The diagnosis is therefore **architectural and mechanistic**, consistent with the Results (**§**3.1–3.4), rather than a species-level water-use generalisation (Crockford & Richardson, 2000; Doerr et al., 2000; Keim et al., 2006; Nilsen et al., 1999).

Takeaway. Tea-tree thickets make soils **functionally drier by re-wiring canopy–litter–soil pathways** after the ground-layer collapses—**not** by unusually high transpiration.

Fire as expression of constraint topology. Fire outcomes in this system are **contingent on the pre-existing constraint architecture**. Where rabbits maintain ground-layer collapse and **conditional corridors remain closed**, fire **amplifies structural simplification** by reducing canopy, litter and moss while favouring grasses and other disturbance-aligned elements (Moxham & Turner 2008). **Fire does not supply the primary mechanism of recovery in**

CMW on calcareous sand systems when these constraints remain unrepaired. This explains why ***Gaudium laevigatum*** **persists across all recorded fire histories** (Moxham & Turner 2008) and why **inland tea-tree thicketing aligns more closely with disturbance and fragmentation than with fire regime alone** (Moxham & Turner 2011).

Tea-tree as a gateway to secondary degradation.

Tea-tree dominance does not merely simplify woodland structure; it re-engineers the disturbance environment in ways that favour secondary disturbance-aligned shrubs with substantially greater long-term consequences. Dense tea-tree canopies reduce ground-layer resistance, homogenise microsites, and generate repeated disturbance pulses (fire, suppression, trampling) that advantage opportunistic woody invaders (Moxham & Turner, 2008). Operationally, the highest-risk pathway is **tea-tree → Polygala**, and best-practice suppression requires **least-disturbance, cool-season, selective control** with zero seed-rain tolerance (Brown, 2025; Roberts et al., 2023).

Among these, *Rhamnus alaternus* (Italian Buckthorn) and *Polygala myrtifolia* are the most consequential secondary colonisers, with **Polygala** representing the highest-risk trajectory (Eyre Peninsula Landscape Board, 2026; Department of Primary Industries & Regions South Australia, 2021/2026).

Buckthorn contributes to further structural closure and competitive exclusion once established (Urban Bushland Council WA, n.d.), however **Polygala presents a qualitatively different management risk**. *Polygala myrtifolia* establishes rapidly under tea-tree–dominated conditions and maintains a **persistent soil seedbank**, with Australian guidance and regional plans recording viability/emergence windows of **~5–10+ years**, necessitating sustained follow-up (Weeds Australia; Urban Bushland Council WA; Eyre Peninsula Landscape Board, 2026). Once this seedbank is established, disturbance events reliably trigger reinvasion, effectively locking sites into a degraded, shrub-dominated state with escalating management costs and narrowing recovery options (Eyre Peninsula Landscape Board, 2026).

In this sequence, tea-tree functions as a **gateway state** sequencing must suppress rabbits and disturbance aligned shrubs before any canopy work rather than a terminal condition. Where tea-tree dominance is allowed to persist, the probability of secondary invasion—particularly by **Polygala**—increases sharply, transforming a reversible structural problem into a long-duration **decades-scale** ecological liability (Moxham & Turner, 2008; Moxham, Cheal, & Turner, 2009). The critical management risk is therefore not tea-tree alone, but tea-tree **enabling** the establishment of disturbance-aligned shrubs whose legacy effects extend well beyond the initial shrub phase (PIRSA, 2021/2026; Eyre Peninsula Landscape Board, 2026).

This gateway dynamic explains why, once tea-tree dominance is established, fire consistently **reinforces** rather than **reverses** degradation on calcareous dunes (see §4.7).

Architectural convergence and invasion risk.
The exceptional management risk posed by *Polygala myrtifolia* arises not only from its persistent seedbank, but from its **architectural convergence with tea-tree**. Intact Coastal Moonah Woodland exhibits a high degree of structural resistance to invasion, maintained by a multi-layered canopy, functional ground-layer, and continuous litter and moss cover (Moxham, Cheal, & Turner, 2009). Rabbit browsing breaches this resistance by collapsing lower-layer architecture, after which tea-tree establishes and re-engineers the site into a dense, shrub-dominated form (Moxham & Turner, 2008).

Polygala is uniquely positioned to exploit this condition because its growth form, canopy density, and disturbance response closely **match the architecture already created by tea-tree** (Weeds Australia). Under these conditions, **Polygala does not invade intact woodland**; it **replaces or co-occupies** an existing shrub framework, recruiting rapidly following disturbance and drawing on a long-lived soil seedbank. Australian germination research shows **high germination (≈93–95%) at 25/15 °C**, broad **pH tolerance (75–100% across pH 4–10)**, tolerance to **moderate salinity (≤100 mM NaCl)**, and **surface-biased emergence** (≈48%)—a profile consistent with rapid recruitment under shrub canopies and post-disturbance pulses (Roberts, Moloney, Monie, & Florentine, 2023). Buckthorn (*Rhamnus alaternus*) contributes to further closure within this pathway (DEW/Eyre Peninsula Landscape Board, 2026), but **Polygala** represents the highest-risk trajectory because its architectural fit and seedbank persistence convert a **rabbit- and tea-tree–mediated** structural shift into a **long-duration, self-reinforcing** degraded state (Eyre Peninsula Landscape Board, 2026; Weeds Australia).

Key point.
Polygala represents the greatest secondary threat because its architecture closely matches that created by tea-tree, allowing it to replace or co-occupy shrub-dominated sites once rabbits have breached the structural resistance of intact woodland (Moxham & Turner, 2008; Moxham et al., 2009; Weeds Australia; Roberts et al., 2023).

4.2. Rabbit-Grazing as the Primary Driver of Thicket Formation.

Tea-tree thickets are **not** an inherent or self-maintaining ecological condition; they arise through **prolonged rabbit-grazing** that selectively removes ground-layer constraints and **redirects regeneration pathways**. In the absence of rabbits, Moonah woodlands maintain a **diverse structural mosaic** because biotic selector gates and structural constraints—**ground-layer continuity, regulated browsing pressure, canopy layering, and hydrological openness**—keep recruitment corridors broad and **prevent shrub-monoculture lock-in**. Under sustained grazing, rabbits **selectively remove seedlings and resprouts** of palatable species while leaving relatively unpalatable shrubs (e.g., tea-tree) largely untouched,

funnelling the system toward monoculture (Mutze, Cooke, & Jennings, 2016; PestSmart, n.d.; Lam & van Etten, 2002).

Once tea-tree becomes dominant, **canopy closure** intensifies interception and shading; the **ground-layer collapses**; and hydrological routing shifts in ways that **reinforce** the structural change—amplifying the dysfunction initially triggered by grazing (Moulton, Hesp, Miot da Silva, Keane, & Fernandez, 2020). Rabbit pressure is therefore **not merely contributory**; it is the **primary driver** that enables tea-tree thicket formation and **locks** the system into a **degraded, low-diversity, low-option** architecture (Mutze et al., 2016; PestSmart, n.d.).

This pattern is **not species-specific** to *Gaudium laevigatum*. In coastal systems where grazing and disturbance **remove recruitment constraints**, disturbance-aligned shrubs with **persistent seedbanks** (e.g., *Polygala myrtifolia*) exhibit the **same monoculture trajectory**, indicating that shrub thicket formation is a **system-level response to constraint failure**, not a species anomaly (Brown, 2025).

As tea-tree stands thicken, they also **modify herbivore and predator dynamics** through changes in physical structure. **Dense thickets provide persistent cover** for rabbits, reducing exposure and allowing grazing pressure to be **maintained spatially and temporally**. Episodic disturbance is thereby converted into **sustained selector pressure**, preventing ground-layer recovery and **re-imposing** the recruitment suppression that enabled thicket formation. Concurrently, increasing stem density and low-visibility shrub architecture **reconfigure understorey access pathways**, placing structural constraints on predator movement and interception. **Reduced access—rather than predator absence**—weakens predation as a regulating pathway. This allows grazing pressure to persist under a **constrained-access regime**. These structural effects are not unique to tea-tree: **dense formations of *Polygala myrtifolia* and *Rhamnus alaternus*** create comparable cover, similarly, altering access geometry. Under dry conditions, rabbits may even **strip cambial tissue** from these shrubs as a moisture source, further coupling herbivore pressure to dense woody architecture and **extending disturbance** into periods when grazing alone would otherwise decline.

Historical mechanism.
Early twentieth-century accounts from the Nepean dunes document not only rabbit-driven grass collapse but the **operational sequence** that converted **sheoak–grassland mosaics** into **"*ti-tree*" monoculture** on calcareous sands: fell and stack a fraction of the scrub; **burn hot** to bare ash; **sow seed onto the still-hot substrate**; install **fencing**; and apply **repeat burns** to suppress resprouting. This **bare-surface, ash-over-sand** treatment created exactly the **SWR-tight, litter-poor, infiltration-closed** conditions that favour thicket persistence. The

modern shrub monoculture is therefore **not a natural endpoint**, but a **historically engineered and rabbit-amplified collapse state** on a sensitive substrate (The Leader, 16 Nov 1912; *The Advocate*, 28 Feb 1925; Boneo–Sorrento corridor).

Historical confirmation.
The same sources describe a rapid **before → after** transition—from **grassy sheoak landscapes** to ***"grassless wastes thickly covered with tall ti-tree"***—following rabbit irruptions, **explicitly linking rabbit arrival to tea-tree spread**. These testimonies provide **direct evidence** that tea-tree dominance is a **rabbit-driven structural collapse**, not a natural or climatically determined vegetation state.

Interpreting the collapse through the EF frame.
Viewed through **Evolutionary Flexibility (EF)**, tea-tree thickets represent a **negative-K, low-option** configuration disclosed under **rabbit opposition (Ω)**. **Restoration succeeds when:**

- **(D + R)** are rebuilt (**diversity + redundancy**);
- **constraints (C / CT)** are re-opened to **expand admissible recruitment corridors**; and
- **coherence (K)** is shifted back toward **buffering**;

before large reductions in dominant biomass are attempted (cf. §§3–4; Mutze et al., 2016; Moulton et al., 2020).

Softened interpretive note (aligned with EF language).
EF is presented here as an **interpretive scaffold** that names the **same causal chain** in architectural terms. Under this view, rabbit pressure functions as an **opposition profile** that **closes recruitment corridors, thins redundancy, and synchronises failure pathways**. The mechanistic synthesis is **independent of EF**; EF is used solely to (i) generalise the diagnosis and (ii) **justify sequencing** that **restores admissible recruitment routes before major biomass reductions** occur. EF **does not introduce new mechanisms**; it provides **architectural language** for the mechanisms described above.

Scope note (driver vs co-factors).
Other disturbances (e.g., inappropriate fire, nutrient enrichment, sand movement) can **co-amplify** thicket dynamics, but in the systems analysed here **rabbits are the enabling driver** that **activates and maintains** the monoculture trajectory; without **opposition relief**, time spent "*waiting*" further **spends latent potential** (Mutze et al., 2016).

Operational takeaway.
Do **not** treat thickets as "*transitions*" that will resolve with time. **Suppress rabbits first**, **stabilise the ground-layer**, and only then **reduce dominant biomass**—otherwise interventions simply **re-expose** seedbanks and regenerating cohorts to the **same suppressive profile**, deepening lock-in (Mutze et al., 2016; Moulton et al., 2020).

Bridge to §4.2.1. Spatial persistence of rabbit pressure. Because rabbit pressure is **spatially heterogeneous**, the degree to which thickets remain locked—or drift toward senescence—depends on **where** and **how long** opposition persists. §4.2.1 maps this heterogeneity and shows when late-stage thinning occurs *without* recovery.

4.2.1 Spatial Persistence of Rabbit Pressure and Conditions Under Which Late-Stage Thinning Occurs.

Continuity from §4.2. Having established rabbits as the **primary driver** of structural lock-in, §4.2.1 examines the **landscape patterning** of that pressure to clarify where late-stage thinning occurs and why it often yields **replacement rather than recovery** in fragmented or propagule-rich contexts.

The persistence—and eventual relaxation—of **rabbit pressure** varies sharply across the landscape, and this spatial patterning governs whether tea tree thickets remain **locked** or enter **late-stage senescence**. Dense *Gaudium laevigatum* thickets are not biologically inert. Over multi-decadal periods, small birds use tea tree as shelter and perches, depositing seeds via defecation and regurgitation; this introduces additional taxa to the understorey, particularly **bird-dispersed shrubs** and small trees, with composition driven by the surrounding propagule pool.

As thickets mature, **stem density**, **canopy closure**, and **litter accumulation** progressively reduce ground-level accessibility. In some contexts, dense tea tree stands eventually become **structurally unusable to rabbits**, producing a late shift in **selector pressure**. This transition is **spatially contingent**. In peri-urban or otherwise human-proximate areas—where rabbit populations are already reduced by control programs, fencing, traffic mortality, predation subsidies, or habitat fragmentation—**functional exclusion** of rabbits from dense thickets can occur earlier and more fully. By contrast, in **remote or less disturbed** landscapes, rabbits commonly remain beneath tea tree for much longer, maintaining **sustained grazing** that suppresses ground-layer recovery and native recruitment. In such areas, tea tree dominance is **prolonged** rather than relaxed, and senescence-driven thinning may be **delayed for decades** or fail to occur within management-relevant time frames (Mutze, Cooke, & Jennings,

2016; Cooke, 2012).

Where rabbit pressure is eventually reduced—whether through **structural exclusion** or **external population decline**—ageing tea tree cohorts may begin to **senesce**, and **localised thinning** arises from stem mortality rather than disturbance. During this phase, **avian-mediated seed deposition** becomes more visible, but composition remains strongly conditioned by neighbourhood propagules. In **fragmented coastal landscapes**, seeds deposited beneath senescing tea tree frequently include **secondary woody weeds** (e.g. *Cotoneaster* spp., *Rubus fruticosus* agg., *Rhamnus alaternus*, *Pittosporum undulatum*) **(Figure 10),** alongside—or instead of—native species (Moxham & Turner, 2011; Moxham, Cheal, & Turner, 2009).

Critically, this transition unfolds over **multi-decadal timescales (~30–60 years)** following **prolonged constraint closure.** During this period, because recruitment corridors remain closed, the **original soil seedbank** and **residual native assets** continue to **decay**. Seeds of disturbance-sensitive grasses, herbs, sedges, and canopy species are progressively exhausted or rendered non-viable, and remnant individuals that initially persist beneath thickets often **senesce without replacement (Figure 11)** (Moxham et al., 2009; Moxham & Turner, 2011; Mutze et al., 2016).

Chronic rabbit disturbance does more than suppress native recruitment; it **actively maintains the surface conditions under which disturbance-aligned shrubs are able to recruit.** Through repeated digging, scraping, and grazing, rabbits remove mosses, litter, fine roots, and palatable ground-layer species, continually re-exposing shallow soil microsites and **preventing progressive burial of surface seedbanks**. This disturbance regime is **persistent rather than episodic**, holding seeds within the upper soil profile where emergence probability is highest.

Germination data for *Polygala myrtifolia* show that seeds are **non-dormant, highly viable, light-independent, and strongly surface-biased,** with emergence declining rapidly as burial depth increases (Roberts et al., 2023). Under sustained rabbit pressure, these recruitment corridors are therefore **not transiently opened and closed, but continuously maintained across seasons**, particularly during cool, moist periods. The result is **ongoing, asynchronous recruitment rather than a single post-disturbance pulse,** allowing *Polygala* to persist and re-establish even where adult plants are suppressed or canopy structure shifts. Rabbit activity therefore functions as a **recruitment amplifier for disturbance-aligned shrubs**, linking ground-layer collapse directly to the germination niche identified by Roberts et al. (2023) and preconditioning the system for secondary shrub dominance unless surface constraints are

restored.

The resulting change therefore represents **replacement rather than recovery of the historical woodland architecture**, and its timing and outcome are strongly mediated by **rabbit persistence** across the landscape. Tea tree thickets **may** thin and be replaced in some contexts, but by that point the **historical option set** has largely been **lost**, and the system is typically routed toward a **different—often more invasion-prone—assemblage (Figure 10),** rather than a return to the original woodland architecture (Moxham & Turner, 2011; Moxham et al., 2009). Comparative cases involving *Polygala myrtifolia*, *Rhamnus alaternus*, and fire are treated diagnostically in the appendices to demonstrate the **generality of the constraint-collapse mechanism,** not to introduce additional causal drivers.

Operational implication.
If **outputs** (e.g. rabbit-grazing pressure) are **not** controlled, neither **time** nor **disturbance** will produce recovery; both will simply **spend remaining latent potential** (Mutze et al., 2016; Cooke, 2012; Moxham et al., 2009).

Constraint release rather than evolutionary novelty.
The initial, non-degraded coastal woodland **evolved under constraints** that limited where and how tea tree could persist, confining it largely to **foredune and disturbance-exposed contexts**. These constraints—**ground-layer density, recruitment filtering, and hydrological openness—did not eliminate tea tree, but prevented its inland dominance. European disturbance** removed or inverted those constraints, **altering which latent strategies could be expressed.** Tea tree thicket formation thus represents the **expression of an existing strategy under an altered constraint topology, not** a change in the species' evolutionary trajectory.

Bridge to §4.3. If the **timing and outcome** of thinning depend on opposition persistence (§4.2.1), then **restoration must be sequenced** to remove opposition and **rebuild constraints** before altering dominant biomass. §4.3 sets that sequence: **Polygala first, ground-layer second, tea tree last.**

Figure 10. Late-stage tea-tree thinning producing replacement rather than recovery in a peri-urban context.

*Senescing **Gaudium laevigatum** no longer maintains exclusive dominance, but the historical woodland option set has been lost. Secondary woody shrubs occupy released space, ground-layer architecture remains absent, and the system is routed toward an invasion-prone assemblage rather than recovery.*

Figure 11. Senesced tea-tree collapse suppressing native assets under chronic disturbance.

*Mature **Gaudium laevigatum** stems have collapsed, forming a dense layer of woody debris over **Leucopogon parviflorus** and **Acacia retinodes var. uncifolia**, both present but physically inhibited beneath the fallen material. Chronic rabbit disturbance and past fire*

exposure have prevented ground-layer recovery, illustrating that tea-tree senescence produces replacement, not recovery, and continues to suppress high-value native species.

canopy. The absence of a ground-layer and the replacement of layered woodland structure illustrate how fire, under chronic disturbance and rabbit pressure, produces ***simplification rather than recovery****, entrenching a low-option tea-tree thicket.*

4.3. Implications for Restoration (Polygala First, Ground-Layer-Safe Thinning).

Continuity from §4.2.1. Because rabbits and disturbance-aligned shrubs (notably *Polygala*/*Rhamnus*) exploit any opening, **thinning without front-loading opposition relief** and **surface-constraint repair** simply **spends latent potential** and entrenches lock-in. The sequence below operationalises this logic.

Rule of order.
Disturbance-aligned shrubs—*Polygala myrtifolia* and *Rhamnus alaternus*—**must be suppressed before any substantive tea-tree removal is attempted**; reversing this order reliably converts thinning into **replacement rather than recovery** (Roberts et al., 2023; Weeds Australia, n.d.).

Effective restoration in Coastal Moonah Woodland **should not begin with wholesale tea-tree removal**. Because thicket formation is maintained by **coupled structural and hydrological mechanisms under rabbit pressure**, management must first **repair missing functions—recruitment pathways, ground-layer architecture, depth-partitioned rooting, and nutrient gating—before** gradually altering dominant structure (Lam & van Etten, 2002; Roper, Carter, & Weaver, 2015).

Restoration framing (explicit).
Restoration is **not** the re-assembly of a target Ecological Vegetation Class. It is the **reconstruction of evolutionary functional pathways and constraint architecture** that historically maintained persistence. **Species composition is an outcome of restored pathways**, not the mechanism by which persistence is re-established (Moxham, Cheal, & Turner, 2009; Moxham & Turner, 2011).

Where disturbance is **biologically maintained**, **population control** and **resource-network collapse** must be treated as a **single intervention**, not sequential or optional actions (Mutze, Cooke, & Jennings, 2016; Cooke, 2012).

Six-Step Restoration Sequence.

Steps 1 and 2 are coupled: rabbit control and suppression of disturbance-aligned shrubs must proceed **together** to close recruitment corridors and stabilise surface processes.

1) Control rabbits to reopen recruitment pathways.

Even low rabbit densities (≤ 5 rabbits ha^{-1}) cause steep declines in native cover and richness and suppress seedling establishment. Lowering grazing pressure is essential to retain any gains in ground-layer recovery (Mutze et al., 2016; Cooke, 2012; PestSmart, n.d.).

2) Front-load suppression of surface-aligned disturbance colonisers (*Polygala myrtifolia* and *Rhamnus alaternus*) before and during thinning.

- *Polygala myrtifolia* exhibits a **disturbance-aligned recruitment strategy**: soil pH is not limiting; germination is high across the coastal temperature range; moisture-stress tolerance is moderate; and emergence is **strongly surface-biased** (Roberts et al., 2023).
- The increased light and small disturbed patches created during thinning open **ideal recruitment corridors** that *Polygala* is **pre-adapted** to exploit—especially where native recruitment remains **pH-constrained** (Roberts et al., 2023).
- A **persistent, multi-year seedbank** produces repeated recruitment pulses unless seed input and surface-emergence pathways are actively **closed**. If suppression is **delayed**, thinning intended to assist native recovery instead **amplifies *Polygala***, rapidly re-occupying newly opened microsites (Roberts et al., 2023; Weeds Australia, n.d.).

As established in §4.2.1, chronic rabbit disturbance does not merely suppress native recruitment but **continuously maintains shallow, exposed soil microsites**. When combined with the strongly surface-biased, non-dormant germination behaviour of *Polygala myrtifolia* (Roberts et al., 2023), any thinning-induced opening reliably re-activates recruitment unless surface constraints are repaired. **This is why suppression of *Polygala* must be front-loaded and coupled with rabbit control before structural thinning is attempted.**

Rhamnus alaternus (Italian buckthorn) must be treated **concurrently**. At low to moderate densities it is straightforward to suppress, but dense evergreen canopies, deep litter beds, and **bird-mediated propagule pressure** require **staged, low-disturbance, in-situ** suppression to prevent creation of **high-light corridors** that favour reinvasion. **Delayed treatment** risks buckthorn becoming the **primary gap beneficiary** (Roberts et al., 2023; Weeds Australia, n.d.).

Method: use **low-disturbance** approaches with **multi-year follow up**, aligned to

seedbank longevity, **propagule pressure**, and **seasonal emergence**, to prevent synchronised recruitment and enable progressive seedbank drawdown (Roberts et al., 2023; Weeds Australia, n.d.).

3) Initiate targeted tea-tree thinning to protect and re-establish the ground-layer.
Use **narrow corridors** and **small patches** to raise understorey light and throughfall while **limiting bare-soil exposure**, which otherwise intensifies **soil-water-repellency (SWR)** and runoff.
Avoid wholesale clearing, which: (i) increases repellency; (ii) triggers capsule opening; (iii) causes dense tea-tree recruitment; and (iv) resets the system into **even thicker thickets** (Lin, Jung, Hsiao, & Hamburg, 2006; Lam & van Etten, 2002; Weber, 2003).

4) Immediately rebuild the ground-layer in thinned or suppressed patches.
Direct seed or plant **grasses, herbs, and sedges**; retain **coarse woody debris**; and deploy **micro-wetting / SWR-amelioration** practices. These steps restore **porosity** and **near-surface moisture retention**, denying *Polygala* the surface-moist microsites it depends on (Roper et al., 2015; Roberts et al., 2023).

5) Reintroduce structural diversity as the ground-layer consolidates.
Re-establish **Moonah, sheoaks (Allocasuarina/Casuarina), Banksia**, and mid-storey species to rebuild:
• **layered architecture**, • **rooting-depth complementarity**, and • **actinorhizal nutrient gating**—thus reinstating the **redundancy** that historically limited tea-tree dominance (Moxham, Sinclair, Walker, & Douglas, 2009; DAFF, 2019).

6) Continue phased tea-tree reduction, synced to diagnostics.
Progressively reduce tea-tree as:
• **ground-layer cover increases**,
• **native recruitment is verified**,
• **Polygala suppression is sustained**.
This sequencing lowers the risk of post-treatment recruitment surges and prevents **resetting to denser thickets** (Lam & van Etten, 2002; Roberts et al., 2023; Weeds Australia, n.d.).

Caution on Fire.
On **calcareous, SWR-prone sands**, generic "*reset*" burns typically on calcareous, SWR-prone

sands: **amplify SWR**, **create recruitment surfaces** for tea-tree and *Polygala*, and **fail to produce recovery** where constraints are degraded **unless**:

1. rabbits are **controlled**; 2) *Polygala* is **contained**; and 3) the **ground-layer** is already **re-established** (Doerr, Shakesby, & Walsh, 2000; Roper et al., 2015). Only then should additional **biomass reduction** be considered.

Rationale and Architectural Logic.
Why *Polygala* first? Because it exploits the very conditions **thinning** is intended to create for natives. When *Polygala* suppression is **paired with rabbit control** and **rapid ground-layer rebuilding**, early **targeted thinning** protects the ground-layer instead of handing the site to colonisers (Roberts et al., 2023; Weeds Australia, n.d.).

Central architectural principle: Restore missing functions before removing the dominant structure.
(Roberts et al., 2023; Weeds Australia, n.d.)

One-line takeaway. Polygala first, ground-layer second, tea-tree last—because only a **rebuilt constraint architecture** can hold recruitment corridors open long enough for thinning to work.

Management implication — asymmetric risk of removal.
Although *Gaudium laevigatum* and *Polygala myrtifolia* **converge** on the same **recruitment-suppressing shrub architecture** under disturbance, the **ecological risk of removal is not equivalent**. Autochthonous coastal systems **developed under historical exposure** to intermittent tea-tree within an **open, layered mosaic**, and many native species retain **conditional tolerance** to its structure where **ground-layer pathways** and **recruitment corridors** remain intact. By contrast, no native species evolved with *Polygala myrtifolia*, and its dominance introduces a **novel architectural state** with **no embedded recovery contingencies**. Consequently, **unsequenced tea-tree removal** can **collapse remaining native pathways**, whereas **delayed or incomplete suppression of *Polygala*** reliably results in **replacement rather than recovery**. This asymmetry explains why *Polygala* must be addressed **first** in restoration sequencing, **even where tea-tree is the visually dominant canopy** (Moxham, Cheal, & Turner, 2009; Moxham & Turner, 2011).

Architectural convergence does not imply ecological equivalence: tea-tree sits within a **historically contingent system**, whereas *Polygala* represents a **novel, non-recoverable routing state**.

Management Rule — Order matters (with autochthonous asset-protection exception).
Rule. Remove **disturbance-aligned shrubs** (*Polygala myrtifolia*, *Rhamnus alaternus*) and

stabilise the ground-layer before reducing tea-tree. Reversing this order **opens recruitment corridors** that favour replacement shrubs and **closes recovery pathways**.

Exception (autochthonous asset protection). Where **high-value autochthonous assets** (e.g., *Melaleuca lanceolata*, *Allocasuarina* spp., **Banksia**, or **intact native ground-layer assemblages**) are being **directly suppressed or lost** beneath tea-tree, **limited, localised tea-tree reduction may be undertaken first**, provided it is **low-disturbance, in situ**, and **immediately paired** with *Polygala/Rhamnus* suppression and **ground-layer stabilisation**. **Broad or unsequenced** tea-tree removal remains **contraindicated**.

Definition (assets). "*Assets*" refer **exclusively** to **autochthonous species and assemblages with embedded recovery potential**; disturbance-aligned shrubs and structurally dominant tea-tree are **not** considered assets under this definition.

System-scale qualifier (predator mediation in continuous systems).
In **large, continuous** coastal systems with established predator guilds and low edge effects, **vegetation structure can influence rabbit behaviour** by mediating **predation risk**. In such contexts, dense shrub thickets may function as **refugia** rather than controls on grazing, and **limited structural opening** can **reduce rabbit pressure** by increasing predator access and altering rabbit spatial use.

This mechanism is **context-dependent** and does **not** override the sequencing rule: any thinning undertaken for this purpose must be **low-disturbance** and **concurrent** with suppression of disturbance-aligned shrubs (*Polygala*, *Rhamnus*) and **stabilisation of the ground-layer**. Predator facilitation is **not** a substitute for **direct rabbit control** and is **not** expected to operate reliably in **fragmented or peri-urban** remnants (Mutze et al., 2016; Cooke, 2012).

Coupled strategy: population control + resource-network collapse.
Downward pressure on rabbit-driven disturbance is most effective when **direct rabbit control** and **vegetation-based constraint of rabbit diet and shelter** are applied **together**. Field observations at Boneo indicate that rabbits persist not simply as a function of population size, but through access to a **supporting resource network**—including **invasive grasses**, **woody shrubs** such as *Rhamnus alaternus*, and **dense *Polygala myrtifolia* thickets** that provide **forage, dry-season moisture, and structural refuge**. Addressing rabbit impacts therefore requires **simultaneous action** on **both components** of this system.
Direct population control alone reduces rabbit numbers but, without concurrent suppression of **food and harbour plants**, remaining individuals retain the capacity to **persist, forage efficiently, and maintain chronic soil-disturbing behaviour**. Conversely, **vegetation control alone** is undermined where rabbit pressure continues to **remove ground cover,**

expose soil, and reactivate seedbanks. **Applied together**, these interventions act **synergistically**: vegetation suppression **constrains dietary supplementation and shelter**, while population control **reduces grazing and digging intensity**. The outcome is **collapse of the disturbance feedback loop** that sustains invasive dominance (Mutze et al., 2016; Cooke, 2012).

Framed this way, **rabbit management is not standalone**, but an **integral component of disturbance architecture** within the **Method of Least Disturbance**. Rabbits function as **maintenance agents of invasive feedback loops**, and effective restoration depends on **disrupting both the animals and the resource networks** that enable their impact. **Integrated application**—rather than reliance on either population suppression or vegetation control alone—is therefore essential for **durable ecological outcomes**.

Bridge to §4.4. Even with correct order (***Polygala*** **→ ground-layer → tea-tree**), outcomes still depend on **method choice**. §4.4 shows *why* selective **in-situ** control preserves shade, litter, and surface roughness, thereby **decoupling germination cues** and preventing seedbank synchronisation that would otherwise reset the system.

4.4. Selective Chemical Control and Seedbank Dynamics: Why Method Choice Determines Ecological Trajectory.

Continuity from §§4.1–4.3. With hydrological **re-wiring** (§4.1) sustained by **rabbit opposition** (§4.2) and sequenced **constraint repair** established (§4.3), the final determinant is **how** removal interacts with **seedbanks**. Selective control prevents **synchronised pulses** that would undo sequencing and **re-open** lock-in pathways.

Disturbance, Soil-Water-Repellency, and Why Method Choice Matters.

Degradation of Coastal Moonah Woodland is consistently associated with disturbance-driven processes that simplify vegetation structure, increase bare ground, and erode native ground-layer components, rather than with the presence of invasive species alone (Moxham & Turner, 2009; Moxham, Cheal & Turner, 2009; Moxham & Turner, 2011). Higher-quality remnants retain intact physiognomy, including canopy cover, litter accumulation, and moss- and herb-rich ground-layers that buffer soil microclimate and regulate hydrological function. Management guidance therefore emphasises minimising soil and structural disturbance and retaining in situ vegetation architecture as a prerequisite for recovery (Moxham et al., 2010).

On calcareous dune systems, this guidance is mechanistic rather than precautionary. Disturbance determines whether rainfall functions as a regenerative input or is converted into runoff, bypass flow, and preferential infiltration through the activation of soil-water-repellency (SWR). Removal of canopy cover, litter, and surface roughness exposes hydrophobic soil horizons, causing rainfall to bead, run off, or bypass the biologically active surface layer rather than infiltrating evenly. This disrupts soil-moisture availability for native recruitment while concentrating moisture in microsites that favour disturbance-aligned colonisers.

Within this context, weed control methods must be evaluated not by tool type (chemical versus non-chemical) but by their hydrological and structural consequences. Clearance-based approaches such as cutting and removal, mechanical extraction, or fire commonly open canopy, remove litter, and increase surface exposure, intensifying SWR expression and generating bare-ground pulses. Under these conditions, management actions intended to facilitate recovery instead act as disturbance re-initiators, converting rainfall into an invasion-facilitating pulse rather than a recovery resource and reliably favouring reinvasion in systems operating near hydrological and recruitment thresholds (Moxham & Turner, 2011).

It is this hydrological context that determines whether shrub suppression suppresses invasion or amplifies it by synchronising germination cues across persistent seedbanks.

Where *Polygala* or buckthorn seedbanks remain active, tea-tree removal functions as a recruitment trigger—not a restoration action.

This asymmetry explains why visually dominant species are not always the correct first-order management priority in degraded Coastal Moonah Woodland.
Given this asymmetry, restoration outcomes are determined not only by **sequencing** but by **method choice**, because removal methods differ sharply in how they interact with **seedbank activation** and **surface-constraint architecture**. Selective chemical control (**in situ suppression that retains biomass**) is not a convenience; it is a **structurally required response** to the conditional behaviour of soil seedbanks in degraded coastal systems. Manual removal that exposes soil without retaining structure behaves mechanistically like non-selective disturbance, regardless of whether chemicals are used.

In Coastal Moonah Woodland (CMW) and analogous coastal environments, the dominant **constraint failure** is not merely canopy suppression; it is the **activation and persistence of disturbance-adapted seedbanks**. Management outcomes are therefore determined **not** by shrub removal per se, but by the **architectural consequences** of how removal interacts with germination cues and fragility gates.

Seedbanks as Conditionally Activated Systems.

Soil seedbanks operate as **conditionally activated reservoirs**, shifting among **dormant**, **germinable**, and **exhausted** states in response to cues including:

- surface light penetration
- diurnal temperature oscillation
- soil-moisture pulses
- oxygen diffusion
- microbial activity

Disturbance does not simply expose seeds. It **synchronises germination cues**, converting a temporally staggered seedbank into a **pulsed recruitment event**. On sandy, low-organic, water-repellent substrates, synchronisation is especially strong.

Broad or non-selective removal methods—slashing, grubbing, wholesale canopy opening, or fire—commonly trigger synchronisation by:

1. abruptly increasing surface light;
2. amplifying temperature variability;
3. producing sharp wetting fronts following rainfall;
4. reducing microbial attrition via litter loss.

The combined effect is **mass recruitment dominated by disturbance-aligned colonisers**, resetting the system to the same **low-option architecture** that management aims to reverse.

How Selective Chemical Control Alters Seedbank Behaviour.

Selective, in-situ control (e.g., **drill-and-fill, basal bark, targeted stem spray**) **decouples** germination cues. By neutralising incumbent shrubs while retaining:

- standing biomass
- litter continuity
- surface roughness
- shade

…selective methods:

1. prevent uniform light shock;
2. buffer temperature oscillations;
3. absorb rainfall pulses before they interact with bare mineral soil;
4. maintain microbial processes that drive seed decay.

Under these moderated conditions, seedbank expression becomes **asynchronous rather than pulsed**, enabling follow-up control to track emergence without system reset.

Species-Specific Implications.

Polygala myrtifolia

Empirical work shows:

- a **non-dormant seedbank** with very high germination across autumn–spring temperatures,
- **no light requirement**, and
- a **strong surface-emergence bias** that collapses with burial depth (Roberts et al., 2023; Weeds Australia, n.d.).

Implications:

- **Broad disturbance + surface exposure → dense, synchronised recruitment.**
- **Selective in-situ suppression →** removes seed input **without opening site-wide recruitment corridors**, forcing **gradual emergence** over multiple seasons and enabling **cumulative seedbank drawdown** rather than reinvasion lock-in.[3]

***Rhamnus alaternus* (Italian buckthorn).**

Field and experimental evidence show:

1). broad thermal germination range;
2). emergence declines sharply with shallow burial (~5 cm);
3). seed rain highly concentrated beneath adults;
4). recruitment strongly microhabitat-filtered;
5). seedbank persistence ≥ 5 years;
6). reinvasion primarily **bird-mediated** (DAFF, 2019; Weeds Australia, n.d.; Australian weed-management guidance).

Implications:

- **Non-selective removal →** landscape-scale edge formation and reinvasion windows.

[3] **Methods authority.** Unless otherwise stated, operational guidance for **Polygala** suppression (timing, selectivity, least-disturbance protocol) follows Brown (2025), based on a decade of applied control in Coastal Moonah Woodland on calcareous sands. External sources are cited where they extend seed ecology, persistence, or policy context.

- **Selective, in-situ control** → neutralises seed sources while preserving shade/litter buffering, keeping emergence **asynchronous**, **diagnosable**, and biased toward **autochthonous pathways**.

Comparative Evidence Summary.

Feature	*Polygala myrtifolia*	*Rhamnus alaternus*
Dormancy / readiness	Non-dormant; high germinability	Germinates across broad regimes
Light requirement	Light & dark	Microhabitat filtered; seed rain beneath adults
Surface vs burial	Strong surface bias; none at ~8 cm	Emergence declines with ~5 cm burial
Moisture stress	Strong decline below ~−0.6 MPa	Early survival constrained by drought/microsite
Seedbank persistence	Multi-year	≥ 5 years
Dispersal	Near parent + disturbance-aligned	Bird-dispersed; edge-driven
Management implication	Avoid non-selective disturbance; selective/manual with multi-year follow-up	Selective cut-and-paint/basal bark; avoid large-scale edge creation
Sources	Roberts et al., 2023; Weeds Australia, n.d.	DAFF, 2019; Weeds Australia, n.d.

Architectural Interpretation (EF–CT–FL Frame).
Within the **EF–CT–FL** framework, selective chemical control prevents **synchronisation of fragility gates**. Instead of reopening all recruitment corridors simultaneously, activation is confined to **small, diagnosable microsites within intact surface architecture**. Seedbanks are allowed to **fail by attrition** rather than succeed through pulsed recruitment. Disturbance thereby shifts from acting as a **system opener** to functioning as a **controlled filter**.

Why selective control is structurally required:
Non-selective removal **collapses surface constraints**, whereas selective suppression **preserves** the very conditions under which rebuilt constraints can function.

Anchor sentence:
Selective chemical control **prevents synchronised germination cues**, converting persistent seedbanks from **pulsed recruitment systems into gradually exhausting reservoirs** subject to microbial decay and targeted follow-up.

Operational Steps (Method-Critical Refinement of §4.3 Sequencing)

1. **Initiate targeted tea-tree thinning *only after rabbit control and suppression of disturbance-aligned shrubs (Polygala/Rhamnus) are active*, to protect and re-establish the ground-layer.**

Use **narrow corridors and small patches** to increase understorey light and throughfall while limiting bare soil exposure that aggravates **SWR** and runoff on calcareous sands. **Avoid wholesale clearing**: it increases SWR, triggers serotinous capsule opening, and produces dense tea-tree recruitment (Lin et al., 2006; Lam & van Etten, 2002; Weber, 2003).

2. Immediately rebuild the ground-layer in thinned or suppressed patches.

Direct seed or plant **grasses, herbs, and sedges**; retain coarse woody debris; deploy **micro-wetting / SWR amelioration** techniques. These actions restore porosity and moisture buffering, denying *Polygala* the **surface-moist microsites** it prefers (Roper et al., 2015; Roberts et al., 2023).

3. Reintroduce structural diversity as the ground-layer consolidates.

Re-establish **Moonah, sheoaks, Banksia**, and mid-storey taxa to rebuild **layered architecture**, **depth-partitioned rooting**, and **actinorhizal nutrient gating** (Moxham et al., 2009; DAFF, 2019).

4. Continue phased tea-tree reduction, synced to diagnostics.

Reduce tea-tree progressively as:

- ground-layer cover increases,
- native recruitment is verified,
- *Polygala* suppression is sustained.

This sequencing prevents **post-treatment recruitment surges** and avoids resetting to **denser thickets** (Lam & van Etten, 2002; Roberts et al., 2023).

Caution on Fire.

On **calcareous, SWR-prone sands**, generic "*reset burns*" typically:

- amplify water repellency,
- create recruitment surfaces for tea-tree and *Polygala*, and
- fail to produce recovery when constraints are degraded

unless:

1. rabbits are controlled,
2. *Polygala* is contained, and
3. the ground-layer is already re-established.

Only then should **additional biomass reduction** be considered
(Doerr, Shakesby, & Walsh, 2000; Roper et al., 2015).

Empirical programs show canopy opening without prior suppression of disturbance-aligned shrubs produces **replacement monocultures**, not recovery (Brown, 2025).

Rationale.

Making *Polygala* the **first-order priority** prevents it from exploiting the very conditions thinning is designed to create for natives. When *Polygala* suppression is paired with **rabbit control** and **rapid ground-layer rebuilding**, early targeted thinning becomes **ground-layer protection**, not disturbance that hands the site to colonisers (Roberts et al., 2023; Weeds Australia, n.d.).

Core architectural principle: Restore missing functions **before** removing the dominant structure.

One-line takeaway:
Non-selective disturbance resets the system; selective chemical control preserves the architecture needed for recovery.

Warren Management on Steep, Highly Disturbed Slopes: Collapse, Blockage, and Constraint Failure.
This section addresses **moderate-to-steep slopes** (dune faces, escarpments, embankments, sloping woodland margins) where **gravity-driven soil movement, runoff concentration, and erosion** are active.

In many degraded coastal woodlands on slopes, rabbit warrens are not randomly distributed. They are commonly associated with **remaining structural and biological integrity**—fallen timber, litter islands, persistent root systems, and remnant native ground flora (*Tetragonia implexicoma*, *Rhagodia candolleana*, native grasses/herbs). In these contexts, a warren often indicates **residual ecosystem function**, not complete collapse.

Why collapsing warrens often worsens outcomes.
On slopes where rabbits remain, warren collapse acts primarily as a **disturbance pulse with geomorphic consequences**, not effective control. Collapse:

- disrupts root mats, coarse debris, and litter islands that stabilise slopes;
- exposes bare mineral soil rapidly mobilised by rainfall;

- initiates rilling, soil creep, and slumping;
- synchronises germination cues for disturbance-aligned shrubs and grasses;
- does **not** remove rabbits.

Rabbits typically respond by excavating **new burrows upslope or laterally. This expands the disturbance footprint** propagating erosion into previously intact microsites.

Limitations of blocking warrens.

Blocking entrances (soil, rock, brush, mesh) still disturbs soil and commonly **redirects digging** into adjacent stabilised microsites. Where rabbits remain active, blocked warrens are abandoned in favour of **newly excavated burrows**, expanding disturbance and increasing slope instability.

Thus, both collapse and blockage share a core limitation: they modify burrow infrastructure **without removing opposition**, while simultaneously weakening surface constraints.

Constraint-Based Alternatives for Steep Slopes.

On steep slopes retaining native ground flora and structural elements:

- **Prioritise rabbit population reduction** before any soil-disturbing works.
- **Retain fallen timber and root systems** that contribute to slope cohesion.
- **Suppress disturbance-aligned shrubs** to prevent capture of newly exposed microsites.
- **Stabilise the ground-layer** (litter, coarse debris, rapid re-establishment of natives) to progressively reduce burrow admissibility.

Under this sequence, warrens may **lose viability** as resistance and vegetation structure recover, reducing the need for direct intervention.

Implications for Management on Steep Slopes.

Where rabbits persist because **residual structure** and **palatable ground flora** remain, blanket warren collapse or blocking is often **counterproductive**. These actions remove stabilising constraints **without** removing opposition, increasing both **disturbance and erosion** while leaving rabbit pressure largely intact.

Warren intervention on slopes should be treated as **earthworks with ecological and geomorphic consequences**, not a standalone control method. It should only be undertaken where:

- rabbit populations are **already being reduced**, and
- **immediate surface stabilisation** is feasible.

Forward pointer. The selective-control logic in §4.4 closes the loop back to §4.1: preserving shade, litter, and roughness **interrupts** the interception–SWR–preferential-flow cascade while the ground-layer is rebuilt, ensuring that **structural change follows constraint repair**, not the reverse. This is the architectural core of the study's EF diagnosis and the reason "***restore functions before removing the dominant structure***" remains the governing rule.

4.5. Management Implications: Staged Reduction Rather Than Complete Removal (with Ground-Layer and Moonah Understorey Protection Guidance).

Continuity from §§4.1–4.4

The mechanistic synthesis established earlier shows that tea-tree thickets arise from **interacting hydrological and structural mechanisms**—high canopy interception (§4.1), hydrophobic litter and **soil-water-repellency** (SWR) (§4.1), shallow **near-surface pulse capture** (§4.1), **ground-layer collapse** (§4.1), and persistent **rabbit-driven selector pressure** (§4.2). Together they **reconfigure hydrological pathways**, producing a **functionally drier, low-infiltration soil system** (Crockford & Richardson, 2000; Doerr, Shakesby, & Walsh, 2000; Keim, Skaugset, & Weiler, 2006; Nilsen et al., 1999; Mutze, Cooke, & Jennings, 2016). As §§4.2–4.3 demonstrated, these pathways remain locked until **opposition is reduced** and **constraint architecture is rebuilt**.

Sequencing rule (gateway risk → order of operations).

Because tea-tree functions as a **gateway state**—with **Polygala myrtifolia** the highest-risk consequence due to its persistent seedbank and rapid recruitment under shrub architecture—**sequencing must suppress rabbits and disturbance-aligned shrubs before any canopy work** (Brown, 2025; Weeds Australia, n.d.; Eyre Peninsula Landscape Board, 2026).

Why large-scale "*reset*" removal backfires on calcareous sands.

Gaudium laevigatum is a disturbance-adapted coloniser: **large-scale removal (cutting, slashing, fire) typically triggers mass seed release and dense recruitment** on calcareous sands, resetting the system to a thicket **unless constraints are repaired first** (Brown, 2025; Moxham & Turner, 2008). On water-repellent dune sands, bare-surface exposure also **increases runoff, erosion and repellency**, degrading hydrological function and favouring shrub/grassy dominance (Doerr et al., 2000; Roper et al., 2015).

What works instead (staged reduction after constraint repair).

After **rabbit suppression** and containment of **Polygala/other disturbance-aligned shrubs**, a **staged structural reduction** provides a feasible pathway to rebuild the ground-layer, recover

infiltration niches and reopen woodland architecture—**without triggering dense, disturbance-driven cohorts** (Brown, 2025; Roberts et al., 2023).

Constraint-Focused Sequencing.
(Cross-references: This sequence depends on the logic established in §§4.2–4.4: opposition removal (4.2), spatial persistence (4.2.1), and suppression of disturbance-aligned shrubs + ground-layer rebuilding before thinning (4.3–4.4).)

Dependency note. Steps 1–3 **must** be underway before any substantive tea-tree reduction (Step 4); reversing this order reliably converts thinning into replacement rather than recovery.

1. Control rabbits to reopen recruitment pathways.

Even ≤ 5 rabbits ha^{-1} cause steep declines in native cover and suppress seedling establishment; rabbit pressure functions as the **primary selector** maintaining monoculture dominance (Mutze et al., 2016; Cooke, 2012).
→ **Constraint reopened:** recruitment gates.

2. Rebuild the ground-layer.

Re-establish grasses, herbs, and sedges; retain coarse woody debris; apply micro-wetting/SWR amelioration on calcareous sands to restore porosity, infiltration, aeration, and moisture retention (Roper et al., 2015).
→ **Constraint rebuilt:** water-holding architecture + microbial floor.

3. Reintroduce structural diversity.

Re-establish **Moonah, Banksia, and sheoaks** (Allocasuarina/Casuarina) to restore:
• rooting-depth complementarity
• canopy layering
• actinorhizal N inputs
• system redundancy
that historically constrained tea-tree dominance (Moxham et al., 2009; DAFF, 2019).
→ **Constraint restored:** layered architecture + nutrient gating.

4. Thin tea-tree gradually once Steps 1–3 are in place.

Use **narrow corridors and small patches** to increase understorey light and throughfall while avoiding bare-soil creation, which intensifies SWR and runoff.
Avoid wholesale clearing, which:
• increases repellency
• triggers serotinous capsule opening

• drives dense tea-tree recruitment
• resets the system into **even thicker thickets**
(Lam & van Etten, 2002; Lin, Jung, Hsiao, & Hamburg, 2006; Weber, 2003; *The Victorian Naturalist*, 2013).
→ **Constraint sequencing:** dominant structure removed **last**, not first.

Protecting Existing Ground-Layer and Moonah Understorey Values During Thinning.
(Cross-reference: This follows directly from §4.1's ground-layer collapse mechanism, §4.2's selector pressure, and §4.3's sequencing logic.)

Tea-tree expansion suppresses both native grasslands and Moonah understorey assemblages through **shading**, **high interception**, and **litter accumulation**, while rabbits act as "*asset protection*" for tea-tree by selectively removing palatable recruits (Weber, 2003; Nilsen et al., 1999; Mutze et al., 2016).

Implications for practice:

- **Use fine-scale, low-disturbance methods** (selective stem removal, hand cutting, narrow openings) to avoid bare soil and prevent SWR escalation (Nilsen et al., 1999; Roper et al., 2015).
- **Pair initial thinning with early Polygala suppression** to prevent exploitation of newly lit microsites. Maintain shade and litter continuity where possible to avoid seedbank synchronisation (Lam & van Etten, 2002; Roberts et al., 2023; Weeds Australia, n.d.).
- **Prioritise rabbit control under Moonah canopies**, which often function as refugia enabling rabbits to repeatedly clip palatable recruits (Mutze et al., 2016; Cooke, 2012).

These measures **protect existing assets** rather than creating recruitment corridors for colonisers.

Hypothesis: Sheoak Legacy Effects and Italian Buckthorn Establishment.
(Cross-reference: connects with §4.2.1 on propagule-driven replacement and §4.4 on seedbank and micro-site architecture.)

Sheoaks (Allocasuarina/Casuarina spp.) are **actinorhizal nitrogen-fixing trees**, contributing substantial nitrogen to nutrient-poor coastal soils (Diem & Dommergues, 1990; Duhoux & Dommergues, 1985). Nitrogen fixation is well-documented across the family, with nodulation strongly influenced by phosphorus availability (Reddell & Bowen, 1985). Sheoaks enrich soil via nitrogen-rich litter and root turnover, and in other actinorhizal systems these effects **persist as fertility legacies** even after canopy loss (Binkley & Giardina, 1998).

Hypothesis.
Italian buckthorn (*Rhamnus alaternus*) shows elevated establishment probability in **former sheoak zones** on calcareous sands because these sites retain **long-term nitrogen**

enrichment and modified microbial/structural properties. Even after sheoak recruitment failure, these legacy footprints make exposed dune ridges functionally similar to nutrient-enriched gullies. As a nitrogen-responsive, bird-dispersed shrub, buckthorn is hypothesised to exploit these enriched microsites.

Predictions:

1. Ridge-top buckthorn sites will show **higher plant-available N and microbial activity** than adjacent ridges lacking sheoak indicators (charcoal, cones, root remnants).
2. Buckthorn will be **disproportionately associated** with ridges showing multiple independent sheoak legacy signals under comparable propagule pressure.

Falsifier. If buckthorn occurrence does **not** correlate with independent sheoak-legacy indicators under similar propagule pressure, the hypothesis is rejected.

This hypothesis provides a testable mechanism explaining buckthorn presence in **unexpected ridge-top positions**.

Takeaway for §4.5.

Remove constraints first, protect assets second, reduce tea-tree last—otherwise thinning rebuilds the very thickets it aims to dismantle. **Planned fire on calcareous dunes is only low-risk after** rabbits are suppressed, disturbance-aligned shrubs are contained, and the ground-layer is rebuilt; otherwise burns predictably simplify structure and do not displace *Gaudium laevigatum*.

Operational caution for planned fire on calcareous dunes.
Planned fire should be considered **only after rabbits are suppressed, disturbance-aligned shrubs are contained,** and the ground-layer is rebuilt. Where these conditions are not met, burns predictably simplify structure, reducing canopy, litter and moss while increasing perennial grasses and exotic elements, and do not displace *Gaudium laevigatum* (Moxham & Turner 2008; Moxham & Turner 2011).

4.6. Convergent Behaviour of *Gaudium laevigatum* and *Polygala myrtifolia* Under Disturbance.

Continuity from §§4.1–4.5.
§§4.1–4.5 established the structural template under which dominance emerges:

1. **hydrological re-wiring** (interception → SWR → preferential flow) (§4.1)
2. **opposition-maintained corridor closure** via rabbits (§4.2–4.2.1),
3. **disturbance-aligned shrubs exploiting opened microsites** (§4.3),
4. **seedbank synchronisation risk under non-selective removal** (§4.4), and

5. the need for **constraint-first, structure-last staging** (§4.5).

Against this backdrop, the behaviour of *Gaudium laevigatum* and *Polygala myrtifolia* is best understood as **convergent expression of the same architectural opportunity under sustained disturbance**, not species-specific anomaly.

Convergent Structural Architecture (link to Box 2).
As shown in Box 2, shrub dominance in degraded coastal systems is a **repeatable architecture**: dense canopy, hydrophobic litter, surface-biased recruitment, and suppressed ground-layer function. Under disturbance and grazing, *Gaudium laevigatum* and *Polygala myrtifolia* consistently converge on this architecture, despite their taxonomic distance and different evolutionary origins (Weeds Australia, n.d.; Florabase DBCA, 1995).

1. Recruitment Biology and Disturbance Alignment.

Polygala — surface-biased emergence + persistent seedbank
P. myrtifolia expresses a disturbance-aligned germination profile characterised by:

- very high germination at 25/15 °C,
- germination across a broad soil-pH range,
- no obligate light requirement,
- moderate tolerance of moisture stress, and
- strong surface-biased emergence, with no emergence from burial at ~8 cm (Roberts et al., 2023).

A persistent, multi-year soil seedbank produces repeated recruitment waves whenever canopy openings or surface disturbance occur (Weeds Australia, n.d.; PIRSA, 2026).

Tea-tree — disturbance-released mass seeding + cohort establishment
Gaudium laevigatum is an obligate seeder, typically killed by fire or mechanical damage, with woody fruits that release seed en masse following disturbance. Post-disturbance recruitment is frequently prolific and even-aged, producing dense cohorts that rapidly re-establish closed shrub structure (Florabase DBCA, 1995; Lam & van Etten, 2002).

Cross-reference (§4.4). This parallel disturbance-aligned recruitment explains why non-selective clearing or fire synchronises emergence and resets degraded systems to shrub carpets unless seed input is neutralised and surface constraints are retained.

2. Hydrological Mechanisms That Converge (link to §4.1).

Both species generate **dense canopies** and **persistent litter layers** that:

- intercept a large fraction of rainfall (≈ 20–50 %; Crockford & Richardson, 2000),
- promote **hydrophobic litter** and **SWR**,
- divert infiltration into **preferential flow** that bypasses biologically active horizons,
- maintain **shallow, discontinuous wetting fronts**.

Hydrophobic litter and SWR are well-documented in dune systems (Doerr, Shakesby, & Walsh, 2000), and create self-reinforcing surface dryness and **cyclic vegetation–soil feedbacks** (Siteur et al., 2016).

Cross-reference (to §4.1):

This is the exact hydrological re-wiring described earlier—interception → repellency → bypass flow → shallow pulse capture—which both taxa can generate independently.

3. Ground-Layer Suppression and Feedback Lock-In.

As thickets consolidate:

- light at the soil surface declines,
- infiltration remains shallow,
- moisture persistence decreases,
- ground-layer species lose cover and recruitment windows.

These feedbacks jointly **lock-in monoculture dominance** (Crockford & Richardson, 2000; Doerr et al., 2000).

For *Polygala myrtifolia*, evergreen foliage and thick litter physically obstruct seed–soil contact (Weeds Australia, n.d.);
for *Gaudium laevigatum*, hydrophobic litter and high interception markedly reduce throughfall and infiltration (Florabase DBCA, 1995).

4. Persistence Strategies Under Disturbance.

Both species rely on **seed-driven recruitment**, not strong resprouting:

- *P. myrtifolia*: persistent, multi-year seedbanks (Weeds Australia, n.d.; Roberts et al., 2023).

- *Gaudium laevigatum*: post-disturbance seed pulses from serotinous fruits (Florabase DBCA, 1995; Lam & van Etten, 2002).

Thus, **non-selective clearing, fire, or heavy thinning** typically produces **dense recruitment carpets** unless constraints and seed input are simultaneously controlled.

Cross-reference (to §4.4):

This is precisely why selective, in-situ suppression is required to avoid **seedbank synchronisation** and system reset.

Why They Co-Dominate Degraded Coastal Mosaics.

1. Trait match to disturbance

Surface-biased emergence (Polygala) and fire-released mass seeding (tea-tree) align with disturbance regimes typical of coastal dune systems (Roberts et al., 2023; Lam & van Etten, 2002).

2. Hydrostructural reinforcement

Interception + SWR + preferential flow jointly reduce near-surface moisture and constrain ground-layer recovery (Crockford & Richardson, 2000; Doerr et al., 2000; Siteur et al., 2016).

3. Seedbank persistence and adjacency

Polygala's multi-year seedbank and tea-tree's abundant post-disturbance rain ensure **rapid re-occupation of canopy gaps** (Weeds Australia, n.d.; Florabase DBCA, 1995).

Cross-reference (link to §§4.2–4.2.1):
Rabbit pressure closes recruitment corridors long enough for both taxa to **capture and hold** disturbed microsites, extending monoculture persistence.

Management Corollary (Link to §§4.3–4.4).
Because both species **capitalize on disturbance** and then **engineer the surface environment** against native re-entry, **non-selective removal or untimed burning is high-risk**: it synchronises emergence, resets seedbanks, and restarts the monoculture cycle (Lam & van Etten, 2002; Weeds Australia, n.d.).

The **lower-risk path** is:

- **selective, in-situ suppression** that preserves shade and litter continuity while neutralising seed input (§4.4),
- paired with **rabbit suppression** (§4.2–4.2.1), and
- **immediate ground-layer rebuilding** (§4.3, §4.5).

This sequencing prevents surface-opening pulses that would otherwise be colonised by *Polygala* or tea-tree.

Takeaway.

Gaudium laevigatum and ***Polygala myrtifolia*** **converge functionally** because both**:**

1. seed into disturbance**,**
2. re-engineer canopy–litter–soil processes (interception + SWR) that starve the surface of water and light, and
3. use persistent seed inputs to re-occupy gaps—locking degraded coastal systems into shrub-dominated states unless treatments are selective, sequenced, and surface-aware (Crockford & Richardson, 2000; Doerr et al., 2000; Florabase DBCA, 1995; Roberts et al., 2023).

4.7. Fire in Coastal Moonah Woodland: Why "*Reset*" Burns Usually Fail.

Continuity from §§4.1–4.6.
The preceding sections established that Coastal Moonah Woodland (CMW) collapse is driven by **interacting hydrological and structural mechanisms** (§4.1), maintained in a **locked configuration by rabbit opposition (Ω)** (§4.2–4.2.1), exacerbated by **disturbance-aligned shrubs** (§4.3), intensified by **seedbank synchronisation under non-selective removal** (§4.4), and only reversible through **constraint-first, structure-last sequencing** (§4.5).
Against this diagnostic backdrop, fire cannot **in these calcareous, water-repellent, low-N dune systems** be treated as a neutral or resetting tool be treated as a neutral or resetting tool.
On **calcareous, water-repellent, low-N dune systems**, fire typically **amplifies the very dynamics that produced collapse unless constraints have been repaired in advance**.

These observations **extend, rather than contradict**, evidence from calcareous dune systems: on such substrates, **increasing fire frequency simplifies structure without eliminating tea-tree**, **(Figure 12)** indicating that **fire primarily acts as an amplifier of a rabbit-maintained, ground-layer-depleted state** (Moxham & Turner 2008).

Context.
CMW occupies **calcareous, leaching-prone sands** historically supporting a **Sheoak–Moonah–Banksia mosaic** with a grassy ground-layer (Moxham, Turner, Walker, & Douglas,

2010). Under sustained rabbit pressure, many remnants shifted toward **tea-tree dominant, low-option** architecture. On this substrate, fire **reinforces** the hydrological and structural failures described earlier unless the **full constraint-repair sequence** is undertaken first. Moxham et al. (2010) emphasise that fire on calcareous dunes is rarely benign and tends to **amplify functional dryness**.

Where tea-tree has opened the system to secondary shrubs—particularly **Polygala**—fire acts on a pre-compromised architecture and **amplifies** simplification unless the gateway is closed first (Brown, 2025; Moxham & Turner, 2008).

Historical Signal.
Early 20th-century descriptions document a **before → after** shift: grassy sheoak landscapes transitioning to dense ti-tree dominance following rabbit irruptions (Moxham & Turner, 2009). A contemporaneous 1889 traverse between Sorrento and Cape Schanck provides a natural experiment: within a rabbit-proofed enclosure, **Sheoak and wattles regenerated rapidly and densely**, demonstrating that **recruitment failure—not edaphic limitation—drove collapse** under open rabbit pressure (*The Australasian*, 1889).
This directly supports the **opposition-closure** logic in §§4.2–4.2.1: fire effects cannot be interpreted without first recognising the primary constraint—**browsing pressure**.

Point Nepean Evidence and Feedbacks to Fire Proneness.
At Point Nepean, increased fire frequency shifted CMW from a **layered woodland** to **simplified grassy woodland**, characterised by:

- reduced canopy and mid-storey cover;
- reduced litter and moss;
- fewer obligate seed regenerators;
- increased perennial grasses
  (Moxham et al., 2010).

Least-burnt sites retained **Melaleuca lanceolata**, moss beds, and low fuels; frequently burned sites became **structurally simplified**. Tea-tree remained common across all fire histories, and *Polygala myrtifolia* occurred in both recently burnt and long-unburnt degraded sites (Moxham & Turner, 2009; Moxham et al., 2010).

Interpretation.
The simplified, disturbance-maintained states described in §§4.2–4.6 become **more fire-prone**, **(Figure 13)** reinforcing the hazard rather than reducing it—precisely the opposite of what "*reset*" burns intend. Because **total richness** did not change consistently across fire histories while **structural/functional attributes** degraded and **exotics increased**, the monitoring framework effectively **measured variation within an already reduced state** rather than detecting architectural recovery or loss. Treat **native richness**, **structural indices**, and

functional composition as the primary diagnostics; use total richness only as a **supplementary** descriptor.

Substrate Rule: Short-Interval Fire on Calcareous Sands.
On **calcareous dune sands**, repeated fire functions as a **stress multiplier**:

- each burn **increases water deficit**,
- amplifies nutrient limitation (especially lime chlorosis),
- and suppresses epicormic/lignotuber recovery relative to acidic or deeper soils (Parsons & Specht, 1967; Parsons & Uren 2013).

Classic trials show *Eucalyptus baxteri* becomes **chlorotic and stunted** on calcareous sand but **vigorous** on siliceous sand, indicating that alkaline substrates impose a physiological penalty that **narrows post-fire recovery windows**.

Cross-reference (§4.1).
This penalty compounds the hydrological re-wiring (interception → SWR → bypass flow) already operating under tea-tree and *Polygala* dominance.

Imperata cylindrica: Survivorship Misread as Historical Dominance.

Imperata cylindrica (blady grass) illustrates how **disturbance-tolerant remnants** are misinterpreted as historical baselines.
Imperata persists because it tolerates **nutrient stress and fire**, not because it historically dominated dunes. Studies show Imperata expansion is constrained by **soil chemistry and nitrogen availability**, and fire alone does **not** promote dominance (Butler, Lewis, & Chen, 2021).

On calcareous dunes where sheoak loss reduces **biological nitrogen inputs**, Imperata's persistence reflects **constraint failure**, not original structure.
Where Moxham et al. show repeated disturbance simplifies CMW, Butler et al. show Imperata reflects **nutrient-limited survivorship**, not pre-disturbance composition.

Frequency-Amplified Failure: Broader Evidence.
Short-interval fire can cause regeneration failure **even on non-calcareous substrates**.
Examples include:

- **Wilsons Promontory**: > 1,200 ha of collapsed eucalypt forest after repeated short-interval fires, with warnings of permanent stand loss under one more reburn (Parks Victoria, 2023).
- **Reburn studies**: antecedent canopy scorch increases subsequent severity and alters fuel structure (Collins et al., 2021).

- **High-severity, short-interval wildfire** reduces species richness and depletes soil seedbanks in resprouting eucalypt forests (Kasel, Fairman, & Nitschke, 2024).

These results align with the **EF logic**: repeated disturbance reduces (D + R), deepens fragility gates, and pushes K negative.

Scope Condition: Do Not Generalise to Siliceous Dunes.
Siliceous coastal dunes in southwest WA show **rapid post-fire recovery** (≈ 6–12 months), stable surfaces, and community dominance by pre-fire composition—*but only on siliceous substrates* (Shumack, Hesse, & Turner, 2017/2018).
These results do **not** apply to calcareous dunes, which carry the nutrient penalty and hydrological constraints described by Parsons & Specht (1967).
Thus, responses observed on siliceous dunes are **not** transferable to calcareous CMW.

Mechanism Link: Why Fire Reinforces Collapse in CMW.
Heat and disturbance **strengthen or reveal SWR** in sandy profiles, forcing water into **preferential flow paths** while newly lit, bare microsites favour **disturbance-aligned colonisers** (Doerr, Shakesby, & Walsh, 2000).

In remnants already simplified by rabbits (§4.2), these effects reinforce a **low-option architecture**, pushing systems toward **tea-tree thicketing or *Polygala* flushes**, not recovery (Moxham et al., 2010).

Tea-tree litter adds hydrophobic compounds; post-fire ash and litter loss reduce microbial seed decay, promoting **synchronised recruitment** (Doerr et al., 2000).

Cross-reference to §4.4.
This is the same seedbank synchronisation mechanism that makes non-selective clearing high-risk.

Geomorphic Note.
On calcareous dune limestones where **wetness is lens-bound**, each burn:

- intensifies near-surface water deficit,
- heightens SWR,
- strips stabilising ground-layer cover,
- destabilises lens expression, and
- accelerates collapse toward coloniser-dominated thickets.

This pattern matches the siliceous vs calcareous contrast documented across southern Australia (Parsons & Specht, 1967; Moxham & Turner, 2009).

Implication (EF Terms).
In EF framing:

- generic burning reduces **(D + R)**,
- drives **K** negative,
- tightens **fragility gates** in the **FL**,
- and reveals a collapse architecture unless sequenced repair is already underway.

The repair sequence must follow the **same order established in §4.3–4.5**:

1. **rabbit suppression →**
2. **Polygala containment →**
3. **ground-layer rebuild →**
4. **reintroduction of deep-rooted functional types (sheoaks, Banksia, Moonah).**

Where fuel management is necessary near assets, the **least-disturbance path with targeted weed suppression** is the only low-risk option.
Broad "*reset*" burns on calcareous dune sands **typically backfire**, reinforcing collapse rather than repairing it (Doerr et al., 2000; Moxham et al., 2010).

Takeaway for §4.7.

On calcareous, **rabbit-simplified systems, fire is not a reset mechanism—it is a constraint multiplier that locks collapse in** unless the full EF repair sequence is completed first. On calcareous substrates fire is conditional: where constraints remain intact it reinforces simplified states, and only after constraint repair can fire avoid reproducing the same grassy or shrubby trajectory (Moxham & Turner 2008).

Figure 12. Long-term post-fire collapse and replacement by tea-tree.
A dead Moonah ***(Melaleuca lanceolata)****—burnt decades earlier—lies collapsed in a ridge-top stand now dominated by* ***Gaudium laevigatum****. Attempts by* ***Leucopogon parviflorus*** *to re-establish have failed, with stems suppressed or broken beneath the dense tea-tree.*

Figure 13. Landscape pulse of tea-tree mortality on a ridgeline following a low-rainfall period.

Widespread crown death in ***Gaudium laevigatum*** *(mid-distance) increases elevated fine fuels and creates large, open recruitment surfaces. Without prior constraint repair (rabbit suppression, ground-layer rebuild) and selective, staged thinning, mass removal or broad* ***"reset"*** *actions on calcareous sands tend to re-instantiate hydrological closure and shrub dominance rather than restore woodland function.*

Field note: Mass die-off increases fuel and opens recruitment corridors but does not repair constraints; without rabbits suppressed and the ground-layer rebuilt, mass removal simply spends latent potential and rebuilds the shrub state.

Table 4.7. Species-level responses to fire frequency and time-since-fire in Coastal Moonah Woodland.

Arrows (↑ ~ ↓) indicate directional change along the fire gradient. Responses are expressed **under prevailing rabbit herbivory**, which acts as a chronic background selector affecting recruitment across all categories; mechanistic implications are developed in § 4.7.1.

Table scope. Species-level signals along the fire gradient recorded for CMW on calcareous dunes (compiled from Moxham & Turner 2008/2011; Moxham et al., 2010).

Species	Common name	Status	Matrix signal (by status)	Function	Evidence
Rhamnus alaternus	Italian buckthorn	Introduced	↑	Exotic woody (bird-dispersed)	**E3** (compilation in file)
Aira spp.	Hair-grass	Introduced	↑	Exotic grass	**E2** (exotics ↑ with frequent fire)
Catapodium rigidum	Fern grass	Introduced	↑	Exotic grass	**E2**
Centaurium spp.	Centaury	Introduced	↑	Exotic forb	**E2**
Cerastium spp.	Chickweed	Introduced	↑	Exotic forb	**E2**
Conyza spp.	Fleabane	Introduced	↑	Exotic forb	**E2**
Cotoneaster spp.	Cotoneaster	Introduced	↑	Exotic woody	**E2/E3** (exotics ↑; woody coloniser)
Dipogon lignosus	Dolichos pea	Introduced	↑	Exotic climber	**E2/E3** (exotics ↑; climber)
Ehrharta erecta	Ehrharta	Introduced	↑	Exotic grass	**E2**
Lycium ferocissimum	African boxthorn	Introduced	↑	Exotic woody	**E2/E3** (exotics ↑; woody invader)
Polygala myrtifolia	Myrtle-leaf milkwort	Introduced	↑	Exotic woody (persistent seedbank)	**E2/E3** (exotics ↑; file details on seedbank)
Rubus fruticosus agg.	Blackberry	Introduced	↑	Exotic woody	**E2/E3**
Hypochaeris glabra	Cat's ear	Introduced	↑	Exotic forb	**E2/E3** (exotics ↑; coloniser)
Oxalis spp.	Oxalis	Introduced	~	Exotic forb	**E2/E3** (exotics ↑, variable)
Pittosporum undulatum	Pittosporum	Introduced (in CMW)	~	Exotic woody	**E3**
Clematis microphylla	Small-leaved clematis	Native	~	Climber	**E1** (constant)
Convolvulus erubescens	Pink bindweed	Native	~	Climber	**E1/E2** (constant/common)
Cynoglossum australe	Australian hound's-tongue	Native	~	Forb	**E1** (constant)
Pimelea serpyllifolia	Thyme rice-flower	Native	~	Small shrub	**E1** (constant)
Swainsona lessertiifolia	Coast swainson-pea	Native	~	Forb (legume)	**E1** (constant)

Dichondra repens	Kidney-weed	Native	~	Ground-cover forb	**E1** (constant)
Austrodanthonia spp.	Wallaby grass	Native	~	Native grass	**E1/E2** (constant/common group)
Austrostipa spp.	Spear grass	Native	~	Native grass	**E1** (constant species group)
Ficinia nodosa	Knobby club-sedge	Native	~	Sedge	**E3**
Lepidosperma gladiatum	Coast sword-sedge	Native	~	Sedge (stabiliser)	**E2/E3** (often stable)
Olearia axillaris	Olearia	Native	~	Shrub (resprouter)	**E3**
Anthosachne scabra	Wheat-grass	Native	↑	Native grass	**E1/E2** (grasses ↑; listed)
Lachnagrostis billardierei	Coast blown-grass	Native	↑	Native grass	**E1/E2** (grasses ↑; listed)
Poa poiformis	Poa	Native	↑	Native grass	**E1/E2** (grasses ↑; listed)
Senecio odoratus	Scented groundsel	Native	↑	Native forb (ruderal)	**E1** (increaser)
Solanum laciniatum	Kangaroo apple	Native	↑	Native shrub (ruderal)	**E1** (increaser)
Daucus glochidiatus	Australian carrot	Native	↑	Native forb	**E1** (listed as increaser)
Poa labillardierei	Tussock-grass	Native	↑	Native grass (facultative resprouter)	**E1** (strong increaser)
Alyxia buxifolia	Sea box	Native	↓	Fire-sensitive shrub	**E2** (shrub/canopy decline with frequent fire)
Banksia integrifolia	Coast banksia	Native	↓	Obligate seeder (canopy)	**E2** (obligate seeders/canopy ↓)
Pomaderris paniculosa	Pomaderris	Native	↓	Obligate seeder (shrub)	**E2** (obligate seeders ↓)
Pultenaea canaliculata	Pultenaea	Native	↓	Obligate seeder (legume shrub)	**E2**
Thuidiopsis furfurosa	Golden weft-moss	Native	↓	Moss (surface buffer)	**E1** (moss higher in least-burnt)
Leucopogon parviflorus	Coast beard-heath	Native	↓	Small tree/shrub (obligate seeder)	**E1** (more abundant in least-burnt)
Melaleuca lanceolata	Moonah	Native	↓	Canopy tree (obligate seeder)	**E1** (dominant in least-burnt)
Allocasuarina verticillata	Drooping sheoak	Native	↓	Obligate seeder; dune stabiliser	**E2** (canopy/seeders ↓)
Hibbertia sericea	Silky guinea-flower	Native	~	Shrub	**E1** (intermediate signal)

Parietaria debilis	Parietaria	Native	↑	Ground-layer forb	**E3**
Rubus parvifolius	Native raspberry	Native	↑	Native shrub (resprouter)	**E3** (resprouts, edges/disturbed)
Correa spp.	Correa	Native	↑	Shrub (resprouter)	**E3**
Rhagodia candolleana	Seaberry saltbush	Native	↑	Stabiliser (litter/fines trap)	**E3**
Tetragonia implexicoma	Bower spinach	Native	↑	Stabiliser (ground-layer)	**E3**
Adriana quadripartita	Rare bitter bush	Native	↓	Shrub	**E3** (trait/compilation in file)
Carex breviculmis	Grass-sedge	Native	↓	Sedge (ground-layer)	**E3**
Crassula sieberiana	Sieber crassula	Native	↓	Small herb (ground-layer)	**E3**
Lagenophora stipitata	Bottle-daisy	Native	↓	Small forb	**E3**
Ranunculus sessiliflorus	Small-flowered buttercup	Native	↓	Moist-microsite annual	**E3** (moist habitats, fire-sensitive by exclusion)
Stackhousia monogyna	Creamy candles	Native	↓	Forb (ground-layer)	**E3**
Wurmbea latifolia	Wurmbea	Native	↓	Geophyte (forb)	**E3**
Hydrocotyle laxiflora	Stinking pennywort	Native	↓	Moist microsite forb	**E3** (benefits from disturbance, not direct fire)
Acacia uncifolia	Coast wirilda	Native	Native: peak at intermediate (~30 yrs), lower at extremes	Obligate seeder (small tree)	**E1** (intermediate maximum reported)
Gaudium laevigatum	Coast tea-tree	Native	~	Woody coloniser	**E1** (constant across gradient)

4.7.1 Fire on Calcareous Dune Sands: Constraints, Feedbacks, and Trajectory Shifts.

Continuity from §§ 4.1–4.7. Sections 4.1–4.6 showed that degraded Coastal Moonah Woodland (CMW) stands on calcareous sands are held in place by a **hydro-structural lock-in** (canopy interception → soil-water-repellency → preferential flow → shallow pulse capture), maintained by **rabbit-driven opposition** and exploited by **disturbance-aligned shrubs** (notably *Polygala myrtifolia* and coastal tea-tree). Section 4.7 established that **fire intensifies these conditions rather than reversing them**.

Bridge to practice. Section 4.7 explained why generic burns fail in degraded CMW. Section 4.7.1 now sets out the **calcareous-sand mechanisms** that make failure more likely and faster, clarifying when fire should be deferred until **rabbits are suppressed, colonisers contained, and the ground-layer rebuilt**. This section applies the same architectural logic specifically to calcareous dune sands, showing why their physicochemical constraints make "*reset*" burning especially high-risk.

Structural change, not richness.
Across calcareous dune systems supporting CMW, **fire frequency** and **time since fire** strongly affect **structure and composition**: least-burnt sites retain woodland/open-forest architecture with deeper litter and moss, whereas frequently burnt sites simplify toward grassy or shrubby states. In these datasets, **canopy and mid-storey cover, litter, moss, and obligate seed-recruiters decline** with increasing fire frequency, while **native perennial grasses and exotics increase**. Importantly, **overall species richness does not differ significantly** across fire histories; only **diversity and dominance** metrics shift (Moxham & Turner, 2008, unpublished).

Why "*total richness*" misdiagnoses state on calcareous dunes. In the Point Nepean dataset, fire simplified CMW from layered woodland/open forest toward grassy/shrubby states—with declines in **canopy/mid-storey, litter, moss, and obligate seed-recruiters** and increases in **native perennial grasses and exotics**—yet **total species richness showed no consistent difference** among fire histories. A tally that includes exotic species can therefore **mask or offset native losses**, making an already reduced state appear stable. For calcareous dunes, **total richness should not be used as a condition index**; report **native richness separately** and prioritise **structural and functional metrics** (canopy/mid-storey cover; litter/moss continuity; obligate-seeder vs resprouter balance; dominance structure; exotic/grass cover).

Box 4.7.1A — Rabbits as the Primary Selector Driving Decline in Coastal Moonah Woodland

Scope. Coastal Moonah Woodland on the southern Mornington Peninsula exhibits a vegetation pattern consistent with **European rabbits (*Oryctolagus cuniculus*) acting as a strong selector** on palatable native species. The community includes shrubs, small trees, forbs, sedges, and ground-layer herbs that are highly palatable to rabbits; long-term rabbit presence is known to suppress recruitment of these taxa even at low densities (e.g., Cooke & McPhee, 2007; Mutze, Cooke & Jennings, 2016).

Threat-abatement documents and exclosure studies consistently report that rabbit browsing prevents regeneration of palatable species, collapses ground-layer diversity, and shifts vegetation toward dominance by browse-resistant shrubs. These interpretations apply to **calcareous** dune sands supporting CMW and **do not** generalise to **siliceous** dune systems where post-fire recovery can be rapid (see § 4.7)

Observed pattern in CMW. The species currently declining or absent in CMW at Tootgarook and Boneo fall entirely within this rabbit-sensitive guild. These include *Acacia uncifolia*, *Alyxia buxifolia*, *Banksia integrifolia*, *Leucopogon parviflorus*, *Pomaderris paniculosa*, *Pultenaea canaliculata*, *Allocasuarina verticillata*, and palatable herbs and forbs such as *Ranunculus sessiliflorus*, *Stackhousia monogyna*, *Wurmbea latifolia*, *Lagenophora stipitata*, and *Hydrocotyle laxiflora*. Their absence from the seedling and juvenile layers, combined with the senescent-only structure of surviving adults, is diagnostic of **chronic browsing pressure**, not natural demographic fluctuation.

Moonah clarification (stage-specific browsing). Although adult Moonah (*Melaleuca lanceolata*) may persist, **seedlings and juveniles are palatable and are selectively browsed by rabbits**, resulting in recruitment failure and a **senescent-only** stand structure under sustained rabbit pressure. This is the mechanism by which Moonah appears "*present*" yet fails to replace itself in degraded CMW.

Contrast with browse-resistant taxa. In contrast, **coastal tea-tree (*Gaudium laevigatum*)** and woody weeds such as *Polygala myrtifolia* and *Rhamnus alaternus* are comparatively **browse-resistant** and **accumulate biomass** under rabbit pressure. This divergence—**palatable species suppressed, unpalatable species dominant**—is the hallmark of rabbit-driven selection (as recognised under the EPBC-listed threatening process, *Competition and Land Degradation by Rabbits*).

Exclosure evidence. Long-term **exclosure studies** provide empirical confirmation: where rabbits are excluded (even with kangaroos present), **palatable shrubs/trees recruit**, **ground-layer diversity recovers**, and **structural complexity re-establishes**. Where rabbits persist, systems **remain locked** in browse-resistant shrub dominance. **(See Australian Government TAP (2016) and CISS (2023) for syntheses and experimental detail)**.

Tea-tree is fire-persistent (so fire ≠ primary cause)

Within this fire gradient, **coastal tea-tree (*Gaudium laevigatum*)** is present under all regimes, from long-unburnt to frequently burnt sites, indicating **persistence rather than fire dependence**. This pattern is inconsistent with fire alone as a sufficient explanation for inland tea-tree thicket formation; other mechanisms must account for **recruitment opportunity, lock-in, and replacement** (Moxham & Turner, 2008, unpublished).

Interpretation for § 4.7.1. The convergence of (1) species-level palatability, (2) recruitment failure, (3) dominance of browse-resistant shrubs, and (4) alignment with exclosure outcomes provides a coherent causal reading: **rabbits are the primary selector removing palatable species from CMW**, while **fire acts as an amplifier** on calcareous sands, simplifying structure and increasing exposure. The resulting configuration—dense tea-tree, woody weeds, and a depauperate ground-layer—is a **rabbit-maintained state shift**, not a historical norm.

Table 4.7.1 — Rabbit-sensitive species recorded as declining in CMW.

Species	Common name	Fire response	Rabbit sensitivity	Status
Acacia uncifolia	Coast wirilda	Declines	Highly palatable; recruitment suppressed	Native
Alyxia buxifolia	Sea box	Declines	Palatable shrub; seedlings removed	Native
Banksia integrifolia	Coast banksia	Declines	Juveniles highly palatable	Native
Leucopogon parviflorus	Coast beard-heath	Declines	Palatable; fails to recruit	Native
Melaleuca lanceolata	Moonah	Declines	**Seedlings & juveniles palatable; recruitment suppressed; adults persist**	Native
Pomaderris paniculosa	Pomaderris	Declines	Extremely palatable	Native
Pultenaea canaliculata	Pultenaea	Declines	Palatable pea-shrub	Native
Thuidiopsis furfurosa	Golden weft-moss	Declines	Sensitive to grazing/trampling	Native
Allocasuarina verticillata	Drooping sheoak	Declines (variable)	Seedlings browsed	Native
Adriana quadripartita	Rare bitter-bush	Likely declines	Palatable	Native

Carex breviculmis	Grass-sedge	Likely declines	Palatable sedge	Native
Crassula sieberiana	Sieber crassula	Likely declines	Palatable herb	Native
Lagenophora stipitata	Bottle-daisy	Likely declines	Highly palatable	Native
Ranunculus sessiliflorus	Small-flowered buttercup	Likely declines	Highly palatable	Native
Stackhousia monogyna	Creamy candles	Likely declines	Browsed to ground level	Native
Wurmbea latifolia	Wurmbea	Likely declines	Highly palatable	Native
Hydrocotyle laxiflora	Stinking pennywort	Likely declines	Browsed; partial recolonisation	Native

Rabbit browsing, regeneration filtering, and fire–herbivory interactions.
Rabbit browsing acts as a selective filter in Coastal Moonah Woodland, removing palatable native species from the regeneration pool while browse-resistant or disturbance-aligned taxa expand. The groups that decline most strongly—obligate-seeding shrubs and small trees such as *Acacia*, *Banksia*, *Pomaderris*, *Pultenaea*, and *Leucopogon*, together with fine ground-layer components—mirror functional patterns documented along fire gradients on calcareous dunes, where these taxa decrease as grasses and disturbance-aligned species increase (Moxham & Turner 2008; 2009). **The shared mechanism is a restructured regeneration environment: rabbits act continuously and selectively, removing the cohorts required for woodland persistence. (Figure 14.)**

The impacts are strongly stage-specific. Mature individuals may persist for decades, creating an illusion of stability, while seedlings and juveniles are consistently removed, producing senescent-only stands with missing age classes. This pattern is evident in Moonah (*Melaleuca lanceolata*), Sheoak (*Allocasuarina verticillata*), Coast Wirilda (*Acacia uncifolia*), and other palatable taxa that remain present as adults but fail to recruit across degraded remnants. Chronic browsing and trampling further collapse the ground-layer by reducing litter and moss continuity, homogenising microsites, and eliminating the moist, sheltered niches required for both herb and woody seedling establishment. **Reduced moss/litter continuity consistently aligns with simplified structure and grassy/shrubby shifts even when total richness appears unchanged.**

As palatable natives decline, competitive release allows browse-resistant species—including coastal tea-tree (*Gaudium laevigatum*) and disturbance-aligned shrubs and weeds—to accumulate biomass and dominance. Because these gains can numerically offset losses of woodland species, total richness may remain superficially stable while functional and

structural diversity collapse. **This "*false stability*" masks degradation and obscures the underlying reorganisation of system architecture.**

These dynamics align with emerging Australian research on pyric herbivory and fire–grazing interactions. Studies show that fire and herbivory interact non-linearly, with outcomes governed by feedbacks between post-fire forage quality, selective grazing, and fuel re-assembly rather than by fire regime alone (Reid et al., 2022; 2023). In northern savannas, fire elevates forage quality and attracts herbivores, whose selective grazing of post-fire regrowth then reshapes fuel structure and influences subsequent fire behaviour. Fire spread and intensity are controlled more by fuel structure and continuity than by total biomass, such that systems with lower biomass but continuous, fast-curing fuels can burn more readily than higher-biomass systems (Cruz et al., 2016). **Long-term grazing and disturbance-aligned grasses can raise fuel hazard and fire intensity even as standing biomass declines** (Setterfield et al., 2013; Walker & Morgan 2022; Traversa et al., 2020).

From a conservation perspective, these interactions explain why fire management frequently fails where herbivory pressure persists. Landscape-scale experiments in northern Australia show that reducing fire extent and frequency improves biodiversity outcomes only where grazing pressure is removed; continued grazing selectively suppresses post-fire ground cover and negates the benefits of altered fire regimes (Legge et al., 2019). **Managing fire in isolation produces an illusion of success: short-term responses can conceal longer-term structural lock-in when browsing remains.** Recent syntheses accordingly emphasise integrated fire–grazing frameworks rather than single-threat approaches (Legge et al., 2019; Xu et al., 2026).

Taken together, the rabbit-driven patterns in Coastal Moonah Woodland and the broader pyric-herbivory literature converge on a general principle: **herbivory sets the post-disturbance rules, and fire then operates within those constraints.** Where selective browsing suppresses regeneration, disturbance reinforces rather than reverses altered states. As a result, maintenance or recovery of native plant diversity in Coastal Moonah Woodland requires rabbit suppression prior to—or in place of—disturbance-based management. Without addressing chronic browsing pressure, fire and other interventions predictably accelerate simplification rather than restore woodland structure.

Figure 14. Rabbit-driven pathway to tea-tree dominance, with fire as a secondary amplifier (Coastal Moonah Woodland)

Rabbits selectively suppress the palatable ground-layer.
Sustained rabbit browsing prevents recruitment of palatable grasses, forbs, and shrubs—even at low densities—by repeatedly removing seedlings and juvenile cohorts, thereby shifting regeneration opportunities toward browse-resistant or opportunistic taxa (PestSmart, n.d.; Foundation for Rabbit-Free Australia, 2023).

Regeneration gates close for palatable natives; tea-tree gains a selective advantage.
With cohorts of obligate-seeding shrubs and small trees (e.g. *Acacia*, *Banksia*, *Pomaderris*, *Pultenaea*, *Leucopogon*) suppressed, competitive and microhabitat checks on tea-tree weaken; seedlings that are avoided or tolerated accrue a persistent recruitment advantage. On calcareous dunes, the functional groups that decline under browsing pressure are the same groups shown to decrease along fire gradients, while grasses and disturbance-aligned taxa increase, indicating a shared constraint on regeneration rather than a fire-initiated cause (Moxham & Turner, 2008; Moxham, Cheal, & Turner, 2009).

Tea-tree expands into dense shrub canopies (thicketing): a replacement state, not a fire-driven climax.
Inland closed tea-tree canopies on calcareous dunes are classified as transition or replacement states that arose following disturbance; tea-tree persists across the full fire gradient at Point Nepean, demonstrating that dominance cannot be attributed to fire regime alone (Moxham & Turner, 2008; Moxham et al., 2009).

Only after tea-tree dominance is established does fire become important—reinforcing, not initiating, the state.
Frequent fire on calcareous sands simplifies structure, with declines in canopy and mid-storey cover, litter, and moss and increases in grasses, while *Gaudium laevigatum* remains present across fire histories (Moxham & Turner, 2008). Fire behaviour in such systems is governed more by fine-fuel structure and continuity than by total biomass (Cruz et al., 2016), and continued grazing can further bias post-fire recovery against ground-layer re-establishment, stabilising the shrub-dominated state unless herbivory is reduced (Legge et al., 2019).

Interpretive note.
This sequence aligns with pyric-herbivory evidence from northern Australia, where fire elevates forage quality and attracts grazers, and selective grazing of post-fire regrowth subsequently reshapes fuels and future fire outcomes (Reid et al., 2022; Reid et al., 2023). Where herbivory persists, the ecological benefits of fire management are frequently negated, highlighting the necessity of suppressing rabbits before—or in place of—disturbance-based interventions (Legge et al., 2019; Xu et al., 2026).

Context

CMW occurs on **calcareous, low-nutrient, leaching-prone sands**, historically forming a **Sheoak–Moonah–Banksia** mosaic with a grassy ground-layer. Many extant remnants occupy calcarenite dune systems on the Mornington/Nepean Peninsula, with structure varying by landscape position and disturbance history (Moxham & Turner, 2009; Moxham, Turner, Walker, & Douglas, 2010). **Rabbit-driven collapse** has shifted numerous sites toward tea-tree-dominant, low-option architecture. Under these conditions, **broad burning is rarely neutral** and typically simplifies structure further unless constraints are repaired first (Moxham et al., 2010).

Historical signal

Reconstructions indicate:

- Open, grassy **Sheoak** structure on dune rises.

- **Moonah** thickets in sheltered swales, **not** inland tea-tree dominance.
  (Moxham & Turner, 2009)

Thus, historical references to "*dense scrub*" inland refer to **Moonah**, not *Gaudium laevigatum*.

Point Nepean evidence

With increasing fire frequency, CMW shifted from layered woodland/open forest toward simplified grassy woodland:

- canopy and mid-storey cover declined,
- litter and moss declined,
- obligate seed-regenerators declined,
- perennial grasses increased,
  while least-burnt sites retained Moonah, extensive moss beds, and low fuels (Moxham et al., 2010). Across all fire histories:

- coastal tea-tree remained common,
- *Polygala myrtifolia* persisted in both recently burnt and long-unburnt degraded stands (Moxham & Turner, 2009; Moxham et al., 2010).

Interpretation. This matches the § 4.7 diagnosis: **disturbance-maintained states become more fire-prone and more simplified**, reinforcing the configuration fire is intended to reverse.

Substrate rule: fire behaviour on calcareous sands

On calcareous dune sands, **repeated short-interval burns** act as **stress multipliers**:

- strip woody layering and ground-layer buffering (litter, moss),
- favour grasses and disturbance-aligned shrubs,
- narrow recruitment windows for canopy species and obligate seed-regenerators,
  driving a trajectory toward **grassy woodland/shrubland** (Moxham et al., 2010).

Patch-scale outcomes deteriorate where remnants are:

- small,
- poorly connected,
- surrounded by infrastructure/urban matrices—
  conditions that elevate exotic woody shrubs and disturbance colonisers. In contrast, **native richness increases with remnant size, connectivity, and adjacent native cover** (Moxham et al., 2010).

Physiological substrate penalty (lime chlorosis)

Calcareous sands impose physiological constraints on many eucalypts via **lime chlorosis**, reducing:

- growth rates,
- nutrient assimilation,
- post-fire recovery.

Classic experiments showed:

- *Eucalyptus baxteri* becomes severely chlorotic and stunted on calcareous sand but vigorous on siliceous sand,

- *Eucalyptus diversifolia* shows comparatively less penalty,
  demonstrating that alkaline sands **narrow recovery windows and reduce tolerance** to frequent fire (Parsons & Specht, 1967; Parsons & Uren 2013). Southern Victorian dune comparisons show that stand dynamics diverge across **calcareous vs siliceous** systems under interacting $CaCO_3$, fire, drought, and browsing (Moxham & Turner, 2009).

Mechanism summary

At Nepean, **loss of litter and moss** and **declines in Moonah/obligate seeders** under frequent burning reduce:

- near-surface buffering,
- microbial activity,
- structural layering.

In fragments already **simplified by rabbits** (§§ 4.2–4.2.1), this compounds **recruitment failure** and favours repeated capture by disturbance-aligned taxa, **locking stands into low-option architecture** (Moxham et al., 2010). In parallel, hydrophobicity in sandy profiles—strengthened or revealed by heat—promotes:

- preferential flow,
- surface moist microsites,
- coloniser recruitment (Doerr, Shakesby, & Walsh, 2000).

This is the same **SWR → bypass flow** mechanism established in § 4.1.

How fire should now be interpreted in calcareous-dune CMW.

1. **Fire is a structure filter, not a primary remover.** At Point Nepean, increasing fire frequency reduced canopy/mid-storey, litter, moss, and obligate seeders and

increased grasses/exotics, with no consistent difference in total richness—a filtering/replacement signal, not evidence that fire alone did the original removal.

2. **Tea-tree persistence shows fire ≠ cause.** *Gaudium laevigatum* occurs across all fire histories (fire-persistent, not fire-dependent). Inland thickets fit a sequence where **rabbits depress woodland recruitment,** and **fire amplifies** the simplified state.

3. **Rabbits drive cohort failure; fire collapses the scaffolding. Rabbits truncate *seedling and sapling* cohorts of Moonah (*Melaleuca lanceolata*), Sheoak, *Acacia*, and other palatable obligate seeders (primary removal), while adult trees may persist in a senescent state.** Fire then strips litter and moss, opens the surface, and rewards grasses/exotics, tightening the **hydro-structural lock-in** on calcareous sands (SWR → bypass flow → pulse capture), further narrowing recruitment windows. Result: **woodland → grassy/shrubby** trajectory with exotics ↑—a **foreshore-like template inland**.

4. **Why richness failed as a KPI.** Because "*increasers*" (grasses/exotics) numerically offset losses of woodland species, **richness can look flat while architecture and function collapse**. The Nepean dataset explicitly shows strong structural/functional shifts with fire even when richness does not change.

Operational rule (the line to govern decisions).

If **rabbits are active**, any burn is **high-risk**. **Suppress rabbits first**, contain colonisers (*Polygala*, *Rhamnus*), **rebuild the ground-layer**, and only then reassess whether fire has any role—on calcareous-dune CMW it typically **does not deliver recovery** and instead **locks in** the grassy/exotic state.

What to track instead of richness (management diagnostics).
Use metrics that match the Nepean signal and the matrix:

- **Structure:** canopy & mid-storey cover; litter/moss continuity (predictors of infiltration/soil buffering).
- **Functional groups:** obligate seeders (Moonah, Banksia, *Leucopogon*, etc.) vs facultative resprouters (direction shows lock-in).
- **Dominance:** Shannon and % dominance (these shift with fire when richness does not).
- **Composition risk:** exotic and perennial grass cover (early warning of structural truncation).

One-paragraph drop-in (Discussion § 4.7.1).

Reinterpreting fire under rabbit pressure. Evidence from Point Nepean shows that increasing fire frequency reconfigures structure and function—**canopy, mid-storey, litter, moss, and obligate seed-recruiters decline while native perennial grasses and exotics increase**—with **no consistent difference in total richness** across fire histories. Because *Gaudium laevigatum* persists across the fire gradient, fire is best read as an **amplifier of a rabbit-thinned state** rather than the primary remover of woodland architecture. On calcareous dune sands this amplification couples with hydrophobicity and preferential flow to **lock degraded stands into grassy/shrubby trajectories**, preventing re-entry of obligate seeders and moss beds. Management should therefore **suppress rabbits first**, contain colonisers, and rebuild ground-layer continuity; using fire as a reset **exacerbates** the very structure it is intended to reverse.

Two-line policy.

Fire in Coastal Moonah Woodland is a state-lock, not a cure. It **amplifies rabbit-driven cohort failure** by filtering out woodland structure and favouring grasses/exotics—often with **no change in richness** to warn managers; therefore calcareous-dune CMW should be treated as a **fire-exclusion** vegetation type, with risk reduction achieved through **weed suppression and structural retention**, not burning.

Implications for practice.

Under the architectural logic developed in §§ 4.1–4.6, generic burning **reduces options and tightens fragility gates** unless a sequenced repair is already underway.

The low-risk sequence is:

1. Suppress rabbits (remove opposition).
2. Contain disturbance-aligned shrubs (*Polygala*, *Rhamnus*).
3. Rebuild the ground-layer.
4. Reintroduce deep-rooted functional types (sheoaks, Banksia, Moonah). (Moxham et al., 2010)

One-line takeaway for § 4.7.1. Fire on calcareous dunes **amplifies collapse trajectories** unless rabbits are suppressed, colonisers contained, and ground-layer and structural functions rebuilt first.

4.8. Comparative Intactness and Baseline: Mornington Peninsula vs South West Victoria.

Continuity from §§4.1–4.7.

The preceding sections showed that collapse in CMW is produced by a coupled architecture—hydrological re-wiring (§4.1), rabbit-driven corridor closure (§§4.2–4.2.1), disturbance-aligned shrub dominance (§4.3), seedbank synchronisation risk (§4.4), and substrate-amplified failure under fire (§§4.7–4.7.1).

Bridge to practice. If §§4.6–4.7.1 diagnose how degraded CMW becomes locked into low-option architecture, §4.8 establishes *what the functional baseline actually is* by contrasting the heavily modified Mornington Peninsula with the most intact Coastal Moonah Woodland in south-west Victoria—clarifying the end-state architecture that restoration must rebuild toward.

Purpose.

This section establishes a functional baseline for Coastal Moonah Woodland (CMW) by contrasting the highly modified Mornington Peninsula (MP) with the most intact statewide remnants in south-west Victoria (SWV). The comparison grounds tea-tree thicket formation as a **disturbance-driven replacement state**—not a historical norm—and clarifies the structural and hydrological attributes restoration must rebuild toward.

4.8.1 Evidence of pervasive modification on the Mornington Peninsula.

On the MP, CMW formerly covered **~12,500 ha**, but today **< 1,000 ha** remains (≈ 10%), and most residual stands are **significantly degraded** (Moxham & Turner, 2009). This contraction aligns with Shire-wide estimates that **only 6–7%** of indigenous vegetation persists, with **few original tree stands** surviving (Mornington Peninsula Thematic History, 2013).

The **mechanism of simplification** is historically documented. Nineteenth-century lime-burning for Melbourne's construction boom led to widespread clearing of **Moonah, Sheoak, and Coast Banksia** for kiln fuel. The cleared mosaic was subsequently **captured by dense coastal tea-tree ("*tangled scrub*")**, which now dominates the Nepean dunes (Mornington Peninsula Thematic History, 2013).

In ecological terms, this shift represents a transition from **layered woodland with grassy/moss ground-layers** to a **single-layer thicket** with:

- low porosity;
- reduced infiltration windows;

- hydrological closure, and;
- narrowed recruitment opportunities;

This is consistent with the hydrological and structural preconditions for collapse identified elsewhere in this report.

On the Nepean calcarenites:
humans created the initial opening → rabbits kept recruitment closed → tea-tree re-engineered canopy–litter–soil processes (interception + SWR) into a stable low-option architecture.
This triad explains both the **pace** and **persistence** of thicket formation on the MP.

Concordant floristic signals include **elevated exotic cover**, **bare-ground**, **litter dominance**, and a prevalence of **disturbance colonisers** (and stabilisers under altered conditions)

such as *Gaudium laevigatum*, *Rhagodia candolleana*, and *Tetragonia implexicoma* (Moxham & Turner, 2009).

Although Point Nepean retains the largest MP stands (> 300 ha), their relative integrity reflects **restricted access (military/quarantine history)** rather than an unmodified trajectory (Mornington Peninsula Thematic History, 2013; Moxham & Turner, 2009).

Interpretive note.
This evidentiary bundle supports the thesis that **tea-tree thickets in MP CMW are post-settlement, disturbance-maintained architectures**, not intrinsic climax states (cf. §§ 4.6–4.7.1).

4.8.2 South-west Victoria as the functional baseline.

In contrast, SWV CMW exhibits:

- **higher native species richness and functional diversity;**
- **greater moss and canopy cover**, and;
- **better condition with fewer adjacent disturbances**

(Moxham & Turner, 2009).

The largest statewide tracts occur in the **Discovery Bay region**, where continuous or semi-continuous **Moonah–Sheoak–Bursaria** complexes persist (Moxham & Turner, 2009).

Palaeoecological evidence indicates **millennia-scale continuity (~7,000 years)** of dominant vegetation types across the hind-dune landscape, strengthening SWV's role as a **reference**

system for structure and process (Moxham & Turner, 2009). SWV therefore represents not an aspirational target but an empirically observed expression of intact constraint architecture on calcareous dunes.

Implication.
Where MP expresses **hydrologically tight, low-option thickets** (reduced infiltration, preferential flow, ground-layer collapse), SWV retains **layering, ground-layer continuity, and microclimatic buffering**—the very attributes required for infiltration continuity, seed-safe sites, and diverse recruitment.

4.8.3 Hydrological and structural lessons from the contrast.

1. **Ground-layer integrity governs moisture residence.**

   SWV's moss-rich ground-layers and litter continuity slow leaching and stabilise near-surface humidity on calcareous sands. MP thickets, by contrast, show **higher bare-ground**, **fragmented litter/moss matrices**, accelerated **surface dryness**, enhanced **SWR**, and **preferential flow** (Moxham & Turner, 2009; Mornington Peninsula Thematic History, 2013).

3. **Canopy layering regulates infiltration windows.**
   SWV's layered woodland (Moonah ± Sheoak ± Bursaria) creates **microtopography and shade** that increase safe-site heterogeneity.
   MP tea-tree thickets reduce **structural porosity** and **soil-contact niches**, narrowing post-disturbance recruitment windows (Moxham & Turner, 2009; Mornington Peninsula Thematic History, 2013).

4. **Disturbance history predicts hydrology.**
   On the MP, historical **fuel-wood extraction, fire, rabbits, and urban-edge pressures** explain contemporary low-infiltration states and disturbance-aligned shrub dominance (*Gaudium laevigatum*), consistent with hydrological mechanisms described in **§** 4.6 (Mornington Peninsula Thematic History, 2013; Moxham & Turner, 2009).

4.8.4 Management corollary (sequencing anchored to the baseline).

Because SWV demonstrates the **structural and hydrological end-state** that maintains open infiltration and diverse recruitment, MP restoration must first **rebuild architecture**, then reduce tea-tree.

Required sequence:

1. **Suppress rabbits** to reopen recruitment corridors and stop ground-layer attrition. (Historical + contemporary evidence: Mornington Peninsula Thematic History, 2013; Moxham & Turner, 2009.)
2. **Reconstruct the ground-layer** (moss/herb continuity, litter retention, microtopography) to restore porosity and moisture-holding architecture characteristic of higher-quality CMW.
(Moxham & Turner, 2009.)
3. **Reintroduce structural diversity** (Moonah ± Sheoak ± Banksia where appropriate) to recover layering, shade, and wind attenuation—widening infiltration windows.
(Moxham & Turner, 2009.)
4. **Only then**, undertake staged reduction of tea-tree, avoiding bare-soil pulses and synchronised flushes that re-instantiate thicket states.
(Trajectory evidence: Mornington Peninsula Thematic History, 2013; Moxham & Turner, 2009.)

One-line takeaway.
SWV shows the **empirical functional baseline; MP expresses** a **disturbance-maintained** thicket **architecture.** Restoration on **MP** will not **converge on baseline** conditions **unless constraints are repaired before canopy simplification**, restoring the layered, porous, ground-layer-anchored architecture that supports infiltration and recruitment (Moxham & Turner, 2009; Mornington Peninsula Thematic History, 2013).

4.8.5 Immediate Priority: Rabbit Control and Weed Removal to Safeguard Assets and Seedbanks.

Action is **time-critical**. Given the Peninsula's severe contraction and fragmentation of CMW (≈ 10% of pre-European extent, with many stands degraded), any remaining structural assets—**mature Moonah/Sheoak, intact moss/herb ground-layers**—and their seedbanks require urgent protection (Moxham & Turner, 2009; Mornington Peninsula Thematic History, 2013).

Immediate requirements:

- **Suppress rabbits immediately** to stop continual seedling and ground-layer attrition, reopen recruitment corridors, and prevent further hydrological tightening on calcareous sands. Without rabbit control, regeneration windows remain closed even when thickets are thinned (Mornington Peninsula Thematic History, 2013; Moxham & Turner, 2009).
- **Remove disturbance-aligned weeds rapidly** (e.g., *Polygala myrtifolia, Rhamnus alaternus,* other exotics, **selectively where they threaten assets** *Gaudium laevigatum*), **prioritising low-disturbance methods** that retain litter/moss continuity and avoid bare-ground pulses that trigger synchronised flushes. (Moxham & Turner, 2009).

Bottom line.
Every month of delay increases the chance that small, fragmented remnants tip irreversibly into low-option, weed-dominated thickets, eroding the last workable seedbanks and structural assets. Urgent, sequenced **rabbit control + weed removal** is essential to preserve remaining pathways back to a layered, porous woodland with open infiltration and diverse recruitment (Moxham & Turner, 2009; Mornington Peninsula Thematic History, 2013).

4.9. Foreshore Template Reset: Mechanism, Geomorphic Outcomes, and Species-Level Consequences (with She-oak as Co-architect).

Continuity from §§4.1–4.8.
The preceding sections showed how hydrological re-wiring (§4.1), rabbit-maintained corridor closure (§§4.2–4.2.1), disturbance-aligned shrub dominance (§§4.3–4.6), fire-amplified collapse on calcareous sands (§§4.7–4.7.1), and landscape-scale simplification on the Mornington Peninsula (§4.8) collectively produce **foreshore-like conditions inland**.
Bridge to §4.9. *This section explains how those conditions are recreated—mechanistically—through rabbits, unsequenced clearing, and ground-layer loss; why the resulting ecological–geomorphic template favours repeated tea-tree re-establishment; and which native species and functions are displaced when inland systems are forced into a foreshore operating mode.*

4.9.1 Mechanism — how rabbits and un-sequenced clearing recreate the foreshore template inland.

Human intervention can inadvertently **translate the foreshore template inland**—the same structural state manufactured historically by rabbits and clearing. In many Coastal Moonah Woodland (CMW) remnants, functionally critical understorey species such as ***Rhagodia candolleana*** (seaberry saltbush) and ***Tetragonia implexicoma*** (bower spinach) are still being removed during weed control or "*tidying*" works. These are native stabilisers and functional scaffolds, not targets with their roles in:

- **surface stabilisation** (trapping fines and stitching mobile sand),
- **litter capture** (building roughness and moisture-holding matrices), and
- **microclimate buffering** (shading calcareous sands, protecting moss/herb carpets).

On calcareous sands, their loss **exposes hydrophobic mineral surfaces**, **breaks litter continuity**, and **resets recruitment filters**—operationally equivalent to chronic grazing pressure.

Cosmetic interventions alone do not restore function. Ornamental or short-lived plantings can increase visual diversity, but they **do not** rebuild infiltration pathways, microsite redundancy, or ground-layer porosity. Likewise, **early-stage physical removal** (pulling, grubbing, scraping) of disturbance-aligned shrubs **restarts bare-ground pulses**, **intensifies SWR**, and **primes seedbank synchrony**.

Use selective suppression instead: low-disturbance, **in situ** herbicide that neutralises targets **while retaining shade, litter, moss and microtopography**. Suppression prevents exposure pulses, avoids synchronised recruitment, and **blocks re-imposition of the foreshore template**.

These well-intentioned but mis-sequenced actions—ornamental replacement and physical removal—**carry the foreshore template inland**, **re-locking a low-competition state** that favours ***Gaudium laevigatum*** and other disturbance-aligned elements.

Rabbits and repeated disturbance act in parallel. Continuous grazing suppresses seedlings, mosses, and herbs, maintaining open, **low-competition** surfaces analogous to coastal foreshores. Repeated **substantive tea-tree clearing without prior constraint repair** recreates the same template by **exposing bare soil** and **continually resetting recruitment filters**. In both cases, inland calcareous dunes become **functionally transformed** into foreshore-like environments—conditions to which tea-tree is **pre-adapted**. **(Figure 15)**

Once established, tea-tree **re-engineers canopy–litter–soil processes**:

- **increased canopy interception** (reduced throughfall to the ground-layer),
- **enhanced soil-water-repellency (SWR)** via hydrophobic litter accumulation, and
- **reduced surface porosity** (fewer seed-safe, moisture-holding microsites),

locking the system into a **low-option thicket**. Under these conditions, loss of ground-layer cover and litter continuity accelerates:

- **runoff** (shallow pulse capture rather than deep infiltration),
- **aeolian deflation** (export of fines and seed), and
- **stripping of the biologically active surface layer**.

Moisture residence declines, **seed-safe sites disappear**, and recovery becomes progressively **less feasible**. This coupled ecological–geomorphic feedback explains why

chronic rabbit pressure and **unsequenced clearing** favour repeated **tea-tree re-establishment** and drive ongoing **topsoil loss** and **structural simplification**, rather than recovery.

Bottom line. Exposure resets on calcareous sands don't just "*tidy*" a site—they **translate inland surfaces toward a foreshore operating mode**, where SWR, bypass flow, and seed-safe site loss become the default.

Hydrological note.
On sandy, low-organic profiles, hydrophobic surface layers **reduce matrix infiltration**, increase **preferential flow and runoff**, and **promote erosion** (rainsplash, sheetwash, wind detachment).
These effects intensify when cover is reduced and heat/dryness fluctuate; thus **exposure events** (physical removal, scalping) have outsized consequences on calcareous dune sands.

Operational implication.

- **Do not** front-load physical clearing (pulling, grubbing, scraping).

- **Do** sequence: **rabbits → ground-layer → structural re-layering → selective suppression** of disturbance-aligned shrubs; **tea-tree as spot-work only** where ground-layer recovery requires it.

- **Keep** stabilisers (*Rhagodia*, *Tetragonia*). **Suppress** targets **in situ** with **low-disturbance herbicide** so architecture is preserved while seed input is neutralised.

Cross-link. This foreshore-template reset is the same surface-dominated hydrology described in §§3.1–3.4 and the seedbank synchronisation risk in §4.4.

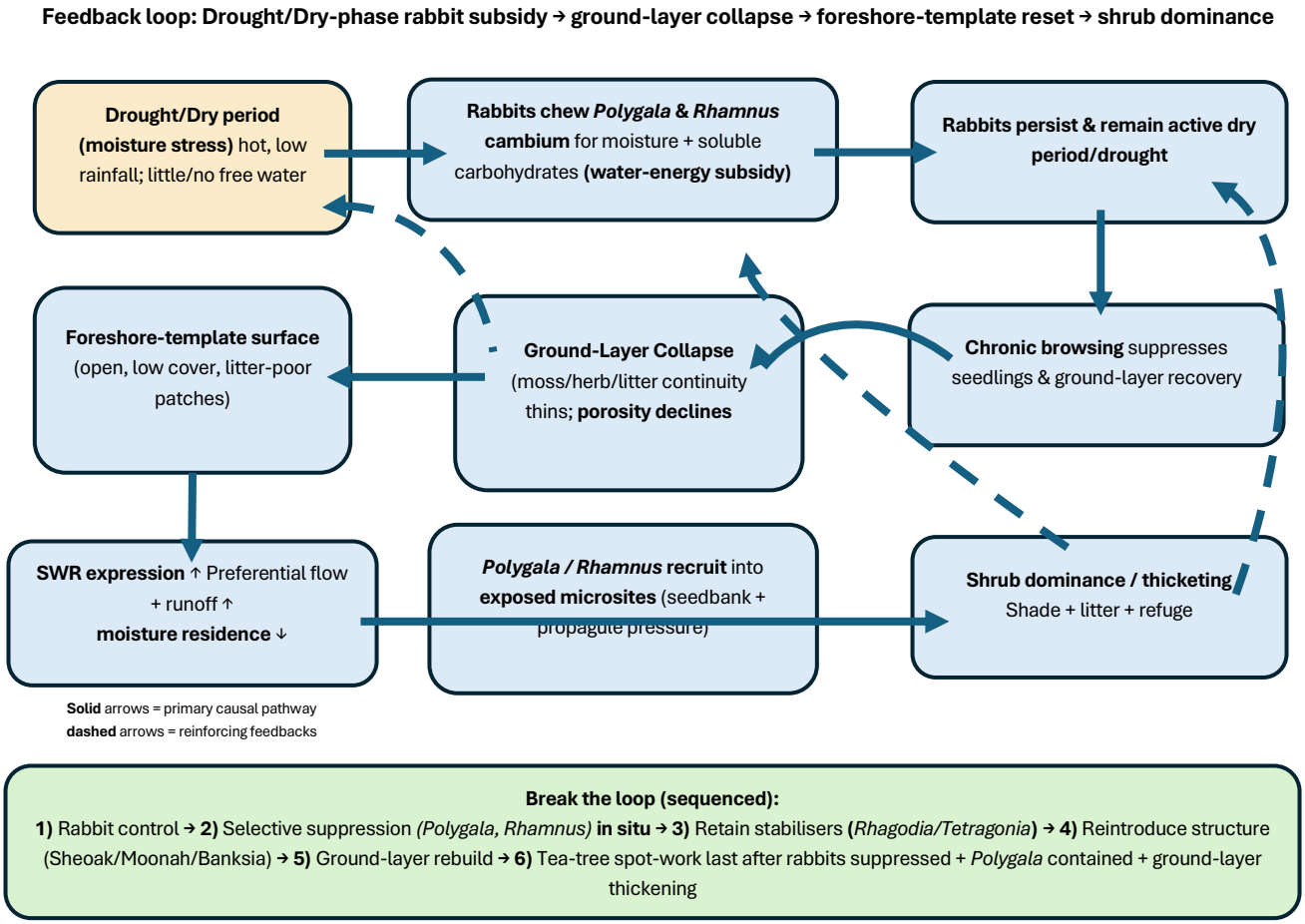

Figure 15. *Feedback loop linking* ***drought/dry-period moisture stress*** *(little/no free water) to rabbit persistence via cambium chewing on* ***Polygala myrtifolia*** *(moisture + soluble carbohydrate subsidy), continued browsing pressure, ground-layer collapse, and SWR-driven hydrological closure. The resulting foreshore-template surface favours recurrent recruitment of disturbance-aligned shrubs* ***(Polygala, Rhamnus),*** *reinforcing shrub dominance. Solid arrows indicate primary causal processes; dashed arrows indicate reinforcing feedbacks.*

4.9.2 Geomorphic outcomes — why erosion and topsoil loss follow.

Erosion and topsoil loss are the **inevitable geomorphic outcome** of the foreshore template when it is recreated inland. Where rabbits and repeated disturbance maintain **low-cover, low-porosity surfaces**—fragmented moss/litter continuity, suppressed ground-layer rooting, exposed hydrophobic sand **(Figure 16**)—the **biologically active horizon is progressively stripped** by runoff and wind.

Diagnostic implication. Where erosion is observed on inland calcareous dunes, the foreshore template has already been reinstated; geomorphic loss is therefore a **state indicator**, not a secondary impact.

On calcareous dunes, the loss of organic fines and surface structure has outsized effects. With each exposure pulse, the system:

- **loses moisture residence** (rapid drying and reduced storage capacity);
- **eliminates seed-safe sites** (fewer shaded, humic, or buffered microsites), and;
- **tightens recruitment windows** (shorter viable emergence periods, greater desiccation risk).

These vulnerabilities are **amplified under SWR**. Hydrophobic surface layers **impede infiltration**, force water into **preferential flow paths**, and increase **runoff concentration** on exposed surfaces. Even minor rainfall events produce **high-energy sheetflow**, accelerating rainsplash, sheetwash, and subsequent **aeolian deflation**. The result is a **ratcheting loss of the surface layer** that formerly moderated temperature, retained moisture, and supported recruitment.

This pattern is not abstract—it mirrors the **statewide contrast**.
Across the Mornington Peninsula, CMW remnants exhibit **higher bare-ground and exotic cover**, consistent with a foreshore-template surface. In contrast, Southwest Victoria remnants retain **denser moss carpets, deeper litter, and more continuous canopy cover**—a configuration that **buffers against surface loss**, maintains porosity, and protects the biologically active layer. **(Figure 17)**

The geomorphic signal therefore confirms the mechanism:
when the foreshore template is reproduced inland, erosion is not a symptom but an architectural outcome of the state itself.

Figure 16. *Highlighted footprint on a sloping calcareous sand surface showing* ***shallow wetting over a hydrophobic profile****. The circled area marks a thin, cohesive surface layer that adhered to the sole during stepping, while* ***dry, non-cohesive sand remains immediately***

***beneath and around it**. This sharp vertical contrast demonstrates soil-water-repellency (SWR): moisture is retained at the surface, downward infiltration is impeded, and effective drought conditions persist below the surface even after wetting events. On slopes, this promotes runoff, erosion, and rapid loss of the biologically active layer.*

***Figure 17.** The intact ground-layer illustrates the architectural state that prevents collapse on calcareous dunes. Litter continuity, moss cover, and embedded native graminoids bind fines, buffer near-surface humidity, and maintain porous infiltration pathways. Where this structure persists, SWR expression is muted, erosion is constrained, and recruitment corridors remain open. Its loss discloses a collapse of surface architecture, not a transient disturbance effect—through rabbit-grazing or aesthetic clearing—marks the transition to foreshore-template conditions and initiates the collapse sequence described above.*

Cross-link. This is the same interception → **SWR** → bypass-flow mechanism described in §§3.1–3.3 and §4.1, expressed geomorphically.

4.9.3 Which native species are being suppressed or lost under foreshore-template conditions?

Canopy / small trees (decline under frequent disturbance).

- **Moonah (*Melaleuca lanceolata*)** — cover highest in least-disturbed stands; declines under frequent disturbance.

- **Coast Beard-heath (*Leucopogon parviflorus*)** — common in least-disturbed stands; declines as ground-layer and litter continuity collapse.

- **Coast Wirilda (*Acacia uncifolia*)** — obligate seeder; fails to recruit where inter-disturbance intervals are too short and surfaces remain open/bare.
  In degraded stands following disturbance, *A. uncifolia*, *M. lanceolata*, and *Pimelea serpyllifolia* are often absent despite being diagnostic of the community.

Ground-layer (first to be lost; key to recovery)

- Moss carpets (e.g., *Thuidiopsis furfurosa*) decline under disturbance/frequent fire.

- Grassy/herb matrices thin or vanish (*Dichondra repens*, *Austrostipa flavescens*; diagnostic *Wurmbea latifolia*, *Parietaria debilis*).
  Loss of these layers removes **seed-safe microsites**, capillary bridges, and surface roughness that resist aeolian deflation.

Native stabilisers (often mis-removed)

- *Tetragonia implexicoma* (bower spinach).

- *Rhagodia candolleana* (seaberry saltbush).

These species trap fines, shade sands, retain litter islands, and protect microsites. **Do not clear them**: removal recreates the foreshore template and accelerates losses.

4.9.4 Baseline mosaic (expanded) and the under-stated role of She-oak.

Before clearing and the shift to tea-tree thickets, the calcareous dune arc carried a **Moonah–She-oak–Banksia mosaic**, with:

- **Drooping She-oak (*Allocasuarina verticillata*)** prominent on landward hind dunes/dryland positions, and
- **Moonah** more common on seaward faces.

This pattern is supported by pollen records and floristic surveys in SWV and at Wilsons Promontory (Drooping She-oak woodland persisting over millennia). The mosaic remains clearest today in **Discovery Bay–Nelson**, where species richness and moss/canopy cover exceed those on the MP.

Why Sheoak matters (five roles + hydrological role clarified).

1. **Actinorhizal nitrogen boundary.**
   Sheoaks host *Frankia* symbionts that fix nitrogen on nutrient-poor calcareous sands, maintaining low-nutrient conditions and preventing shifts toward disturbance-aligned shrubs/exotics (Diem & Dommergues, 1990; Duhoux & Dommergues, 1985; Reddell & Bowen, 1985).
2. **Structural layering & microclimate.**
   On hind dunes, Sheoak (or mixed Moonah–Sheoak) provides wind attenuation, fine litter inputs, and cooler, buffered near-surface microclimates that protect moss carpets and seed-safe microsites (Moxham, Turner, Walker, & Douglas, 2010).
3. **Surface processes & sand stability.**
   Sheoak litter and root matrices add surface roughness, trap aeolian fines, and "*stitch*" the surface, slowing erosion and stabilising dune soils (Moxham & Turner, 2009; Moxham et al., 2010).

Hydrological role (inserted):
By maintaining fine-root porosity, shading sands, and supporting moss carpets, Sheoak suppresses SWR expression and reduces preferential-flow intensity—directly countering the hydrological architecture that drives foreshore-template formation (Doerr, Shakesby, & Walsh, 2000; Moxham et al., 2010; Roper, Carter, & Weaver, 2015; Siteur et al., 2016).

4. **Recruitment scaffolding for companions.**
   Mixed canopies correlate with higher moss cover and lower bare-ground in least-disturbed stands; disturbance closes the recruitment windows required by *Acacia uncifolia*, *Pimelea serpyllifolia*, and other diagnostic species (Moxham & Turner, 2009; Moxham et al., 2010).
5. **Regional baseline evidence.**
   SWV retains this pattern: in Discovery Bay and at Wilsons Promontory, Drooping Sheoak dominated hind dunes over millennia, with Moonah on dune faces—demonstrating stable co-dominance rather than incidental presence (Moxham & Turner, 2009).

What was lost, and why.
Historic lime-burning targeted **Moonah, She-oak, and Banksia**, clearing layered woodland and enabling tea-tree capture of Nepean dunes. Subsequent disturbance/rabbits suppressed She-oak recruitment by **collapsing ground-layer porosity** and keeping surfaces open. In

frequently disturbed Nepean quadrats, canopy/moss decline while bare-ground/grasses/exotics increase, shifting toward **grassy shrubland** and closing the windows She-oaks require (obligate seeder + ground-layer dependence).

4.9.5 Management corollary — what to keep, what to fix, what to avoid.

1. **Rabbits first.**
   Stop seedling and ground-layer attrition; without this, She-oak and *A. uncifolia* cannot re-establish cohorts.

2. **Apply selective suppression — not physical removal — of *Polygala* and *Rhamnus* once constraints are released and the ground-layer thickens.** Suppress targets **in situ**, retain shade and litter, avoid exposure pulses, and prevent seedbank synchrony. **Tea-tree is sporadic spot-work only**, guided strictly by ground-layer needs, and never a primary intervention on calcareous sands. **Disturbance aligned shrubs function as drought subsidies**—providing both water and carbohydrates—allowing rabbits to persist and continue suppressing the ground-layer when recovery would otherwise begin. **(Figure 18, 19)**

3. **Retain native stabilisers.**
   Do **not** "*tidy out*" *Tetragonia implexicoma* and *Rhagodia candolleana*. Use them as **functional scaffolding** while constraints are repaired.

4. **Reintroduce structural diversity.**
   Where seed sources are limited, plant/overseed *Allocasuarina verticillata* into landward hind-dune lenses and pair with Moonah and Banksia to recover rooting-depth complementarity and the actinorhizal N-boundary.

5. **Rebuild the ground-layer.**
   Restore moss/herb/litter continuity and microtopography to extend moisture residence and blunt SWR–runoff coupling.

6. **Only then reduce tea-tree, staged and low-disturbance**, to avoid bare-soil pulses, weed surges, and re-imposition of the foreshore template.

This sequence breaks the drought-phase rabbit subsidy loop illustrated in Fig. 9

One-line takeaway for §4.9.
Unsequenced clearing and grazing recreates the foreshore template inland; only constraint repair (rabbits → ground-layer → stabilisers → structural diversity) prevents tea-tree rebound and geomorphic degradation.

Figure 18. Field observation confirms this mechanism. *During dry periods, rabbits actively chew the living cambium of young Polygala myrtifolia stems for* ***moisture and soluble carbohydrates****, stripping bark vertically and exposing the sapwood. This behaviour* ***sustains rabbit populations through drought****, even as native herbs, mosses, graminoids, and juvenile canopy species are eliminated. The consequence is a s****elf-reinforcing collapse sequence****:*

rabbits suppress the ground-layer that once moderated moisture and infiltration, while drought conditions drive rabbits to harvest Polygala as a combined ***water–energy subsidy****. By sustaining rabbits during stress periods, disturbance-aligned shrubs indirectly* ***maintain the low-competition architecture*** *that favours their own persistence and rapid re-assertion under the foreshore template.*

Figure 19. *Buckthorn* ***(Rhamnus alaternus) stem showing rabbit chewing*** *beneath a clustered tea-tree* ***(Gaudium laevigatum)*** *canopy. Localised bark removal and exposed cambial tissue are consistent with repeated rabbit gnawing, indicating use of woody invasive shrubs as a* ***dry-season moisture and carbohydrate source.*** *The sheltered position beneath tea-tree thickets illustrates how dense* ***shrub architecture provides cover that sustains rabbit*** *activity,* ***maintaining chronic soil disturbance and recruitment conditions*** *favourable to disturbance-aligned shrubs.*

4.10. Faunal Pathways Depend on Sequenced Floristics (and Why the "*Foreshore Template*" Silences Them).

Continuity from § 4.9. Having shown how unsequenced clearing and rabbit pressure recreate a foreshore-like template inland (§ 4.9), we now examine its **faunal consequences**, demonstrating that trophic collapse is not a separate process but the **late-stage expression of floristic and hydrological collapse**.

4.10.1 Why fauna are inside the vegetation argument.

The appearance of stability beneath tea-tree thicket is misleading. Once **ground-layer architecture collapses**, and **SWR-driven hydrological closure** sets in, the system carries **fewer admissible routes** for both plants *and* animals (Doerr, Shakesby, & Walsh, 2000; Siteur et al., 2016). Under EF, disturbance progressively **thins the option set**—first floristic routes, then trophic routes—as architectural corridors, prey bases, and moisture-buffered microsites are lost. The same drought-**period moisture stress** phase feedback loop (Fig. 9) explains why faunal routing options collapse once ground-layer continuity is lost.

Rebuilding **sequenced floristics** is therefore a **faunal intervention**. It restores the resource calendars, shelter structure, and movement routes that autochthonous species evolved with on calcareous dunes (Mornington Peninsula Shire & Context, 2013). Layering vegetation is not habitat enhancement—it reinstates routing options for fauna that have already been removed.

On the Mornington Peninsula (MP), repeated disturbance has driven a shift from **layered woodland** toward **grassy/shrubby, high-exposure states**. Canopy and moss decline; bare-ground rises; disturbance-aligned species expand (Mornington Peninsula Shire & Context, 2013). This is a **structural simplification of the system**, not a compositional anomaly.

As SWR intensifies with heat and disturbance, **infiltration declines**, **runoff concentrates**, and the **biologically active surface layer** is stripped (Dekker & Ritsema, 1994; Dekker et al., 2001; Doerr et al., 2000). This removes the moisture and humic buffering that support seedling recruitment **and** the invertebrate prey bases of small birds and mammals.

Implication.
When groundcovers vanish, **faunal decline follows**. Species dependent on moss–herb matrices, litter islands, seed and fruit resources, invertebrate prey, and porous shelter lose their routing options, and communities shift toward **opportunists and generalists** that exploit simplified architecture and human subsidies (Galbraith, Beggs, Jones, & Stanley, 2015).

Faunal restoration cannot be separated from vegetative restoration: fauna return only when the architectural pathways they evolved with are reinstated. **Rebuild the architecture and fauna return; leave the architecture collapsed and they cannot.**

4.10.2 Avian pathways supported by the baseline mosaic (Moonah–She-oak–Banksia + ground-layer).

Under the **baseline mosaic**—Moonah, Sheoak, Banksia, continuous moss and litter, and a diverse herb/graminoid layer—multiple autochthonous avian guilds persist because the vegetation provides **layered routing options** (Mornington Peninsula Shire & Context, 2013):

- **Insectivores** (foliar, bark, litter gleaners) depend on cool, humid boundary layers and **moss–litter continuity**; they peak where disturbance is lowest.

- **Nectar/fruit users** track Moonah flowering, Leucopogon fruiting, and **Rhagodia/Tetragonia** resources that maintain **year-round foraging calendars**.

- **Seed/grass users** rely on *Austrostipa,* and allied graminoids embedded in a **structured ground-layer**, not on bare patches.
- **Perch, nest, and roost users** require the **vertical layering** that increases porosity, shelter, and substrate availability.

Crucially: small insectivorous birds **do not immediately abandon tea-tree thickets**. They continue using tea-tree for **structural cover as long as** the understorey beneath it retains **moss, litter, and native herbs**.
Once disturbance pushes the understorey toward **introduced grasses and ruderal species**, insectivores (thornbills, robins, small honeyeaters) disappear.

Two mechanisms drive this lagged collapse:

1. **Bottom-up collapse.**
   Loss of **moss–litter–herb matrices** reduces invertebrate abundance and diversity, collapsing the food base sustaining small insectivores—even where canopy remains.

2. **Behavioural exclusion.**
   Simplified ground-layers favour aggressive generalists (e.g., Noisy Miners, Common Mynas) whose interference behaviour excludes small birds from the remaining foraging space.

The outcome is a **false persistence signal**: tea-tree appears green and continuous, yet functions as **low-resource, low-shelter habitat**. Use becomes **transient rather than demographically viable**.

Across suburban Melbourne, **Noisy Miners suppress small insectivores** even where native canopy persists, while larger nectarivores (e.g., Red Wattlebirds) can persist where **vertical layering remains intact** (Humphrey, Haslem, & Bennett, 2024).

Field rule (stabilisers).
Rhagodia candolleana and ***Tetragonia implexicoma*** are **native stabilisers, not weeds**. Their removal produces **foreshore-like conditions**, stripping food, shelter, and invertebrate habitat. They must be **retained as functional scaffolding** throughout recovery (Mornington Peninsula Shire & Context, 2013).

4.10.3 What the "*foreshore template*" does to fauna (mechanism → outcome).

1. **Ground-layer loss → trophic collapse**
   Invertebrate base declines; seed-safe microsites disappear; foraging efficiency drops; moss–litter shelter contracts (Mornington Peninsula Shire & Context, 2013).
2. **SWR + bare soil → hydrological + thermal stress**
   Runoff, rilling, aeolian loss of fines; shortened moisture residence; fewer cool/moist refugia for invertebrates and herpetofauna; prey limitation for birds
   (Doerr et al., 2000; Siteur et al., 2016).
3. **Canopy simplification → loss of vertical porosity + phenological narrowing**
   Reduced layering narrows flowering/fruiting calendars and dampens foraging buffers (Mornington Peninsula Shire & Context, 2013).

Mesopredators (structurally caveated).
Simplified habitats (edges, open ground, reduced mid-storey) can increase mesopredator access and encounter rates; but responses are **context-dependent** and governed largely by **structural complexity and subsidies**, not apex removal alone (Jachowski et al., 2020; Prugh et al., 2009). Australian experiments show apex removal does **not** reliably cause mesopredator release; **architecture dominates** (Castle et al., 2021). These patterns indicate that predator effects are mediated by structure and subsidy, not addressable through predator control in isolation.

Why it "*looks stable*."
Thickets appear green and continuous but function as **low-infiltration, low-resource, low-shelter systems**, favouring opportunists (Common Mynas, Spotted Doves, Common Blackbirds). Long-term analyses link myna establishment to declines in small birds and cavity nesters (Galbraith et al., 2015; Grarock et al., 2012).

Corvid context.
Ravens can be significant nest predators in open coastal systems. Little Ravens in peri-urban Melbourne range widely and track mixed resources; exposure is therefore **structure- and subsidy-dependent**, not purely local (Rees et al., 2015; Whisson et al., 2015).

4.10.4 Species at risk (signals visible in the vegetation record).

Canopy/small trees (diagnostic recruitment failure):
Melaleuca lanceolata, *Leucopogon parviflorus*, *Acacia uncifolia*—fail to recruit where inter-disturbance windows are short (Mornington Peninsula Shire & Context, 2013; PestSmart, n.d.).

Ground-layer (first to collapse):
Moss carpets (*Thuidiopsis furfurosa*), *Dichondra repens*, *Austrostipa flavescens*, *Wurmbea latifolia*, *Parietaria debilis*—the moisture-holding, insect-supporting matrix.
(PestSmart, n.d.).

Native stabilisers (often mis-removed):
Tetragonia implexicoma, *Rhagodia candolleana*—retain as **soil and faunal buffers**.
(PestSmart, n.d.).

4.10.5 Re-centring She-oak (the understated co-architect) so avian pathways can return.

Across the calcareous arc, **Drooping She-oak (*Allocasuarina verticillata*)** co-occurs landward with Moonah seaward. SWV remnants retain **higher moss/canopy cover** and **lower bare-ground/exotics** than MP (Mornington Peninsula Shire & Context, 2013).

She-oak contributes:

- **Actinorhizal N-fixing boundaries**, governing nitrogen on nutrient-poor calcareous sands (Sy et al., 2007).
- **Surface roughness + microclimate buffering**, cooling near-surface air and protecting moss carpets/seed-safe microsites.
- **Surface stability**, stitching calcareous sands and slowing erosion.
- **Recruitment scaffolding** for companions; mixed stands correlate with higher moss and lower bare-ground.
- **Baseline continuity**, with hind-dune dominance over millennia at SWV and Wilsons Prom.

Historic fuelwood cutting of Moonah–She-oak–Banksia plus rabbits suppressing recruitment shifted stands toward **avifaunally poor thickets**, despite their "*green*" appearance (Mornington Peninsula Shire & Context, 2013).

4.10.6 Management corollary — sequencing floristics to re-open faunal routes.

> **1. Suppress rabbits first** → halt seedling and ground-layer attrition that maintains foreshore-like surfaces and depletes invertebrates (PestSmart). Rabbit control re-opens juvenile routes and is the precondition for any faunal recovery.

2. Apply *selective suppression*—not physical removal—of *Polygala* and *Rhamnus* → neutralise disturbance-aligned shrubs **in situ**, **retain shade and litter**, avoid bare-soil pulses, and prevent seedbank synchrony. This protects emerging microsites and prevents the foreshore template from re-locking.

3. Retain stabilisers → *Tetragonia implexicoma* and *Rhagodia candolleana* are **faunal scaffolding** and **surface stabilisers**; they supply cover, fruiting resources, invertebrate substrate, and microclimate buffering. Do **not** "*tidy*" them out; removing them recreates foreshore-like templates and collapses food-web layers (Mornington Peninsula Shire & Context, 2013).

4. Rebuild the ground-layer → restore **moss/herb/litter continuity** and **microtopography** to extend moisture residence, blunt SWR–runoff coupling, and **recreate litter–invertebrate mosaics** that sustain foliar, bark, and litter-gleaning guilds. Without this, no avian guild can persist (Doerr et al., 2000; Siteur et al., 2016).

5. Reintroduce structural diversity → sow/plant **Sheoak** in hind-dune lenses and pair with **Moonah/Banksia** to rebuild vertical layering, rooting-depth complementarity, actinorhizal N-boundaries, and **year-round foraging calendars** (Sy et al., 2007). Layering restores routing and resource continuity for small insectivores, nectarivores, and frugivores.

6. Tea-tree is last and local → only then, and **only** as **targeted spot-work**, apply low-disturbance techniques where tea-tree directly obstructs ground-layer formation or shading balance. Avoid bare-soil pulses and weed surges; maintain faunal resources through transition (Doerr et al., 2000).

Urban invader note.
Remove feeding subsidies (backyard seed, waste) adjacent to works. An 18-month suburban experiment showed Spotted Doves and other introduced species increased under feeding, with effects fading once feeding ceased (Galbraith et al., 2015).

4.10.7 What to monitor (fauna-aware indicators, tied to your evidence).

- **Moss cover (%) and litter continuity** — predictors of infiltration, invertebrate availability, and seed-safe sites (Doerr et al., 2000).
- **Canopy layering index** (Moonah ± She-oak ± Banksia) vs. bare-ground % — target least-disturbed Nepean profiles (Mornington Peninsula Shire & Context, 2013).
- **Return of diagnostic flora** (*Acacia uncifolia*, *Pimelea serpyllifolia*, *Leucopogon parviflorus*) as **faunal proxies** (Mornington Peninsula Shire & Context, 2013).

- **Bird point counts by guild** (insectivore, nectar/fruit, seed) + **Noisy Miner abundance** as a suppression signal (Humphrey et al., 2024).
- **Optional invader tallies** (Common Mynas, Blackbirds, Spotted Doves) along edge → interior transects to assess subsidy removal and edge closure (Galbraith et al., 2015).
- **Corvid activity notes** (e.g., Little Raven movement) relative to bare-ground % and subsidies (Whisson et al., 2015).

One-line takeaway for § 4.10.
Faunal collapse in CMW is not a separate process—it is the late-stage disclosure of floristic and hydrological collapse. Rebuilding fauna requires sequenced floristics, structural recovery, and constraint repair, not "*habitat thinning*."

4.11. Continuity vs Aesthetic Reset: Why Removing Stabilisers and Planting Ornamentals Collapses Function.

4.11.1 Continuity is the infrastructure of persistence.

Autochthonous flora and fauna on calcareous dune systems persist because **habitat structure and resource calendars remain continuous through time**, not because a site "*looks neat*" in any given moment. Where **ground-layer continuity, litter–moss matrices, and layered canopies** are preserved, recruitment windows, invertebrate bases, and seasonal bird resources remain open.
Where continuity is repeatedly broken, **option sets thin**, and systems are progressively routed into **low-option architectures**

that may appear green but are **functionally depleted**.

On the Mornington Peninsula (MP), repeated disturbance has driven structural drift from layered woodland to **grassy/shrubby, bare-ground states**—with canopy and moss reduced, and bare-ground and disturbance-aligned species increased—contrasting sharply with the more intact south-west baseline where moss/canopy cover is higher and exotics/bare-ground lower.

4.11.2 The "*aesthetic reset*": how well-intentioned works erase continuity.

In many CMW remnants, ***Rhagodia candolleana*** (seaberry saltbush) and ***Tetragonia implexicoma*** (bower spinach) are removed during weed control or "*tidy-ups*," then replaced—intentionally or by default—with **introduced grasses**, **ornamentals**, or **episodic plantings** (e.g., bulbs). Functionally, this **replaces stabilisers with ornament**, trading functional

architecture for short-term appearance. These (*Rhagodia and Tetragonia)* are native stabilisers and functional scaffolds, not weeds or transitional fillers.

- **Stabilisers are native, characteristic, and frequent across CMW.**
  Statewide records show ***Rhagodia* in 71%** of quadrats and ***Tetragonia* in 66%**; both are **frequent (68–74%)** in urban-edge remnants from a 121-site dataset. They **trap fines**, **hold litter**, **buffer microclimate**, and **protect seed-safe microsites**—the very functions calcareous sands need to keep the biologically active surface in place.

- **Removing stabilisers exposes hydrophobic sand and resets recruitment filters.**
  Bare-surface exposure breaks moss/litter continuity, shortens moisture residence, and re-opens **foreshore-template** conditions (low cover, low porosity, shallow wetting) inland. In this state, disturbance-aligned shrubs and grasses exploit the opening.

- **The exotic suite that follows disturbance is well-documented in CMW:**
  Ehrharta erecta, Lagurus ovatus, Vulpia spp., Aira spp., Polygala myrtifolia, Rhamnus alaternus, Asparagus asparagoides.
  These taxa **increase with disturbance and infrastructure matrices**, **displacing native structure** without restoring ecosystem function.

Method rule (governing): continuity must never be sacrificed to achieve visual tidiness.

- Where shrubs must be controlled, use **selective suppression** (low-disturbance herbicide, *in situ*): the target dies **without** exposing sand; **shade, litter, moss, and microtopography are retained**; there is **no seedbank synchrony** and **no exposure pulse**.

- **Do not** "*tidy out*" stabilisers—**retain *Rhagodia* and *Tetragonia*** as **functional scaffolding** while constraints are repaired (rabbit suppression, ground-layer rebuild, structural re-layering).

Bottom line.
Clearing for aesthetics carries the foreshore template inland—creating **open, low-competition, litter-poor surfaces** that invite ***Gaudium laevigatum*** (tea-tree) re-colonisation and **reinforce thicket formation**. The alternative is **architecture-first**: keep stabilisers, deploy **selective suppression** (not removal), and rebuild the ground-layer matrix that makes recovery admissible.

4.11.3 Mechanism recap — why the reset damages hydrology and soil.

The **foreshore template** (low cover, disrupted litter/moss, bare sand):

- strengthens **soil-water-repellency (SWR)**,
- increases **shallow pulse capture**,
- reduces **infiltration**,
- concentrates **runoff into preferential flow**, and
- accelerates **erosion** (rainsplash, sheetwash) and **aeolian deflation** of organic fines and seedbanks.

These fines form the **biologically active surface** that sustains recruitment and prey bases. Nepean disturbance analyses show **canopy/moss down; grasses/bare/exotics up**, consistent with SWR-driven closure on exposed surfaces.
This is the same interception → SWR → bypass-flow architecture described in §§3.1–3.3 and §4.1, expressed through management behaviour rather than climate.

4.11.4 Continuity for avifauna: sequenced floristics is faunal-pathway repair.

Autochthonous bird guilds—litter/foliar insectivores, nectar/fruit users, seed/ground users—depend on:

- **layered canopies** (Moonah–She-oak–Banksia),
- **litter–moss continuity**,
- a **native herb/graminoid ground-layer**,
- and **microclimatic buffering**.

These conditions are **most intact** in south-west Victoria and **most eroded** on the MP. Removing *Rhagodia/Tetragonia* to "*tidy*" under tea-tree removes:

- food,
- cover,
- microclimate buffers, and

- soil-stabilising scaffolds.

Sequenced floristics—**rabbits → ground-layer → structural diversity → staged tea-tree reduction**—restores the **continuity** that MP avifauna track over decades.

4.11.5 Who is being lost (signals from the vegetation record).

Canopy/small-tree suppression (diagnostic failures)

- *Melaleuca lanceolata*
- *Leucopogon parviflorus*
- *Acacia uncifolia*

After disturbance events, *A. uncifolia*, *M. lanceolata*, and *Pimelea serpyllifolia* are often absent despite being diagnostic of the community.

Ground-layer collapse

- Moss carpets (e.g., *Thuidiopsis furfurosa*)
- Native herb/graminoid matrix (*Dichondra repens*, *Austrostipa flavescens*, *Wurmbea latifolia*, *Parietaria debilis*)

Loss removes **seed-safe microsites** and **invertebrate prey bases**.

Stabilisers to retain (often mis-removed)

- *Tetragonia implexicoma*
- *Rhagodia candolleana*

Retain as **functional scaffolding**; their removal **recreates the foreshore template**.

4.11.6 Re-centring She-oak within continuity.

The baseline mosaic included **Drooping She-oak (*Allocasuarina verticillata*)** on landward hind dunes and **Moonah** seaward. Co-dominance is supported by:

- pollen and floristic records (e.g., Wilsons Prom hind dunes dominated by She-oak over millennia), and

- the south-west baseline (higher native richness, greater moss/canopy cover).

This is the **continuity template** that supports avifauna and soil function. Its loss is **diagnostic of degradation on the MP**.

4.11.7 Operational rules (to protect continuity rather than aesthetics).

Do not remove (native stabilisers)

Tetragonia implexicoma (bower spinach) and Rhagodia candolleana (seaberry saltbush) must be retained under tea-tree. These are native stabilisers that trap fines, anchor litter, buffer microclimate, and provide invertebrate habitat. Removing them recreates the foreshore template.

Do not plant as "*replacements*"

• Ornamental or episodic groundcovers (e.g., bulbs) that add visual diversity but do not rebuild continuity.

• Nursery natives selected for appearance but lacking stabilisation, hydrological, or layering function.

• Introduced grasses such as *Ehrharta erecta*, *Lagurus ovatus*, *Vulpia* spp., and *Aira* spp. These grasses are almost never planted intentionally. They typically arrive via:

- contaminated tools or machinery
- mulch or soil contamination
- edge seed-rain
- bird and mammal vectors
- disturbance-activated seedbanks

None of these replacements rebuild continuity; all create exposure pulses that disturbance-aligned species exploit.

Creating bare soil or removing stabilisers provides exactly the microsites these disturbance-aligned grasses exploit. These species increase with disturbance and do not rebuild continuity.

Do plant (to restore continuity).

• Ground-layer rebuilders: *Dichondra repens*, *Austrostipa flavescens*, *Wurmbea latifolia*, *Parietaria debilis*, native herbs/sedges/graminoids; moss/litter islands where needed.

• Stabilisers (retain and augment): *Tetragonia implexicoma*, *Rhagodia candolleana*.

• Structural species: *Allocasuarina verticillata*, *Melaleuca lanceolata*, local Banksia spp., *Leucopogon parviflorus*, *Pimelea serpyllifolia* — to rebuild layering, shading, root-depth complementarity, and nutrient boundaries.

Do first (sequencing for continuity).

1. Suppress rabbits — stop constant foreshore-template reset and loss of seedlings, moss, and herbs.
2. Rebuild the ground-layer — restore moss/herb/litter continuity and microtopography to extend moisture residence and blunt SWR–runoff coupling.
3. Reintroduce structural diversity — over-seed or plant *Allocasuarina verticillata* (hind-dune lenses) with Moonah/Banksia to recover layering and nutrient boundaries.
4. Stage tea-tree reduction last — use low-disturbance methods only, avoid bare-soil pulses, and retain *Rhagodia/Tetragonia* as scaffolds during transition.

4.11.8 One sentence takeaway for policy and field teams.

Do not trade continuity for cosmetics. Removing native stabilisers and planting ornamentals replicates the foreshore template, tightens SWR-driven hydrological closure, accelerates soil loss, and silences autochthonous bird pathways; sequenced floristics is the only path back to functional continuity on calcareous dunes.

5. Operational Synthesis: From Architecture to Practice.

5.1 Cosmetic restoration and the failure of structure-blind approaches.

Most restoration undertaken on calcareous dunes fails for the same reason the collapse occurred: the underlying **architecture** remains unrepaired. Efforts are typically directed at visible vegetation—clearing shrubs, planting natives, reshaping superficial form—without re-establishing the **functional ground-layer mesh**, **hydrological openness**, or **faunal pathways** that make recruitment admissible.

In this setting, **broad or untimed clearing of *Polygala myrtifolia* and *Rhamnus alaternus* (Italian buckthorn)**, or any action that exposes bare, hydrophobic surfaces **before** constraints are repaired, simply **reopens the collapse template**:
ground-layer attrition → infiltration failure → SWR intensification → coloniser flush → recapture by *Polygala*/*Rhamnus*.

Tea-tree is typically removed **sporadically and locally**; it should be treated as **spot-clearing only**, guided by ground-layer and shading needs, not as the primary target of a restoration program.
Function, not **form**, must be restored first. Cosmetic success can coincide with architectural failure; visible vegetation change is not evidence of recovery.

5.2 Architectural metrics and forward diagnostics (EF = (D + R) + C + K).

Ecological systems do not possess resilience as a trait. A system's future capacity is determined only by the **architecture it carries**:

- **D + R** — the diversity and redundancy of admissible routes,
- **C / CT** — the constraint topology: thresholds, dependencies, feedbacks, and the conditional corridors they define,
- **K** — coherence sign:
    - **+1** = coherence (positive coupling),
    - **0** = neutral,
    - **−1** = incoherence (negative or self-cancelling coupling).

Under opposition (Ω*; realised disturbance pressure), this architecture is interrogated; the system's **verdict** under disturbance is revealed, not stored in advance.

Forward diagnostics must therefore track changes in architecture, not plant cover:

- **Ground-layer continuity and porosity**,
- **Infiltration pathways** (deep vs shallow pulse capture),
- **SWR expression** by depth,
- **Microsite redundancy** (D + R),
- **Constraint gating** (rabbit pressure, herbivory, seed predation),
- **Coherence sign (K)** of canopy–soil–ground-layer interactions.

These determine what the system *can* do next. If these indicators do not improve, no amount of planting or thinning constitutes recovery.

5.3 Monitoring design for calcareous dunes.

Monitoring must directly reflect the collapse mechanism and the architecture required for recovery.

Hydrology and soil function

- SWR class at 0–5 cm, 5–15 cm, 15–30 cm (post-rain and post-drydown).
- Mode of infiltration (proportion of shallow vs deep penetration).
- Microtopographic heterogeneity: runnels, depressions, sheltered pockets.

Ground-layer structure

- Moss/lichen continuity as % cover.
- Herbaceous richness and spatial occupancy.
- Litter depth and distribution (continuous, non-hydrophobic matrix).

Recruitment and option sets

- Seedling emergence in shaded vs exposed microsites.
- Juvenile survival under rabbit exclusion vs ambient browsing.
- Density and type diversity of recruitment microsites.
- Track **post-suppression microsite integrity** (treated vs untreated sub-patches) to confirm **no loss of ground-layer continuity** after chemical treatments

Constraint topology (C)

- Rabbit pressure index (pellet counts, warren density, tracklines).
- Seasonal herbivory on Banksia, Moonah, and Sheoak juveniles.
- Evidence for disturbance-driven synchrony (coloniser flush sequences).

Coherence sign (K)

- Canopy litter effects (hydrophobicity, shading, protection).
- Coupling of canopy interception with ground-layer retention.

- Net effect on microsite diversity (widening or narrowing D + R).

Restoration programs must report trajectories in these architectural metrics.

5.4 Constraint-first implementation(Order Is Non-Negotiable).

(rabbits → ground-layer → structure → *Polygala*/*Rhamnus*; tea-tree last and local),

1. Rabbit suppression
Constraint release must precede all other interventions. Suppress rabbits first to reopen juvenile corridors and prevent ongoing attrition of the ground-layer.

2. Ground-layer reconstruction,
Rebuild continuity, porosity, shading, and seed-safe microsites **without exposing bare soil**. Actions include:

- **Retain/augment stabilisers** (*Rhagodia candolleana*, *Tetragonia implexicoma*).
- **Microtopographic enrichment** and **litter continuity** to slow surface drying.
- **Re-establish moss/herb matrices** to restore infiltration buffers and prey bases.
- **Use selective, least-disturbance herbicides** only where needed to control disturbance-aligned herbs/forbs—**no scraping, grubbing, or scalping** at this stage.

3. Structural diversity reintroduction,
Reintroduce or encourage **Banksia, Moonah, Sheoak** as **functional strata**, restoring:

- depth-partitioned rooting,
- moderated near-surface microclimate and wind attenuation,
- **actinorhizal nitrogen boundaries** (Sheoak),
- layered infiltration buffering and microsite redundancy.

4. Selective suppression of *Polygala myrtifolia* and *Rhamnus alaternus*,
Once (1)–(3) are in place, **selectively suppress targets *in situ*** with **low-disturbance herbicide** to:

- **retain shade and litter** (avoid bare-ground pulses),
- **neutralise seed input**,
- **prevent synchronised recruitment** (seedbank/propagule waves),
- **preserve the recovering ground-layer matrix**.

Terminology note (for contractors and field teams):

- **Selective suppression** = **in-situ herbicide treatment** that kills the target while **retaining** shade, litter, and ground-layer structure.
- **Removal** = **physical extraction** (pulling, grubbing, scraping) that **exposes** hydrophobic sand and **resets** seedbanks.
  On calcareous dunes, **use suppression**, not removal—until late, localised phases where architecture is proven stable and exposure risks are minimal.

Tea-tree work remains **sporadic and local**: **spot-clear** only where it demonstrably obstructs ground-layer recovery or creates problematic shading. It is **not** a primary program target.

Order is non-negotiable. Beginning with physical "*weed removal*" (pulling, scraping, grubbing) on calcareous sands **reinstates** the collapse template by exposing hydrophobic surfaces, intensifying SWR, and inviting coloniser flush.

5.5 Global restoration practice and why it fails (Lithgow et al., 2013).

A global review of dune restoration studies (Lithgow et al., 2013) shows that most projects focus on **structural vegetation metrics**—cover, richness, early growth—while rarely measuring:

- hydrological function,
- nutrient or microbial processes,
- succession,
- constraint dynamics,
- or long-term system behaviour.

Lithgow et al. found:

- **>80%** of projects measured only species composition or cover,
- **<25%** examined ecological processes,
- **~13%** assessed longer-term system behaviour or natural regeneration.

This global pattern mirrors the failures seen on calcareous dunes:
restoration is overwhelmingly **cosmetic**, not architectural.

Your architecture-first sequence corrects this by re-establishing:

- infiltration pathways,
- microsite redundancy,
- constraint topology,
- ground-layer matrices,
- and coherence (K),

before any visible reshaping or large-scale shrub work.

5.6 Policy and program implications (architecture as compliance).

A credible restoration program must encode architectural logic into procurement, monitoring, and audit requirements.

Required reporting metrics

- SWR trajectories at multiple depths,
- Ground-layer structural continuity,
- Rabbit pressure indices and suppression efficacy,
- Microsite diversity and juvenile survival,
- Canopy–soil coherence indicators (K).

Required sequencing in contracts

- No shrub work before rabbit suppression.
- **No bare-ground resets** (no scalping, scraping, mass uprooting).
- **Selective suppression** (low-disturbance herbicide) of ***Polygala*/*Rhamnus*** only **after** constraints are repaired and the ground-layer has measurably thickened.
- **Tea-tree** limited to **spot-clearing** driven by ground-layer needs (evidence-based, site-specific).

Audit-ready architecture tests (post-treatment)

- **SWR trajectory** (0–5, 5–15, 15–30 cm) shows no post-works spike and a downward trend over seasons.
- **Ground-layer continuity** maintained or improved after suppression (no loss of moss/herb/litter coverage).
- **No synchronised coloniser flush** in newly treated sub-patches (verify through seasonal emergence checks).
- **Juvenile survival** of Banksia/Moonah/Sheoak increases under ambient conditions (no net decline versus pre-works).

These requirements convert architecture into practice and replace cosmetic vegetation management with **functionally reconstructive restoration.**

6. Conclusion.

Diagnosis.

Tea-tree thicket formation on the calcareous dunes of the southern Mornington Peninsula represents a structural–hydrological collapse driven primarily by sustained **rabbit-grazing**, then locked in by **hydrological closure**. Chronic herbivory removes grasses, herbs, and juvenile strata, collapsing the **ground-layer** and narrowing recruitment corridors. As tea-tree infills the vacuum, **canopy interception** increases, litter becomes hydrophobic, **soil-water-repellency (SWR)** expresses more strongly, and **shallow near-surface pulse capture** replaces deep infiltration. The result is a functionally drier, **low-option** architecture that continually selects for itself (Crockford & Richardson, 2000; Doerr, Shakesby & Walsh, 2000; Mutze et al., 2016).

This is not a historical norm: it is a **post-disturbance replacement architecture** (Mornington Peninsula Thematic History, 2013; Moxham & Turner, 2009).

Historical mechanism.

Early 20th-century Nepean accounts describe the operational sequence that manufactured the modern degraded state on lime-rich, SWR-sensitive sands: **fell and stack the scrub → burn to ash on a hot northerly day → sow seed onto the still-hot ground and embers → fence → repeat burns** (Leader, 16 Nov 1912).

These actions created the same **bare, litter-poor, SWR-tight, low-infiltration** surfaces that contemporary disturbance and grazing reproduce. Tea-tree dominance is therefore **not** the initiating cause but a **symptom and maintainer** of an engineered, **rabbit-amplified** failure state.

Baseline and contrast.

The **pre-collapse** baseline was a **Sheoak–Moonah–Banksia** mosaic with a moss/herb ground-layer that provided:

1. **depth-partitioned** rooting,
2. **actinorhizal nitrogen boundaries** on nutrient-poor sands, and
3. **porous, buffered infiltration pathways** (Moxham, Sinclair, Walker & Douglas, 2009).
   In south-west Victoria, this architecture persists—**intact moss continuity, higher native richness, layered canopies**—demonstrating the porous, drought-buffered structure that once prevailed on the Mornington Peninsula before lime burning, clearing, and rabbit irruptions dismantled it (Moxham & Turner, 2009).
   Within this mosaic, ***Rhagodia candolleana*** and ***Tetragonia implexicoma*** are **native stabilisers, not weeds**. Their removal recreates **foreshore-like** bare surfaces, accelerating SWR and favouring thicket re-establishment.

Climate-change interaction.
Projected warming, drier cool seasons, more intense short-duration rainfall, and longer fire seasons **multiply the same pathways** that produced collapse:

- intensified SWR and reduced moisture residence;
- higher preferential flow and episodic erosion;
- compressed post-fire recovery windows that favour disturbance-aligned shrubs.

On calcareous dunes, these shifts are not additive but **multiplicative**: warmer, drier intervals deepen hydrophobic layers; intense rainfall increases runoff concentration and loss of fines on exposed surfaces; longer fire seasons extend the period in which **bare-surface recruitment filters** re-activate. The climate signal therefore **deepens architectural vulnerabilities already present**, pushing degraded remnants toward **low-option** architecture faster than repair can keep pace.

Management corollary — repair constraints before exposure; act with selective suppression, not removal.
Restoration on calcareous dunes succeeds only when the collapse mechanism is **reversed architecturally**, not cosmetically. The **constraint-first** sequence (final order) is:

1. **Immediate rabbit control** to reopen recruitment corridors and halt **ground-layer** attrition.
2. **Apply selective suppression—not physical removal—of *Polygala myrtifolia* and *Rhamnus alaternus*.** Suppress **in situ** with **low-disturbance** herbicide so targets die without exposing sand; retain shade and litter, avoid exposure pulses, and prevent seedbank synchrony.
3. **Retain native stabilisers** (*Tetragonia*, *Rhagodia*) as functional scaffolding while constraints are repaired. Do not "*tidy*" them out.
4. **Reintroduce structural diversity**—**Sheoak** (hind-dune lenses) paired with Moonah/Banksia—to restore layering, rooting-depth complementarity, shade, wind attenuation, and the **actinorhizal nitrogen boundary**.
5. **Rebuild the ground-layer**—restore moss/herb/litter continuity and microtopography to extend moisture residence, widen microsites, and blunt **SWR–runoff** coupling.
6. **Tea-tree is last and local**—only then, and only as targeted **spot-work**, apply **low-disturbance** treatment where tea-tree directly obstructs ground-layer formation or shading balance; avoid bare-soil pulses, weed surges, and **re-imposition** of the foreshore template.

This sequencing is not optional. It is the **inverse of the 1912 collapse template**. It restores the architecture within which **deep infiltration, fines retention, and diverse recruitment** become admissible again.

EF framing (interpretive).
Under **Evolutionary Flexibility (EF)**, tea-tree thicket is a **negative K**, **low-option verdict disclosed** under sustained opposition (Ω) from rabbits and disturbance. Recovery is achieved by rebuilding **(D + R)**, reopening constraints **(C/CT)**, and restoring positive coherence **(K)** so that the system carries **latent options forward** rather than collapsing into a single shrub pathway. [**Optional softener:** *EF here is an interpretive scaffold; it does not add mechanisms beyond those demonstrated above.*]

Immediate priority.
With only ≈ 10% of **pre-European** CMW remaining, much of it degraded, the system sits near temporal limits. **Delay** increases the probability of **irreversible routing** into weed-dominated, **low-option** architectures. Under a hotter, drier, more extreme climate, **urgent rabbit control + selective suppression (low-disturbance, in situ)** are essential to preserve the last viable pathways back to a **layered, porous, infiltration-open woodland**.
The future of CMW on the Mornington Peninsula now depends on acting before remaining option sets disappear; architecture can be rebuilt, but only if opposition is first removed and continuity restored.

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Appendix A. EF Alignment (Evolutionary Flexibility Framework).

EF summary

Evolutionary Flexibility (EF) formalises persistence as **EF = (D + R) + C + K**, where **D** (diversity) and **R** (redundancy) provide latent options; **C** (contingency) is the constraint architecture that determines which options remain open when opposition acts; and **K** (coherence, signed) captures whether internal couplings buffer ($K \geq 0$) or amplify ($K < 0$) fragility. In EF, opposition (Ω/Ω^*) "*opens the box*," revealing the verdict of the hidden architecture. **CT** (Constraint Topology) and **FL** (Fragility Landscape) denote, respectively, the conditional corridors and fragility gates through which outcomes are routed. In this study's case (tea-tree thicket formation), rabbit pressure (Ω) discloses a low-option, negative-K assembly via high interception, SWR-driven infiltration loss, shallow pulse capture, and ground-layer collapse (Crockford & Richardson, 2000; Doerr et al., 2000; Keim et al., 2006; Nilsen et al., 1999; Mutze et al., 2016).

A.1 — D + R (Diversity and Redundancy): Options that keep corridors open

Pre-rabbit coastal woodlands were open, grassy systems with a layered tree–shrub mosaic that included Drooping Sheoak (*Allocasuarina/Casuarina*), Coast Banksia, Moonah, and a diverse ground-layer (grasses, herbs, sedges). This delivered vertical and functional redundancy in rooting depth, canopy architecture, and soil building processes—i.e., multiple routes for infiltration, storage, and recruitment (Moxham et al., 2009; Moxham et al., 2010). Functional roles contributed by Sheoaks included actinorhizal nitrogen fixation and landscape stabilisation, indirectly supporting soil fertility and hydraulic stability at dune and riparian interfaces—options that buffered stress and kept corridors open under variable conditions (DAFF, 2019). After rabbit arrival, multi-layer redundancy collapsed: Sheoaks and Banksias failed to recruit; the ground-layer was removed; a shallow-rooted coloniser (tea-tree) dominated the upper profile. The option set shrank from many routes to few—an EF reduction of (D + R) (*The Leader*, 1912; see §4.2).

A.2 — C (Contingency): The conditional architecture that decides what matters when Ω arrives

Constraint release explains inland tea-tree proliferation: clearing and altered fire regimes created foredune-like recruitment surfaces; rabbits removed biological filters; and the resulting microclimate, litter bed, and recruitment thresholds re-architected constraints in favour of tea-tree. In other words, C changed—light, moisture routing, and recruitment thresholds shifted—determining which latent options remained viable once Ω acted (Weber, 2003; Lam & van Etten, 2002).

A.3 — K (Coherence, signed): Whether internal couplings buffer or amplify fragility

Tea-tree thickets express a negative K configuration:
• High interception reduces rain to soil inputs (Crockford & Richardson, 2000; Keim et al., 2006).
• Hydrophobic litter restricts wetting fronts and concentrates preferential flow (Doerr et al., 2000; Siteur et al., 2016).
• Shallow roots pre-empt near-surface pulses, repartitioning pulse water (Lam, 2002; Groom, 2000).
• Ground-layer loss eliminates porosity, microbial activity, and moisture-holding matrices (Nilsen et al., 1999; Weber, 2003).

Restoration targets a shift in K from negative to buffering: relighting the floor (targeted thinning), reinstating ground-layer matrices, and reintroducing deep-rooted functional types that reopen subsurface routes (Lam & van Etten, 2002; Roper et al., 2015).

A.4 — Ω / Ω (Opposition): The opener that reveals the verdict*

Ω denotes realised opposition; Ω* denotes activated opposition under disturbance.
In this system, Ω is rabbit-grazing (with fire/clearing as additional openers). When redundancy is thin and K is negative, even modest Ω discloses collapse (thicket formation).
Landscape-scale work shows vegetation structure and dune stability tracking rabbit abundance and control history—i.e., Ω magnitudes correlate with the ecological verdict disclosed (Mutze et al., 2016; Moulton et al., 2020).

A.5 — CT / FL (Constraint Topology & Fragility Landscape): Routes and gates

• CT (conditional corridors) are redrawn by the five mechanisms: interception narrows the rain-to-soil corridor; SWR constricts infiltrability and promotes preferential flow; shallow roots pre-empt near-surface pulses; ground-layer removal erases biogenic pore networks. The corridor network thins until most routes dead-end (Crockford & Richardson, 2000; Doerr et al., 2000; Keim et al., 2006).

• FL (fragility gates) emerge where small shocks have outsized effects: water-repellent lenses and bare sandy patches convert rainfall to runoff; shaded floors and capsule pulses create recruitment gates that favour colonisers; local failures aggregate to system-scale dysfunction (Doerr et al., 2000; Siteur et al., 2016).

A.6 — Restoration as EF repair: Rebuild architecture before removing the incumbent

EF-consistent sequence (including *Polygala* priority):

1. Reduce Ω (rabbits) (Mutze et al., 2016; Cooke, 2012).
2. Front-load *Polygala myrtifolia* suppression (Roberts et al., 2023; Weeds Australia, n.d.).
3. Targeted tea-tree thinning via small corridors/patches after rabbit control and Polygala suppression are active (Lam & van Etten, 2002; Lin et al., 2006).
4. Immediate ground-layer rebuild with micro-wetting on water-repellent sands (Roper et al., 2015; Roberts et al., 2023).
5. Reintroduce structural diversity (Moonah, Banksia, Sheoaks) (Moxham et al., 2009; DAFF, 2019).
6. Phase further tea-tree reduction once corridors thicken and native recruitment is sustained (Lam & van Etten, 2002; *Victorian Naturalist*, 2013).

A.7 — Diagnostic value (how to use EF in practice)

• **Name the verdict, not the hope:** resilience is a past-tense descriptor applied *after* opposition (Ω); **before Ω acts, the task is architectural diagnosis and design—options (D + R), constraints/constraint topology (C/CT), and routing—expressed here using EF/CT/FL terminology.**

• Map corridors and gates: prioritise microsites where small interventions reopen routes (Doerr et al., 2000; Lin et al., 2006).

• Measure options, not just states: track ground-layer cover/porosity, functional group recruitment, rooting-depth diversity (Moxham & Turner, 2011; Moxham et al., 2010).

• Sequence to thicken routes: pair risky steps (e.g., thinning) with guard actions (*Polygala* suppression, immediate ground-layer work, rabbit control) (Roberts et al., 2023; Weeds Australia, n.d.).

• Track Sheoak recruitment as a leading indicator that (D + R) and K are shifting toward buffering; rising Sheoak survival generally accompanies declining SWR expression at

the surface (DAFF, 2019; Roper et al., 2015).

• Check nodulation on Year 1/2 plantings; where nodulation is absent on ultra-oligotrophic sands, revisit microsite P in future planting pulses to enable early fixation (Sanginga et al., 1989; Nguyen & Pawlowski, 2017).

A.8 – Sheoak Actinorhizal Nitrogen Fixation (Mechanism & Role)

Symbiosis. Sheoaks are actinorhizal nitrogen-fixing trees that host *Frankia* in cortical root nodules; *Frankia* reduces atmospheric N_2 to ammonium transferred to the host. Reported fixation rates in Casuarinaceae can be comparable to legumes under favourable P conditions (Nguyen & Pawlowski, 2017; Obertello et al., 2020; Sanginga et al., 1989).

Why it matters on calcareous, SWR-prone sands.
• Biogenic porosity & infiltration: stable pore networks improve infiltration and gas exchange in the top 10–20 cm (DAFF, 2019).
• N boundary condition (constraint setting): actinorhizal inputs stabilise nitrogen limitation and support microbial processes that maintain surface structure and admissible recruitment corridors (Nguyen & Pawlowski, 2017; Obertello et al., 2020).
• Depth-partitioned routing: Sheoaks thicken the vertical option set and reduce pulse monopolisation by shallow functional types (Moxham et al., 2009; DAFF, 2019).

Couplings and limits (staging for restoration).
• P dependence: extremely low P can constrain nodulation; consider microsite amendments without broad nutrient loading (Sanginga et al., 1989; DAFF, 2019).
• Browsing sensitivity: rabbit suppression and guards/enclosures are prerequisites for recruitment (Mutze et al., 2016; Moulton et al., 2020).

Operational note. Place Sheoak reintroductions after rabbit control, *Polygala* suppression, and the start of ground-layer rebuilding, positioning Sheoaks to stabilise porosity and nutrient boundary conditions while tea-tree is phased down (DAFF, 2019; Roper et al., 2015; Roberts et al., 2023).

Appendix B. Fire Response Trends in Coastal Moonah Woodland (Compressed Matrix).

Notes: Trends summarise CMW patterns on calcareous, SWR-prone sands. Response varies with fire interval, severity, and post-fire grazing/weed pressure. Interpret with site context. Where rabbits and disturbance-aligned shrubs persist, repair constraints (rabbit suppression, Polygala containment, ground-layer rebuild) **before** any biomass reduction. (Roper et al., 2015; Doerr et al., 2000).

Functional group / species	Typical trend after fire	Mechanism link (short)	Key sources
Moonah (*Melaleuca lanceolata*)	Declines / slow recovery	Recruitment depends on intact microsites; weed/rabbit pressure suppresses seedlings	Moxham & Turner, 2011; Moxham et al., 2010
Coast Wirilda (*Acacia uncifolia*)	Declines	Seedlings vulnerable on repellent sands under grazing	Moxham et al., 2010; Roper et al., 2015
Drooping Sheoak (*Allocasuarina verticillata*)	Declines (variable)	Browsing + low-N sands; loss removes actinorhizal constraint + depth partitioning	DAFF, 2019; Moxham et al., 2009
Ground-layer (grasses/herbs/moss/biocrust)	Declines	SWR intensifies; porosity/microbial loss reduces infiltration and retention	Doerr et al., 2000; Siteur et al., 2016
Coast tea-tree (*Gaudium laevigatum*)	Often increases (recruitment pulse)	Bare, sunlit microsites favour coloniser strategy; later closure suppresses ground-layer	Lam & van Etten, 2002; Weber, 2003
Banksia integrifolia	Often declines with short intervals	Interval-sensitive recruitment on repellent sands	Weber, 2003; Roper et al., 2015
Polygala myrtifolia	Strong increase	Persistent seedbank + high germination on exposed surfaces	Roberts et al., 2023; Weeds Australia (n.d.)

Ehrharta erecta	Increase	Disturbance coloniser capturing bare, repellent microsites	Weber, 2003; Roper et al., 2015
Lycium ferocissimum / *Rubus fruticosus* agg.	Increase (edges, corridors)	Bird-dispersed; thrives in lit disturbed edges	Weber, 2003

Reading the matrix: "*Declines*/*Increase*" refers to typical short- to medium-term patterns in CMW on calcareous sands. Where rabbits and *Polygala* are contained and the ground-layer is rebuilt, native recruitment can recover; otherwise colonisers dominate and re-lock the low-option architecture (Moxham et al., 2010; Roper et al., 2015).

Appendix C. Cross-System Convergence: Italian Buckthorn as a Symptom of Constraint Collapse.

Opening note (tone/positioning).
Italian buckthorn is examined here as a **structurally convergent response to constraint collapse**, not as an independent invasive driver with unique ecological effects. This appendix offers a brief comparative note showing how the architectural logic described for inland tea-tree dominance also manifests in other degraded coastal and peri-urban systems. Italian buckthorn (*Rhamnus alaternus*) is used **not** as an additional focal species, but as a **diagnostic analogue**: shrub monocultures commonly arise from **constraint failure**, not exceptional species-level aggressiveness.

C.1 Architectural lineage and latent pioneer logic.

Italian buckthorn behaves as a system-dominating shrub **when** constraints fail, because it expresses the **latent architecture of a disturbance-adapted lineage** under collapsed filtering. In intact ecosystems, pioneer-leaning tendencies are **constrained** by canopy structure, ground-layer continuity, browsing pressure, and disturbance regimes; **when those constraints fail, the underlying architecture is disclosed and dominance follows**. *(Scope note: this context does not require species-specific nitrogen symbiosis claims; buckthorn is treated here through structural filters rather than lineage mechanisms.)*

C.2 Trait expression under constraint failure.

Under degraded conditions, buckthorn expresses traits that are adaptive in disturbed systems and destabilising once dominance is achieved:

- rapid establishment on nutrient-poor soils;

- evergreen canopy that suppresses recruitment pulses;
- shade tolerance enabling **self-closure**;
- bird-dispersed propagules sustaining **propagule pressure**;
- high root allocation capturing water and nutrients in simplified surface profiles.

C.3 System-level failure and selector breakdown.
Buckthorn proliferates where **selector logic** is disrupted, including:

- loss of browsing gates;
- rabbit-driven suppression of native recruitment pathways;
- inappropriate disturbance regimes;
- canopy fragmentation increasing recruitment windows;
- nutrient enrichment associated with disturbance.

C.4 Positive feedbacks and monoculture lock-in.
Once established, buckthorn generates reinforcing feedbacks: dense shade suppresses seedlings, evergreen litter alters near-surface moisture/chemistry, and dispersal maintains pressure. **This mirrors inland tea-tree dominance:** monoculture emerges **because** the constraints required to maintain dynamic balance are absent.

C.5 Implications for interpretation and management.
Buckthorn **reinforces the central argument**: shrub monocultures arise from **constraint collapse**, not intrinsic species properties. Durable recovery depends on **restoring constraint networks** so pioneer dominance is no longer favoured; buckthorn then **declines as a consequence of architectural repair**, not simply repeated removal.

C.6 Constraint-preserving treatment as a prerequisite for autochthonous recruitment (M.O.L.D. application).
Field application supports that buckthorn must be **actively treated** to achieve recruitment and recovery of autochthonous species. In multiple coastal and peri-urban sites, buckthorn was **selectively treated in situ** using the M.O.L.D. framework—**neutralising canopy**

suppression while retaining standing biomass to preserve microsite architecture and prevent **bare-surface recruitment windows** that favour secondary invasion. These outcomes indicate that the incumbent must be **neutralised in a constraint-preserving manner**; treatment is a **necessary enabling step**, not the primary driver of recovery.

Closing tweak.
The emergence of buckthorn dominance **reinforces** this study's central finding: **once constraint architecture is lost, selection favours architectures aligned with exposure, rapid capture, and corridor closure—regardless of species origin**.

C.7 Mini-Matrix — *Rhamnus alaternus* (Italian buckthorn) as a diagnostic of constraint collapse

Dimension	Before constraints fail (intact architecture)	After constraints fail (constraint-collapse, foreshore-template operating mode)	Constraint-preserving management (sequenced)	Diagnostic signals to track
Filters & corridors (CT)	Browsing gates, layered canopy (Moonah–Sheoak–Banksia), and a continuous ground-layer keep recruitment corridors **narrow and specific**; microsites are **shaded, humic, seed-safe**.	Browsing gates lost (rabbit-grazing), canopy fragmentation, and ground-layer collapse **widen recruitment windows**; **bare, sunlit, water-repellent** surfaces favour buckthorn establishment.	**1) Suppress rabbits** to re-close juvenile corridors; **2) retain/augment stabilisers** (*Tetragonia*, *Rhagodia*) to rebuild microsite continuity; **3) selective, in-situ buckthorn suppression** (low-disturbance) to neutralise seed rain without exposure pulses; **4) rebuild ground-layer**, then reintroduce structural diversity.	Return of **moss/litter continuity**, decline in **bare-ground %**, reduced **synchronised emergence** beneath treated canopies; **juvenile survival** of autochthonous species increases without caging.
Hydrology (SWR & routing)	Near-surface buffering from litter/moss and biogenic porosity supports **matrix infiltration**; **SWR expression muted**; shallow pulses dissipate into depth-partitioned profiles.	Hydrophobic surface layers, **preferential flow**, high **runoff**; short moisture residence; repeated **exposure pulses** reset recruitment filters and favour evergreen shrub capture.	Keep shade/litter in place during treatment (**no bare-soil creation**). If needed, **micro-wetting / SWR amelioration** in small patches after in-situ suppression to protect reforming ground-layer.	**SWR class by depth** (0–5, 5–15, 15–30 cm) trending down; **shallow : deep infiltration ratio** improves; **sheetflow/rilling** observations decline.
Propagule pressure	Bird-dispersed arrival occurs, but **unsuitable microsites** + browsing prevent build-up.	**Edge/urban matrices** supply constant seed rain; suitable exposed microsites → **rapid establishment** and local seed input → self-reinforcement.	**Contain seed sources first** (selective in-situ suppression of fruiting adults), then **reduce edges**/light corridors; maintain **stabiliser cover** to deny surface recruitment.	Falling **seedling density** in treated sub-patches; **asynchronous trickle** (not pulses) during follow-up.
Feedbacks (K, signed)	Positive coherence (**K ≥ 0**): layering, stabilisers, and browsing gates integrate; redundancy is	Negative coherence (**K < 0**): evergreen shade + litter, exposure-driven microsites, and high seed rain **synchronise**;	Actions that **shift K toward buffering**: restore layering (Sheoak/Moonah/Banksia), thicken ground-layer, hold shade/litter while neutralising buckthorn **in situ**.	**Coherence probes**: does added shade/litter now **increase** (not decrease) microsite diversity? Are **D + R** (options) rising in the juvenile layer?

	usable, failures localise.	redundancy strands; monoculture **lock-in**.		
Outcome expectation	Buckthorn arrival **fails to dominate**; autochthonous cohorts re-enter; shrub balance remains dynamic.	Buckthorn **captures and holds** sites; other shrubs follow; ground-layer stays thin; faunal pathways quieten.	**Constraint-first, structure-last** sequence prevents re-locking; buckthorn **declines as a consequence** of architectural repair, not repeated exposure-heavy removals.	**No post-treatment coloniser flush**, improving **juvenile mix** of Moonah/Sheoak/Banksia; **faunal guild use** responds to re-layering.

Usage note. Treat this matrix as **diagnostic**, not predictive. It shows how buckthorn signals **constraint architecture**—and how **constraint-preserving suppression** plus sequenced floristics prevent re-locking while autochthonous recruitment re-enters.

Appendix D. Cross-System Convergence: *Polygala myrtifolia* as a Surface-Exploiting Symptom of Constraint Collapse.

Opening tweak (tone/positioning).
Polygala myrtifolia is treated here as a **surface-exploiting coloniser** that expresses dominance **only after** constraint architecture has collapsed, rather than as a primary cause of degradation. This appendix provides a **diagnostic note** illustrating how non-native shrubs with disturbance-adapted architectures **converge functionally** with native colonisers (e.g., inland tea-tree) under constraint failure. *P. myrtifolia* is included as a **confirmatory analogue**: dominance emerges from **architectural opportunity**, not intrinsic "*invasiveness*."

D.1 Latent coloniser architecture and disturbance alignment.

P. myrtifolia dominates because it is aligned with **surface disturbance, high light, and simplified surface architecture**. Its success reflects a **match between recruitment biology and altered constraint topology**, not broad competitiveness across intact ecosystems. Traits become decisive when **ground-layer buffering, browsing gates, and soil-surface stability are lost**.

D.2 Trait expression under simplified constraint regimes.

Under constraint thinning, *P. myrtifolia* expresses:

- **high germination** across broad conditions;
- **surface-biased emergence**;
- **persistent multi-year seedbank**;
- **rapid juvenile growth** and **canopy closure**;

- **shade tolerance** that suppresses ground-layer recovery.

D.3 Constraint collapse and selector misalignment.
P. myrtifolia proliferates where selector logic shifts toward **surface capture**, including:

- **rabbit pressure** removing native ground-layer pathways;
- **disturbance events** creating exposed microsites;
- **loss of dense ground-layer cover**;
- **canopy fragmentation** increasing light at the soil surface.

D.4 Positive feedbacks and surface lock-in dynamics.
Once established, *P. myrtifolia* reinforces dominance via **shade**, **litter obstruction**, **seedbank persistence**, and **ongoing ground-layer suppression**, **locking the system into a surface-dominated, low-option architecture**.

D.5 Interpretive and management implications.
P. myrtifolia dominance **signals surface-constraint failure**; removal alone often worsens the problem by **creating new recruitment surfaces**. Management requires **constraint restoration concurrent with suppression**: **rabbit reduction**, **immediate ground-layer rebuild**, **avoidance of bare soil**, and **suppression aligned with seedbank longevity**. Under repaired constraints, *P. myrtifolia* **loses its advantage**.

D.6 Surface constraint-preserving treatment as a prerequisite for native recruitment (M.O.L.D. application).
P. myrtifolia must be **actively treated** to enable recruitment and recovery of autochthonous species. **In-situ** treatment under the M.O.L.D. framework **retains plants during decline** to prevent soil exposure and preserve microsite buffering **while eliminating seed input and canopy suppression**. Where treatment was absent, restored constraints were **insufficient** to overcome seedbank pressure; where treatment preserved architecture, **native recruitment occurred into stabilised microsites** rather than being displaced by renewed emergence. **Treatment is therefore a precondition** enabling constraint restoration to function.

Closing tweak.
Under this interpretation, Polygala dominance reflects the same **exposure-driven recruitment logic** observed in tea-tree thickets and post-fire systems—**indicating constraint failure rather than species-specific pathology**.

D.7 Mini-Matrix — *Polygala myrtifolia* (diagnostic of surface-constraint failure).

Dimension	Before constraints fail (intact architecture)	After constraints fail (surface-exploiting mode)	Constraint-preserving management (sequenced)	Diagnostic signals to track
Filters & corridors (CT)	Browsing gates, layered canopy, and continuous ground-layer keep **microsites shaded, humic, seed-safe**; surface windows are **rare/brief**.	Gates removed (rabbits), canopy fragmentation, ground-layer loss produce **bare, sunlit, water-repellent** surfaces with **frequent pulses**.	**1) Suppress rabbits**; **2) retain/augment stabilisers** (*Tetragonia*, *Rhagodia*); **3) selective, in-situ Polygala suppression** (no exposure pulses); **4) rebuild ground-layer**; **5) restore structural layering**.	**Reduced bare-ground %**, **return of moss/litter continuity**, **asynchronous** (not pulsed) emergence in treated sub-patches; rising **juvenile mix** of Moonah/Sheoak/Banksia.
Hydrology (SWR & routing)	**Matrix infiltration** with near-surface buffering; **SWR muted** by litter/moss; shallow pulses bleed into depth-partitioned profiles.	**SWR-tight** surfaces; **preferential flow**, high **runoff**; short moisture residence; **exposure events** reset filters and favour *Polygala*.	Keep **shade/litter** during suppression; apply **micro-wetting/SWR amelioration** in small patches **after** in-situ kills to protect reforming ground-layer.	**SWR class by depth** trending down; **shallow:deep** infiltration ratio improves; **rilling/sheetflow** notes decline.
Propagule pressure	Arrival occurs, but unsuitable microsites + browsing prevent build-up.	**Persistent seedbank** + constant edge seed rain → **synchronised flushes** on exposed surfaces.	**Neutralise seed sources first** (selective in-situ on fruiting adults); deny surface recruitment with continuous **stabiliser cover**.	Seedling density beneath treated canopies **falls**; emergence becomes **trickle/trackable**, not pulses.
Feedbacks (K, signed)	**K ≥ 0**: layering + stabilisers integrate; redundancy usable; failures localise.	**K < 0**: evergreen shade + litter obstruction + surface microsites **synchronise**; redundancy strands; **lock-in**.	Actions that **shift K toward buffering**: rebuild ground-layer, re-layer canopy, hold shade/litter while neutralising *Polygala* **in situ**.	**Coherence probes**: does shade/litter now **increase** microsite diversity? Are **D + R** (options) rising in juveniles?
Outcome expectation	*Polygala* **fails to dominate**; autochthonous cohorts re-enter; shrub balance remains dynamic.	*Polygala* **captures and holds** gaps; ground-layer stays thin; seedbank re-primes after disturbance.	**Constraint-first, structure-last** sequence prevents re-locking; *Polygala* declines **as a consequence** of architectural repair, not repeated exposure-heavy removals.	**No coloniser flush** post-treatment; improving **juvenile survival** without cages; **faunal use** rises with re-layering.

Usage note. Treat this matrix as **diagnostic**, not predictive. It shows how *Polygala* signals **surface-constraint architecture**—and how **constraint-preserving suppression** plus sequenced floristics prevent re-locking while native recruitment re-enters.

Appendix E. Restoration as Constraint Architecture Recovery under Conditional Survival.

E.1 Purpose and scope.

This appendix formalises restoration logic implied by EF–CT–FL. Because persistence is disclosed only when opposition (Ω) acts on latent architecture, restoration cannot be defined as re-assembling historical species compositions. Restoration is concerned with **re-establishing constraint architecture** that keeps admissible routes open when disturbance occurs. Vegetation classifications describe outcomes observed while constraints were intact; they do not specify the constraints themselves. **Restoration targets architecture, not states.**

E.2 Outcomes versus constraints (a necessary distinction).

Outcome states: observed assemblages and structures expressed under a particular historical configuration of constraints.
Constraint architecture: positioned thresholds, dependencies, gates, and routing rules (CT), together with coherence (K), that determine which pathways remain admissible when opposition acts.
In EF terms, outcomes are verdicts; **architecture is what is carried forward prior to testing**.

E.3 Why composition-based restoration fails under constraint collapse.

When constraint architecture has collapsed (e.g., chronic grazing, surface destabilisation, hydrological rerouting), reintroducing species **alone** does not restore persistence. Species fail not because they are "*out-competed*," but because required corridors are no longer admissible under prevailing CT and K. Two failure modes follow:

1. **Silent attrition:** individuals persist briefly, then fail when opposition acts because corridors close sequentially.
2. **Maintenance dependence:** persistence occurs only through continuous external intervention, indicating CT and K remain misaligned.
   In both cases, the eliminative verdict is **architectural**, not competitive.

E.4 Constraint architecture as an evolutionary product.

Constraint architecture is retained through evolutionary filtering. In pre-collapse Coastal Moonah systems, pathways produced an architecture in which surface stability limited exposure-driven recruitment; vertical routing distributed water access; nutrient boundary conditions prevented single-axis selection; browsing pressure functioned as a selector gate rather than a continuous interaction. When constraints were removed, selection shifted toward architectures aligned with exposed surfaces, shallow routing, and rapid closure—**regardless of species origin or nativeness**.

E.5 Eliminative filtering, not competition.
Competition is not treated as a causal mechanism. What is labelled "*competition*" is the **post-hoc label** applied to eliminative filtering after disturbance closes access to essential pathways. Selection operates by closing corridors, synchronising gates, stranding redundancy, and driving viable routes to zero. Restoration does not aim to improve competitive balance; it aims to **prevent eliminative collapse** by restoring admissible routing under Ω.

E.6 What must be restored (architectural targets).
Restoration targets the re-expression of constraint classes, including:

1. **Biotic selector gates** (grazing positioned as a gate, not a constant force)
2. **Surface admissibility constraints** (preventing exposed microsites from default recruitment corridors)
3. **Structural routing constraints** (layering and interception positioning thresholds)
4. **Resource boundary constraints** (preventing nitrogen or water pulses from becoming dominant selectors)
   These constraints operate jointly; repairing one while leaving others collapsed does not restore admissibility.

E.7 Intervention logic under conditional survival.
Intervention is required when incumbent structures actively block corridors. Dominant shrubs may need **neutralisation without collapsing remaining constraints**, but neutralisation must preserve surface and structural architecture or new fragility gates are created. This explains why low-disturbance, in-situ suppression can succeed: it removes corridor blockage **without collapsing the constraints required for admissible recruitment**.

E.8 Relationship to EF, CT, and FL.
EF specifies latent architecture carried forward. CT maps admissible corridors and gates. FL identifies where collapse initiates under Ω. Restoration under EF–CT–FL is therefore:

> **the deliberate re-establishment of constraint topology and coherence such that at least one admissible route remains open when opposition acts.**
> Resilience, where it appears, is the retrospective name applied after this condition is met.

E.9 Practical diagnostic statement (for management use).
Where dominance persists despite planting, failure is architectural: recruitment corridors remain closed. Recovery begins when constraints are rebuilt such that the system **selects for autochthonous recruitment without continuous external maintenance**.

Appendix F. Cross-System Confirmation of Constraint-Collapse Dynamics.

The dominance of *Gaudium laevigatum* thickets described in this study reflects a broader pattern of **constraint-collapse dynamics** observed in degraded coastal ecosystems. Long-term restoration of *Polygala myrtifolia* in Coastal Moonah Woodland demonstrates that shrub monocultures emerge following **loss of ground-layer buffering** and **disturbance-mediated opening of surface recruitment corridors**, and that recovery depends on **constraint-preserving, low-disturbance intervention** (Brown, 2025).

Although the species differ in origin and life history, the **architectural conditions enabling dominance are convergent**, supporting the interpretation that tea-tree thickets represent a **system-level response to constraint failure** rather than an inherent or stable vegetation state.

Relationship to fire-frequency literature.

On calcareous dunes, increased fire frequency reduces canopy and **mid-storey** cover, litter, and moss, while increasing perennial grasses, with little net change in total species richness (Moxham & Turner, 2008). *Gaudium laevigatum* persists across all recorded fire histories, indicating that fire regime alone does not explain inland tea-tree dominance (Moxham & Turner, 2008). Inland thicketing aligns instead with disturbance, fragmentation, and altered regimes, and closed inland tea-tree canopies are best understood as **"*transition states*" (sensu Moxham, Cheal & Turner, 2009)—interpreted here as replacement architectures disclosed under disturbance rather than historical reference conditions**. Fire therefore functions as a **conditional amplifier**: where rabbits persist and **ground-layer** architecture is degraded, burns reinforce simplification, and **constraint repair is the prerequisite** for any role of fire in recovery (Moxham & Turner, 2008).

Fire as an Opposition Profile (Ω) in Coastal Moonah Woodland (comparative case).

Fire is treated here as a **conditional opposition profile** acting on an already simplified Coastal Moonah Woodland system, rather than as a primary explanatory driver of change. Evidence from Point Nepean indicates that increasing fire frequency shifts Coastal Moonah Woodland from layered woodland/open forest toward simplified grassy woodland, with reduced canopy/shrub cover, litter, and moss, fewer obligate seed regenerators, and increased grass cover; *Gaudium laevigatum* remains common across fire histories and *Polygala myrtifolia* is common in recently burnt and long-degraded contexts (Moxham & Turner, 2008). Where **constraint architecture is degraded** (weed seedbanks, rabbit pressure, exposed sands), burning commonly removes remaining surface buffering, widens exposure corridors, and synchronises recruitment failure and coloniser **lock-in**. In this respect, fire and tea-tree thicketing represent **different expressions of the same constraint-collapse process**, disclosed under different opposition profiles rather than distinct ecological mechanisms.

Appendix G. Rabbit-Grazing, Seedbank Dynamics, and Fire Potential Under Conditional Restoration.

Appendix G. Rabbit-Grazing, Seedbank Dynamics, and Fire Potential under Conditional Restoration

G.1 Purpose and scope.

This appendix formalises how **rabbit-grazing** alters restoration outcomes by (i) **closing recruitment corridors**, (ii) **shifting seedbank expression from staggered to synchronised emergence under disturbance**, and (iii) **increasing fire susceptibility through structural simplification and fine-fuel prominence**. The intent is to connect grazing pressure, seedbank behaviour (with emphasis on *Polygala myrtifolia*), and fire as **interacting opposition profiles** that disclose **low-option trajectories** in Coastal Moonah Woodland.
This appendix integrates these processes within a single constraint-collapse architecture; it does not introduce additional mechanisms.

G.2 Rabbit-grazing as a recruitment-corridor closer (restoration failure mechanism).

Rabbit-grazing acts as a **selector gate** that repeatedly removes palatable seedlings and resprouts, preventing recruitment of structural taxa and stabilising **ground-layer** recovery. Under persistent browsing, restoration inputs (seed, planting, thinning) do not accumulate into durable structure because newly opened corridors are repeatedly closed before recruits transition from vulnerable to persistent stages. The resulting pattern is **silent attrition**: apparent short-term establishment followed by disappearance prior to functional contribution.
This effect is not reducible to "*competition*" but reflects **conditional admissibility**: corridors for establishment remain open only transiently, and grazing functions as an **opposition profile** that repeatedly forces routes toward zero. **Restoration can initiate under grazing, but the *qualitative character* of recovery remains thin and prone to attrition; it becomes *accumulative* only when grazing is lowered enough to keep corridors admissible across seasons and disturbance cycles.**

G.3 Seedbanks as conditionally activated reservoirs (why disturbance matters).

Soil seedbanks are **conditionally activated reservoirs** rather than passive stores. Disturbance alters the timing and density of emergence by synchronising germination cues (surface light, temperature oscillation, wetting pulses, oxygen availability, and reduced microbial attrition). In degraded coastal sands—where surface buffering is thin and **soil-water-repellency** may be expressed—disturbance can convert staggered emergence into **pulse recruitment** that disproportionately favours disturbance-adapted taxa.
Where rabbit-grazing has already removed ground-layer buffering and reduced surface stability, the probability of synchronised germination increases because exposed microsites

are more common and persistence of shading/litter continuity is reduced. Seedbanks thus act as **amplifiers**, converting a single disturbance event into **multi-season recruitment pressure**.

G.4 *Polygala myrtifolia* seedbank dynamics (empirical anchor).

Empirical germination studies show that *Polygala myrtifolia* seeds are **non-dormant** and capable of high germination under realistic seasonal temperature cycles, with emergence occurring in both light and darkness and across wide soil pH. Emergence is **strongly surface-biased**, with highest emergence at the soil surface and sharply reduced emergence with increasing burial depth, including absence of emergence from deeper burial in experimental profiles.

These traits imply that **exposed or lightly disturbed surfaces** created by clearing, fire, grubbing, or trampling constitute **high-admissibility recruitment corridors** for *Polygala*. Where rabbit-grazing prevents native ground-layer re-closure, those corridors remain open across subsequent seasons, sustaining reinvasion and reinforcing a **low-option architecture**.

Management implications identified by Roberts et al. align with this logic: prevent seed set, control seedlings on emergence, and use careful manual or herbicide approaches; fire may trigger mass germination and therefore requires strict follow-up aligned with native recovery capacity.

G.5 Selective suppression as seedbank control (why method choice determines trajectory).

Selective **in-situ** suppression (e.g., targeted cut-stump or stem-specific application) alters seedbank dynamics by **preventing synchronisation of germination cues**. By retaining standing biomass, litter continuity, and microsite buffering, selective approaches reduce uniform light shock, damp temperature oscillation, and limit creation of exposed moist surfaces that favour surface-biased emergence. Under these conditions, seedbank expression becomes **asynchronous rather than pulsed**, enabling targeted follow-up and progressive draw-down while avoiding **site-wide recruitment corridors**.

For *Polygala*, high germination capacity combined with strong surface bias means **non-selective disturbance** is structurally likely to generate recruitment surges, whereas **selective suppression** reduces corridor opening and makes emergence **diagnosable and manageable** through staged follow-up keyed to seasonal windows.

G.6 Fire potential: rabbit-grazing and seedbanks as fine-fuel amplifiers.

Evidence from calcareous dune systems shows that increasing fire frequency shifts Coastal Moonah Woodland from layered woodland/open forest toward simplified grassy woodland, with reduced canopy and **mid-storey** cover, litter, and moss, fewer obligate seed regenerators, and increased perennial grasses; least-burnt sites are associated with Moonah dominance,

moss beds, and low fuel loads.
Rabbit-grazing drives a comparable simplification pathway by preventing recruitment of woody structural taxa and contributing to loss of ground-layer buffering. Once structure is simplified, seedbanks (notably *Polygala*) amplify post-disturbance recruitment into coloniser-dominated ground-layers. This increases **fine-fuel prominence and continuity**, raising ignition likelihood and reinforcing simplified states when fire occurs.

G.7 Integrated causal chain (rabbit–seedbank–fire loop)
Rabbit-grazing closes recruitment corridors by removing palatable seedlings and suppressing ground-layer recovery.

1. Constraint thinning increases exposure (surface instability, reduced shading/litter continuity), widening admissible microsites for disturbance-adapted recruitment.

2. Disturbance synchronises seedbank expression, converting staggered emergence into recruitment pulses, with *Polygala* empirically capable of high germination and strong surface-biased emergence.

3. Coloniser dominance increases fine-fuel prominence while structural buffering declines, increasing fire susceptibility and post-fire simplification pathways.

4. Fire (or other disturbance) acts as an additional opener, reinforcing simplified structure and re-opening recruitment corridors that seedbanks rapidly occupy, while grazing prevents native re-closure.

G.8 Restoration implications (sequencing rule).
Because grazing conditions both the quality and the accumulation of gains, sequencing must prevent corridor re-closure and seedbank synchronisation.

- **Rabbit suppression** should begin early: **recovery can initiate under grazing**, but gains remain thin and vulnerable; **reduction to corridor-keeping levels** (open across seasons and disturbance cycles) is required for recovery to become **accumulative**.

- **Polygala suppression** must be **front-loaded** to prevent seedbank-driven recruitment from occupying newly opened microsites; this is supported by high germination capacity and strong surface-biased emergence under seasonal conditions.

- **Disturbance-intensive interventions** (including broad burning or clearing) should be avoided in degraded remnants unless constraints are already repaired and follow-up is resourced, because disturbance can synchronise recruitment and amplify fine-fuel states.

- **Selective, constraint-preserving suppression** is structurally preferred because it reduces synchronisation and keeps emergence diagnosable, enabling gradual draw-down rather than reset.

G.9 EF / CT–FL interpretation (alignment note).
In EF terms, **rabbit-grazing operates as Ω** that repeatedly closes CT corridors for palatable recruitment; **disturbance (including fire) operates as Ω*** that synchronises FL gates; and **persistent seedbanks provide latent route pressure** that rapidly occupies any reopened corridor. Restoration is therefore the **staged re-opening and thickening of admissible corridors** while preventing synchronised gate activation by managing opposition profiles and seedbank expression.

Brown, C., 2026. *Survival is conditional: Resilience as a retrospective verdict from EF–CT–FL*. Research Square preprint. Available at: https://doi.org/10.21203/rs.3.rs-8965324/v1