

Dynamics and Restoration of Australian Tropical and Subtropical Rainforests

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At a stand level and as a generalization, the dynamics of moist tropical and subtropical rainforests following disturbance can be explained by a few interrelated factors (Swaine and Whitmore 1988; Hopkins 1990; Finnegan 1996; Richards 1996; Terborgh et al. 2002; Wright 2002). First, mature rainforest has a closed canopy and a shady understory. Second, the long-lived trees that dominate mature rainforest are relatively shade tolerant and slow growing, and their seeds typically germinate on dispersal. Third, rainforests also support a suite of shade-intolerant, fast-growing plants (“pioneers”) whose seeds persist in the soil and whose germination is stimulated by the increase in heat and light that accompanies disturbance to the canopy. Fourth, animals are key agents in the pollination, dispersal, and consumption of rainforest plants.

Consequently, in rainforests with an intact fauna, moderate-scale disturbance of the canopy (large tree-fall gaps to blowdowns of several hectares) typically gives rise to the following successional sequence: Pioneers recruit from the seed bank, grow rapidly to form a closed canopy, but do not recruit under their own shade. As the pioneers senesce, they are replaced by slower-growing, shade-tolerant, long-lived trees either present as seedlings at the time of disturbance or subsequently dispersed to the regenerating forest from surrounding areas of rainforest (fig. 14.1). We note that this successional model considerably simplifies variation in plant traits and ecological strategies and does not address issues concerning the maintenance of diversity in rainforests (Tilman 1994; Westoby et al. 2002; Wright 2002). Nevertheless, this model has been widely used to describe the ecology of rainforests and often forms the basis of strategies developed for their exploitation (Hartshorn 1989; Hopkins 1990; Kooyman 1996; Richards 1996; Lugo 1997; Duncan and Chapman 2003; Ganade 2007; Holl 2007).

In this chapter, we consider the utility of successional and alternate models (e.g., King and Hobbs 2006; Cramer 2007) for describing forest dynamics and informing the conduct of restoration projects in rainforest landscapes subject to broadscale anthropogenic disturbance. Such landscapes are characterized by extensive areas of cleared land dominated by grasses, crops and other exotic vegetation, patches of remnant forest, areas of secondary forest on marginal agricultural land, and various types of tree plantations (Richards 1996). Our examples are drawn largely from Australian rainforests, the focus of our research experience. We begin with a brief description of intact Australian rainforests before discussing disturbed systems.

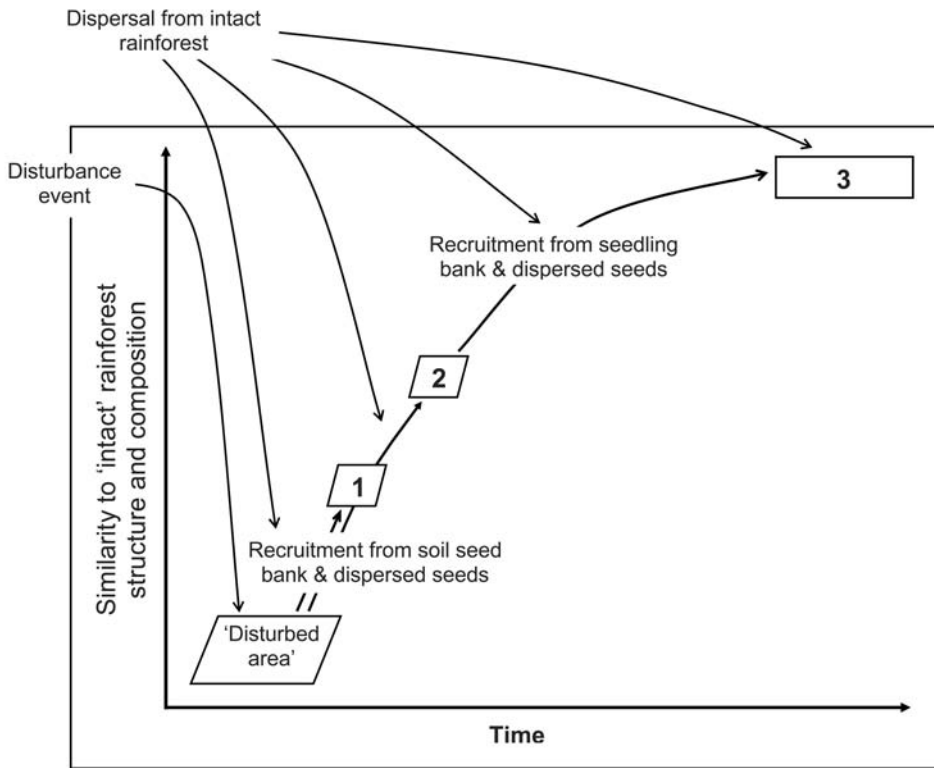


FIGURE 14.1. Model of the dynamics of intact rainforests on fertile soils in tropical and subtropical Australia following disturbance, with sequential stages of recovery dominated by (1) shade-intolerant, fast-growing, short-lived “pioneer” species; (2) longer-lived pioneer trees; and (3) shade-tolerant, slower-growing, long-lived “mature-phase” trees. Stages 1 and 2 are transient, and stage 3 may be persistent.

Environmental Determinants and Dynamics of Australian Rainforests

Until the mid-Tertiary, rainforests covered much of Australia. Currently, they cover around 3 million ha, or 0.4% of the continent, mostly in higher-rainfall areas along the east coast (Cofinas and Creighton 2001). Despite their limited extent, rainforests remain important repositories of biodiversity, supporting, for example, 60% of Australian vascular plant families and 17% of Australian bird species, including many endemic taxa (Lynch and Neldner 2000). From a global perspective, Australian rainforests have some unique characteristics, including the presence of a number of “primitive” angiosperm families (Adam 1992) and a distinctive fauna, such as marsupial frugivores and folivores rather than primates (Primack and Corlett 2005).

At a landscape scale, the composition and structure of Australian rainforests vary primarily with temperature, soil nutrient availability, and rainfall (Webb 1968; Floyd 1990; Kooyman and Rossetto 2006). Distinct forest types, defined in terms of structural attributes or their characteristic floristic composition, are associated with particular combinations of these environmental factors (Webb et al. 1976; Tracey 1982). For example, “complex notophyll vine forests” occur on relatively fertile soils subject to moderate to high rainfall and a “mesotherm” climate

(i.e., lowlands in the subtropics, uplands in the tropics), whereas “simple notophyll vine forests” occur on poorer soils in otherwise similar environments (Webb 1968; Nix 1991).

In the field, transitions between forest types can occur over short distances in conjunction with abrupt changes in environmental conditions. For example, rainforest types can change from “complex” to “simple” from one side of a watercourse to the other, with a change in underlying soil parent materials (Tracey 1982). Similarly, there is often a sharp transition between rainforest and fire-tolerant eucalypt forest, mediated by topographical features that act as a barrier to the spread of fire (Ash 1988).

At a stand level, the dynamics of Australian rainforests vary in response to the intensity and frequency of disturbance events (Hopkins 1990) and also with forest type. In “complex” rainforests on fertile soils, these dynamics tend to follow the successional model presented in figure 14.1, at least for disturbances that open the forest canopy sufficiently to stimulate the regeneration of pioneer species from the soil seed bank (Floyd 1990; Hopkins 1990; Kooyman 1991; Kariuki and Kooyman 2005). In contrast, the species that regenerate after disturbance in “simple” rainforests on poorer soils include many long-lived trees that also occur in mature forest (Floyd 1990; Kooyman 1999).

Dynamics of Australian Rainforests in Anthropogenically Disturbed Landscapes

Australian Aborigines have utilized rainforests for many thousands of years (Horsfall and Hall 1990). Through their use of fire, Aborigines modified the distribution of rainforest, and their hunting- and-gathering practices presumably influenced the distribution and abundance of harvested species (Newell 1999; Bowman 2000; Hill et al. 2000). Nevertheless, the traditional livelihood of the Aborigines relied on the persistence of rainforest and its resources.

European settlers converted extensive areas of rainforest to agricultural land, mainly sugarcane plantations in the lowlands and pasture and horticultural crops in the foothills and uplands (Erskine et al. 2007). Clearing was restricted mostly to forests on fertile soils, and many cleared areas remain under agricultural production. However, in the subtropics, large areas of marginal agricultural land have been abandoned in the past few decades and now support secondary forest (Neilan et al. 2006). There are also around 50,000 ha of monoculture timber plantations and 5,000 ha of mixed-species plantings established on former rainforest land in the Australian tropics and subtropics (Catterall and Harrison 2006; Erskine et al. 2007).

In the following paragraphs, we discuss the dynamics of these remnant forests, secondary forests, and replanted areas (fig. 14.2). Given the long time scales involved in rainforest dynamics and restoration and the paucity of relevant longitudinal studies, we are not in a position to evaluate which type of model “best” describes these systems. Instead, we consider how successional and alternative models draw attention to different aspects of forest dynamics and how these approaches can inform restoration practices.

Rainforest Remnants

Small patches of rainforest have persisted in extensively cleared landscapes in Australia for 50 to 100 years. For example, there are 30 remnants >1 ha of the former “Big Scrub,” a 75,000-ha



(a)



(b)



(c)



(d)

FIGURE 14.2. (a) Remnant rainforest, tropical Australia. (b) Mixed-species rainforest plantation, subtropical Australia. (c) Secondary forest in subtropical Australia dominated by the exotic tree, camphor laurel (*Cinnamomum camphora*). (d) Regenerating rainforest, eight years after the camphor laurel overstory was poisoned.

lowland subtropical rainforest that was cleared between 1860 and 1900 (Adam 1992). Many remnant rainforests have been subjected to disturbance from logging, cattle grazing, fire, and invasion by exotic plants, while all are exposed to an altered physical environment (increased light, wind and temperature variation), particularly on their edges (Lamb et al. 1997; Laurance 1997). Furthermore, it seems likely that the floristic composition of remnants will be impacted by changes in the distribution and abundance of fauna involved in plant regeneration, particularly seed dispersers, seed predators, and herbivores (Wright and Duber 2001; Cordeiro and Howe 2003). For instance, rainforest-dependent frugivorous birds responsible for dispersing the large, fleshy fruits of mature-phase rainforest trees have declined in some subtropical remnants (Moran et al. 2004).

Successional models figure prominently in the approaches developed by practitioners to restore Australian rainforests (Goosem and Tucker 1995; Kooyman 1996; Big Scrub Rainforest

Landcare Group 2005). For example, when applied to remnant rainforests, the model presented in figure 14.1 predicts that the long-term dynamics of remnants may be adversely impacted by dispersal limitation. Consequently, the restoration of “corridors” to facilitate dispersal between remnant forests has underpinned much of the revegetation effort conducted in Australian rainforest landscapes over the past few decades (Lamb et al. 1997; Tucker 2000).

However, successional models do not readily predict some aspects of the degradation of remnant forests. For example, in many subtropical remnants, disturbance of the canopy has resulted in the vigorous growth of exotic vines that smother trees and further disrupt the canopy. These conditions also favor the growth of exotic herbaceous ground covers that can suppress the regeneration of rainforest plants (Floyd 1990; Kooyman 1996; Harden et al. 2004). In such cases, it may be useful to consider alternative models to describe the processes involved in degradation and identify restoration strategies. For example, a “biotic and abiotic threshold” model (Whisenant 2002; King and Hobbs 2006) could be applied to the degradation of remnants driven by the positive feedback among canopy disturbance, the growth of exotic vines, and the spread of herbaceous ground covers. In rainforest, the canopy is considered a key regulator of abiotic conditions, with a closed canopy suppressing light-demanding vines and ground covers (Floyd 1990; Kooyman 1996). Restoration practices that have prioritized the reestablishment of a closed canopy and hence the abiotic conditions characteristic of intact rainforest have proven successful in restoring remnants degraded by exotic vines (Harden et al. 2004; Big Scrub Rainforest Landcare Group 2005). Earlier restoration practices that focused primarily on the control of the herbaceous ground covers were unable to halt the decline of these remnants.

Secondary Forests

Intensive agricultural pursuits in rainforest landscapes have frequently been abandoned because of declining productivity or changes in economic conditions (Richards 1996; Erskine et al. 2007; Ganade 2007). The redevelopment of rainforest following the abandonment of agriculture may be constrained by the destruction of the rainforest seed and seedling banks, the limited dispersal of seeds from remnant forests, predation on dispersed seeds, a reduction in soil fertility, competition from exotic plants, and repeated disturbance from fire and grazing (Hopkins and Graham 1984; Uhl et al. 1988; Hau 1997; Lamb et al. 1997; Holl 1999; Toh et al. 1999; Holl et al. 2000; Erskine et al. 2007). Under these circumstances, abandoned agricultural land may remain covered by exotic grasses and shrubs.

Nevertheless, if abandoned agricultural land is protected from fire and other major disturbances, secondary forest will often eventually replace the grassland (Richards 1996; Corlett 2002). The transition to secondary forest can occur rapidly if land is abandoned shortly after clearing and subsequently protected from disturbance, in which case rainforest plants may regenerate from residual rootstocks and the seed bank, supplemented by dispersal if forests are nearby (Uhl et al. 1988; Richards 1996; Erskine et al. 2007). In other cases, the transition may take decades (Toh et al. 1999; Holl 2007). In disturbed landscapes, the initial colonizers of abandoned land are often exotic plants; consequently, secondary forests dominated by exotic plants now cover large areas of former rainforest land (Ewel and Putz 2004; Zimmerman et al. 2007). In the Australian subtropics, for example, secondary forests dominated by

the exotic tree camphor laurel (*Cinnamomum camphora*) have recolonized around 25% of cleared land in the former “Big Scrub” (Neilan et al. 2006).

The concepts of facilitation and inhibition, inherent in classical successional models, are useful in understanding some of the dynamics of secondary forests (Hopkins 1990; Finnegan 1996; Richards 1996; Ganade 2007; Holl 2007). The presence of trees and shrubs in former agricultural land can facilitate the recruitment of rainforest plants because they attract seed-dispersing animals and suppress grasses that might compete with recruits (Lamb et al. 1997; Toh et al. 1999; Aide et al. 2000; Ganade 2007). Conversely, trees and shrubs also tend to inhibit the growth of recruits through mechanisms such as allelopathy, root competition, and shading (Bazzaz 1979; Tilman 1994; Ganade 2007; Loh and Daehler 2007).

Exotic tree colonizers in abandoned farmland are a particularly interesting case of the tension that exists between the contrasting roles of facilitation and inhibition, with implications for restoration strategies. When exotics are relatively short lived and shade intolerant, as is the case for *Spathodea campanulata*, the dominant colonizer of abandoned land in Puerto Rico, then passive restoration (doing nothing in the expectation that the recruitment of native species will be facilitated by the colonizing trees) may be an effective strategy (Zimmerman et al. 2007). However, when the exotics are long lived, shade tolerant, or capable of altering key environmental conditions such as soil nutrient status (as is the case for the leguminous tree *Myrica faya* in Hawaii; Loh and Daehler 2007), passive restoration is more risky.

In Australia, debate over the management of regrowth dominated by camphor laurel reflects different perceptions of its role in promoting (or retarding) the development of rainforest on abandoned land. Some ecologists have argued for the widespread control of camphor laurel (Floyd 1990), while others have argued for its retention, at least as an interim measure (Neilan et al. 2006). Camphor laurel clearly facilitates the recruitment of rainforest plants to grassland: It establishes among and shades out pasture grasses; when mature, it bears a heavy crop of fleshy fruits that attracts frugivorous birds and bats that disperse the seeds of rainforest plants and exotics to camphor stands (Neilan et al. 2006). However, camphor laurel can potentially live for centuries, during which time it may suppress recruits (Scanlon and the Camphor Laurel Task Force 2000). Given the uncertainty about the long-term trajectory of camphor stands, restoration practitioners have developed selective or patch-scale culling treatments to accelerate the growth of rainforest plants in camphor stands (Woodford 2000; Lymburner et al. 2006; fig. 14.2d).

Identifying the factors that drive or inhibit transitions among grassland, secondary forest, and mature rainforest is an important element in the development of restoration strategies for disturbed rainforest landscapes (Holl 2002). The model presented in figure 14.1 identifies dispersal limitation as a key factor potentially truncating the development of secondary forest. The large seeds of mature-phase rainforest trees that are often dispersed by rainforest-dependent fauna are rarely dispersed to secondary forests isolated from remnant forest (Corlett 2002; Cordeiro and Howe 2003; Moran et al. 2004; Erskine et al. 2007; Holl 2007). However, secondary forest may not progress toward the condition of intact rainforest for other reasons, including dominance of the seed rain by exotic plants (Holl 2007), elevated rates of seed predation or herbivory (Hau 1997; Holl et al. 2000), changes in underlying soil and/or hydrological conditions from past land uses (Zimmerman et al. 2007), and repeated disturbance (Richards 1996).

Alternative conceptual models of the dynamics of secondary forests, such as state-and-transition models (King and Hobbs 2006), can help draw attention to the range of factors driving transitions between different types of vegetation cover in disturbed rainforest landscapes (fig. 14.3). For example, the dispersal of plants from the disturbed matrix can strongly influence the composition of secondary forests, which are usually dominated by small-seeded pioneers and exotic plants (Duncan and Chapman 2002; Neilan et al. 2006).

Replanted Sites

Extensive areas of rainforest have been converted to plantations of timber trees (Lugo 1997). In Australia, plantations in rainforest landscapes are predominantly monocultures of the native conifer *Araucaria cunninghamii*, with smaller areas of mixed-species timber plantations and restoration plantings (Kanowski et al. 2003; Catterall et al. 2004). Restoration plantings typically use a diverse range of species planted at high densities to rapidly attain canopy closure and suppress weeds (Kooyman 1991, 1996; Lamb et al. 1997).

Successional concepts have played an important role in the development of replanting strategies. For example, both timber plantations (when used as part of a restoration strategy) and restoration plantings are intended to facilitate the recruitment of rainforest plants to formerly cleared land (Lamb et al. 1997). Restoration plantings are explicitly based on successional models in terms of their composition (usually a mix of pioneers and mature-phase species) and variation in composition with proximity to remnant forests. Planting designs developed for sites adjacent to remnant forests are comprised mainly of pioneers on the assumption that mature-phase species will readily disperse and recruit to such sites. In contrast, designs developed for more isolated sites include a substantial component of mature-phase species, particularly large-seeded and wind-dispersed trees with limited potential for long-distance dispersal (Goosem and Tucker 1995; Kooyman 1996; Freebody 2007).

Nevertheless, it may be useful to consider revegetation strategies within a state-and-transition framework (fig. 14.3) because successional models do not necessarily address the range of factors that may influence the long-term dynamics of replanted sites. For example, experience has shown that pioneer-dominated restoration plantings often do not recruit an understory of mature-phase rainforest plants as intended, even when located adjacent to remnant forests. Instead, the understory of these plantings often becomes dominated by light-demanding weeds, either present in the seed bank or dispersed from the surrounding matrix, that then suppress the recruitment of rainforest trees (Kooyman 1996; Freebody 2007). Similarly, consideration of landscape-scale factors influencing the dynamics of reforested sites may lead to greater skepticism of claims that plantations can facilitate rainforest regeneration in broadscale restoration programs (Parrotta et al. 1997; Lamb 1998; Lamb et al. 2005). Many tree species grown commercially in plantations (e.g., conifers, eucalypts) do not bear fleshy fruits and hence, when isolated from remnant forests, are unlikely to attract the specialist frugivores that disperse the seeds of mature-phase rainforest plants (Tucker et al. 2004; Kanowski et al. 2005). Consequently, although plantations adjacent to remnant forests may recruit a diverse range of rainforest plants (Chapman and Chapman 1996; Keenan et al. 1997; Lamb et al. 2005), more isolated plantations are likely to be dominated by small-seeded pioneers and exotic plants dispersed from the surrounding matrix (Corlett 2002; Duncan and Chapman 2002).

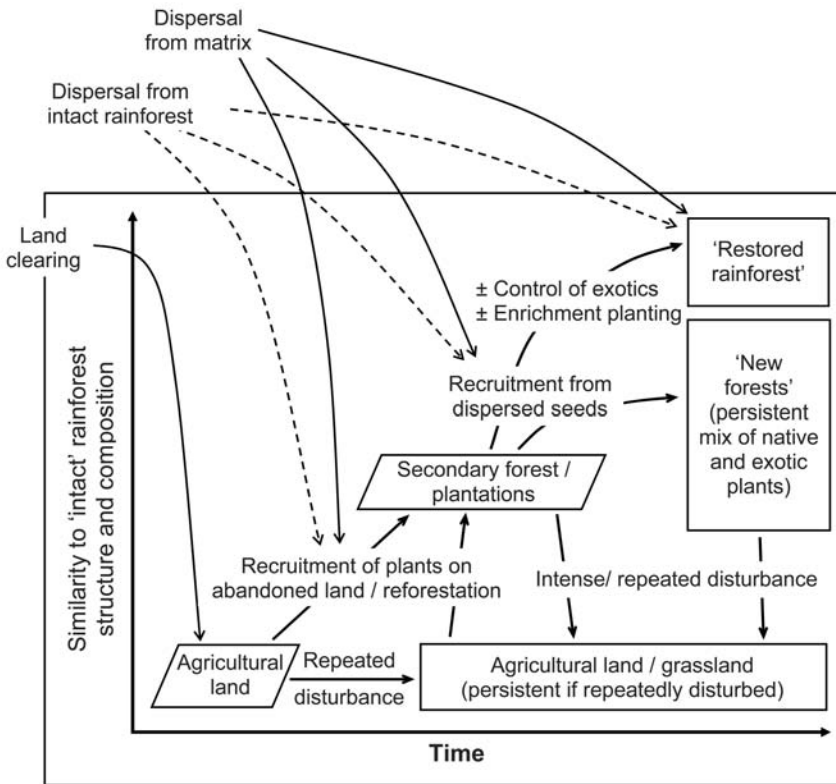


FIGURE 14.3. Model of the dynamics of secondary forests and replanted rainforests in anthropogenically disturbed Australian rainforest landscapes. Rectangular boxes = potentially stable states (persisting for more than one generation of dominant species); parallelograms = transitional states.

Conclusions

Techniques for restoring rainforests to cleared land have been informed by successional models developed from observations of intact rainforests (Floyd 1990; Hopkins 1990; Kooyman 1996). These techniques have been successful insofar as restored sites can develop a rainforest-like structure and provide habitat for some rainforest-dependent biota within one to two decades of establishment (Kanowski et al. 2003, 2006; Grimbacher et al. 2007; Kanowski and Catterall 2007; Catterall et al. 2008). However, few restoration projects have been established long enough to progress to the stage where planted trees have been replaced by species dispersed to the restored site let alone converge on target conditions. As successional models address only some of the factors influencing the dynamics of restored sites in disturbed landscapes, it may be useful to consider alternate models of forest dynamics to inform the long-term management of restored sites (table 14.1).

A state-and-transition model of the dynamics of restored sites (fig. 14.3) suggests that these sites will often require long-term intervention, including the control of exotic plants and the addition of native species, to converge on the condition of intact forest. Because the costs of

TABLE 14.1.
Models of ecosystem dynamics applicable to forested lands within Australian tropical and subtropical rainforest landscapes.

Forest Type	Successional Models	Alternative Models	Application to Restoration
Intact rainforest (extensive areas of rainforest with intact faunal assemblages)	The recovery of forests on fertile soils after disturbance is often described by successional models (fig. 14.1).	None (at the stand scale).	Restoration interventions in intact rainforest are rare, as recovery through autogenic processes is usually assumed. Some heavily logged sites have been treated (e.g., by replanting and vine control) to hasten succession (Kooyman 1999).
Remnant rainforest (small patches of rainforest in otherwise disturbed landscapes)	Successional models identify dispersal limitation as a factor influencing the dynamics of remnant forests.	The degradation of remnants following disturbance of the canopy and invasion by exotic vines could be described by a "biotic and abiotic" threshold model, with the canopy regulating abiotic conditions.	A common landscape-scale target of restoration is the establishment of corridors to improve dispersal between remnants. The primary site-scale target of remnant restoration is reestablishment of the canopy, if disturbed.
Secondary forest (regrowth forests developed after clearing, often dominated by exotic plants)	The concepts of facilitation and inhibition are useful for understanding the dynamics of secondary forests: Established trees may facilitate plant recruitment by attracting dispersers and suppressing grasses but may also inhibit the growth of recruits.	"State-and-transition" models can provide a useful framework for describing the long-term dynamics of secondary forests, as they focus on site- and landscape-scale drivers of the trajectory and stability of secondary forests and alternate types of vegetation cover.	Secondary forests can recover considerable structure and function by autogenic processes but may require intervention (e.g., control of exotics, enrichment planting) to converge on the condition of intact rainforest, depending on the longevity and shade tolerance of colonizing species and the recruitment of rainforest plants.

TABLE 14-1.
Models of ecosystem dynamics applicable to forested lands within Australian tropical and subtropical rainforest landscapes, continued.

Forest Type	Successional Models	Alternative Models	Application to Restoration
Replanted sites (monoculture and mixed-species timber plantations, diverse restoration plantings)	Replanting strategies and techniques draw heavily on successional models. "Pioneer" plantings and timber plantations (when used for restoration) are explicitly intended to facilitate the recruitment of mature-phase rainforest plants.	The long-term dynamics of replanted sites are likely to be contingent on the same site- and landscape-scale factors that influence remnant forests and secondary forests. These dynamics may be usefully described by state-and-transition models.	Techniques for establishing rainforest trees in Australian tropical and subtropical landscapes are well developed. Planting strategies generally assume that sites will converge on intact rainforest through autogenic processes, but long-term intervention may be necessary to control weed invasion and to enrich species composition in cases where dispersal is limited. To be effective, intervention needs to be coupled with a systematic monitoring program.

intervention can be high, particularly if a problem such as weed invasion is not controlled at an early stage, the routine monitoring of restoration projects may need to become a necessary part of their management (Catterall et al. 2008). At present, most Australian rainforest restoration projects are not monitored in any formal way (Kanowski et al. 2008; although for counterexamples, see Kooyman 1996; Tucker and Murphy 1997; Harden et al. 2004).

Once the long-term outcomes of restoration projects are better known (e.g., through more systematic monitoring), there may need to be a reassessment of what constitutes appropriate “target conditions” for restored sites. It may become apparent, for example, that most restoration projects are so small and isolated and so heavily influenced by the disturbed matrix that the structure, composition, and dynamics of restored sites will always tend to diverge from the condition of intact rainforest. If so, it may be necessary to accept stable assemblages of native and exotic plants (“emerging” or “new forests”; Ewel and Putz 2004) as the target for most restoration projects. Alternatively, investment in projects aimed at reestablishing assemblages typical of intact rainforests may need to be restricted to high-value applications (e.g., habitat for threatened species or plantings strategically positioned to act as future seed sources; Kooyman 1996) rather than being used as the default approach across the landscape, as currently tends to be the case.

All models of rainforest dynamics recognize the importance of landscape context in affecting the trajectory of restored sites. To date, much restoration effort in Australia has been expended on the creation of corridors to facilitate dispersal between remnants. However, corridors do not address other landscape-scale factors affecting the persistence of biota in remnants, such as the influence of the surrounding matrix. A better understanding of the relative importance of the extent and configuration of rainforest cover at the landscape scale (e.g., Bennett et al. 2006) and integration of this knowledge into models of rainforest dynamics is required to inform future restoration projects aimed at conserving rainforest biota.

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