TOWARDS A Conceptual Framework for Novel Ecosystems

Lauren M. Hallett¹, Rachel J. Standish², Kristin B. Hulvey², Mark R. Gardener³, Katharine N. Suding¹, Brian M. Starzomski⁴, Stephen D. Murphy⁵ and James A. Harris⁶

¹Department of Environmental Science, Policy & Management, University of California, Berkeley, USA ²Ecosystem Restoration and Intervention Ecology (ERIE) Research Group, School of Plant Biology, University of Western Australia, Australia

³Charles Darwin Foundation, Galapagos Islands, Ecuador, and School of Plant Biology, University of Western Australia, Australia

⁴School of Environmental Studies, University of Victoria, Canada

⁵Department of Environment and Resource Studies, University of Waterloo, Canada ⁶Environmental Science and Technology Department, Cranfield University, UK

3.1 INTRODUCTION

Endangered birds often garner conservation action and the Rodrigues fody (*Foudia flavicans*) is no exception. Dependent on mature-stand forests on the smallest of the Mascarene Islands, the Rodrigues fody (Fig. 3.1) experienced a population crash when the majority of its habitat was converted for agriculture in the 1960s. What was exceptional about the fody was its manner of recovery. Before its population could be completely decimated, it was saved in part by the expansion of fast-growing non-native trees that quickly fulfilled the mature-stand habitat requirement of the bird (Impey et al. 2002; popular coverage and interpretation by Fox 2003 and Marris 2011). Its story highlights three key points we explore throughout this chapter. First, it indicates that novel species interactions should be considered in conservation efforts. Second, it demonstrates that novel ecosystems can provide some of the same functions as their historical counterparts. Lastly, it serves as a cautionary tale: the fody nearly went extinct due to anthropogenic land

Novel Ecosystems: Intervening in the New Ecological World Order, First Edition. Edited by Richard J. Hobbs, Eric S. Higgs, and Carol M. Hall. © 2013 John Wiley & Sons, Ltd. Published 2013 by John Wiley & Sons, Ltd.



Figure 3.1 A male Rodrigues fody (*Foudia flavicans*) displaying. Photograph courtesy of Dubi Shapiro.

vojtisodi vojtis

Restoration threshold

change and native forests are recovering slowly, if at all (Impey et al. 2002). Slowing anthropogenic drivers of ecosystem change, such as land conversion and climate change, is the primary way to reduce the frequency of these types of conservation challenges. Novel ecosystems and associated species interactions may be a significant secondary tool in conservation situations.

This chapter is about when and how to intervene in novel ecosystems. It provides a brief introduction to many of the ideas and concepts addressed in greater detail in later chapters. It is not an argument for the virtue of novel ecosystems per se; given the choice, most of us would opt to mitigate many of the processes driving ecosystem change. In a world of rapid humaninduced change however, the power of the novel ecosystem concept is its pragmatism. Novel ecosystems can serve conservation aims, whether by maintaining species diversity or providing ecosystem services. Here we develop a framework to aid in evaluation of such benefits. We first describe approaches to identify thresholds shifts into novel territory. Second, we consider how functional similarities between novel and historical ecosystems can inform decisions about when and how to intervene in novel ecosystems. We conclude with a discussion of practical considerations and methods for managing these systems.

3.2 THRESHOLDS AND ANTICIPATING DRAMATIC ECOSYSTEM SHIFTS

Novel ecosystems are composed of non-historical species configurations that arise due to anthropogenic

Figure 3.2 Types of ecosystems under varying levels of biotic and abiotic change. A historical ecosystem remains within its historical range of variability; a hybrid ecosystem is biotically and/or abiotically dissimilar to its historical ecosystem but is capable of returning to the historical state; novel ecosystems are biotically and/or abiotically dissimilar to the historical state and have passed a threshold such that they cannot be returned to the historical state. Pathways represent possible directions of change: (1) shifts from historical to hybrid ecosystems that are reversible; (2) non-reversible shifts from historical or hybrid ecosystems to novel ecosystems; and (3) further biotic and abiotic shifts are possible within novel ecosystems. From Hobbs et al. (2009). Reproduced with permission of Elsevier.

environmental change, land conversion, species invasions or a combination of the three. They result as a consequence of human activity but do not depend on human intervention for their maintenance (Hobbs et al. 2006; Chapter 5). Because it can be easier to reverse the effects of some drivers of ecological change but not others, a useful distinction is between hybrid and novel ecosystems. While both hybrid and novel ecosystems are composed of new species combinations and/or abiotic conditions, hybrid ecosystems can more readily be returned to their historical states whereas significant barriers prevent novel ecosystems from returning to their historical states (Fig. 3.2).

This distinction is important for two reasons. First, a primary management goal is often to prevent threshold shifts that result in novel ecosystems. This requires the ability to differentiate a hybrid from a novel ecosystem *before* the shift occurs, and also requires the ability to reverse or control the effects of drivers causing the shift. Second, when a threshold has been crossed that in practice is irreversible, it becomes necessary to develop new management goals for the resulting novel ecosystem other than returning it to its historical state. Later in this chapter we will discuss how to develop management goals for novel ecosystems, but it is first important to characterize possible thresholds. Without a robust consideration of threshold dynamics, it is possible that the novel label becomes over-prescribed with the unintended consequence that the conservation potential of some ecosystems is not fully realized.

Thresholds can be crossed when an increase in a continuous, often exogenous, driver of change, such as nitrogen deposition or climate change, accumulates to a point at which the system can no longer absorb the change and instead shifts into a different state. Identifying these tipping points can help managers prioritize their efforts in hybrid ecosystems (Suding and Hobbs 2009). For example, known thresholds tipped by rising salinity in the Wheatbelt of south-western Australia (Cramer and Hobbs 2002) helped managers decide when to intervene to prevent a large freshwater lake from becoming saline (Froend et al. 1997; Wallace 2003). Managers with extensive ecological knowledge and access to long-term datasets may be better placed than most to make use of the threshold approach in a predictive manner (Bestelmeyer 2006; Bestelmeyer et al. 2011). There will always be uncertainty about the exact location of thresholds however, and for systems characterized by complex dynamics it may not be possible to develop indicators of an impending regime shift (Hastings and Wysham 2010). Consequently, a combination of a threshold approach with risk assessment - what are the consequences if a threshold is crossed? - is needed to help guide decision making (Polasky et al. 2011; Chapter 18).

Species invasions can similarly drive ecosystems across thresholds. Species invasions are often dynamic and difficult to anticipate, and invasion-driven thresholds may be passed before they have even been noticed (Box 3.1). For example, relatively little research has been conducted to show quantitative thresholds of biotic and abiotic impacts of biological invasions on native assemblages (Gaertner et al. 2009). Understanding invasion-related thresholds is further confounded by the time lags between invasion and impact (Sax and Gaines 2008). For example, the non-native quinine tree (*Cinchona pubescens*) now comprises 20% of the cover in shrub lands in the highlands of the Galapagos Islands. This invasion has resulted in a reduction in the abundance of most native plant species but, as yet, no local extinctions (Jäger and Kowarik 2010). Difficulty in projecting the future trajectory of the quinine invasion leaves managers uncertain as to whether the native and non-native species will continue to co-exist or whether the tree invasion will eventually result in extinctions. Species extinctions are clear examples of irreversible change but, in practice, changes in species abundances can also be irreversible if such changes entail additional effects on ecosystem composition or structure (Box 3.1). Such examples underscore the need to couple uncertainty with risk assessment when designing interventions to prevent threshold shifts (Chapter 18).

When the driver of change is external to the site, managers may be able to predict but unable to prevent the system crossing a threshold. For example, nitrogen deposition on nutrient-poor soils can have widespread effects on ecosystem composition and function but, despite known threshold dynamics, managers may be unable to reverse the driver (Bobbink et al. 2010). Consequently, these ecosystems are likely to become novel and management efforts may be better served by curbing the effects of threshold shifts rather than attempting to control the underlying driver (this approach is discussed further in Section 3.6.2 and in Chapter 18). In contrast, when a driver occurs at the site level, such as in the salinity example earlier, managers may aim to intervene in the hybrid system before the threshold is crossed.

Altered fire regimes are a common anthropogenic change that can result in both hybrid and novel systems. In Illinois barrens (a woodland-prairie ecotone), for example, fire suppression shifted plant community composition from prairie to woodland species (Anderson et al. 2000). Reintroduction of fire was associated with an increase in prairie species abundances; after long periods of fire-suppression however, the system passed a threshold such that fire reintroduction was not sufficient to restore historical community composition (Anderson et al. 2000). Although this threshold may still be reversible, the additional costs to restore the historical community are greater if fire reintroductions occur after the system has passed a definitively hybrid state. Sometimes altered fire regime can be the result of other thresholds being crossed; these are very difficult to reverse. For example, invasion of the introduced pasture grass Andropogon gayanus created vastly hotter **Box 3.1** Pragmatic management of remnants of the humid highlands of the inhabited islands of the Galapagos: Are thresholds useful and can we prevent shifts into novel states?

Much of the humid highlands and transition zones of the inhabited islands of Galapagos have been transformed to a novel state by land use and biological invasions (Watson et al. 2009). On the island of Santa Cruz, which was permanently settled in the 1920s, change has been rapid. Although the island has experienced longer-term disturbance from wild stock, the most significant anthropogenic change occurred when much of its native forests were cleared between 1960 and 1980. In the south-eastern part, however, which has less attractive land for agriculture (lower rainfall and more rocky), there remains a small patch of transitional zone forest which could be considered to be hybrid, that is, it still has its original composition and structure. It has a canopy of native trees and intact shrub layers, whose species are still actively recruiting. This forest has small patches of invasive elephant grass (Pennisetum purpureum), Lantana camara and low densities of Cuban cedar (Cedrela odorata) and guava (Psidium quayaba). The most insipid and widespread species is the ground cover, Tradescantia fluminensis, which has a cover of greater than 50%.

Are thresholds a good measure to guide intervention? Has this system shifted from hybrid to novel? The first barrier to answering these questions is that we have very little data on the historical state. Moreover, Galapagos vegetation, especially in drier areas, is inherently variable: species abundances wax and wane with patterns of wet and dry years (Hamann 1975, 1985). Because the invasion process is just beginning it is highly dynamic; consequently, the eventual state of the system is difficult to envision. If we assume the historical state to be something structurally similar to its current state but with all native plant diversity, chemical control could reduce most invasive species to low densities and return the system to its historical state. However, Tradescantia fluminensis invasion has probably crossed a threshold of impact because it competes with and prevents the recruitment of native herbaceous species (M. Gardener, Charles Darwin Foundation, Galapagos, personal observation). This threshold has never been quantified in the Galapagos but has been quantified in New Zealand (Standish et al. 2001). In hybrid ecosystems thresholds are still reversible. However, the disturbance created by trying to remove this species with chemical methods could be highly perverse: it may damage the biodiversity and ecosystem process and could potentially facilitate further invasion by other species. In short, although this system is relatively pristine and can be maintained in its current state, it is novel and not hybrid because it cannot go back to its historical state.

fires than normal, killing native savanna species in northern Australia and resulting in a near monoculture (Rossiter et al. 2003).

Human activity at the site level, such as land conversion and subsequent abandonment, can rapidly push ecosystems past thresholds. It is easier to identify a threshold once it has been passed and, while the specific barriers to recovery can be hard to identify, the fact that a system has crossed some sort of threshold may be obvious. For example, if overgrazed vegetation does not recover after the removal of livestock, managers can probably assume that a threshold is preventing its recovery (Westoby et al. 1989). In this case, the more pertinent question is whether or not the threshold effects are *reversible*. This question is central to restoration ecology. Within that context, descriptions of ecological filters (Hobbs and Norton 2004; Funk et al. 2008) and state-and-transition models (Wilkinson et al. 2005; Rumpff et al. 2011) are common frameworks to test and characterize the presence of thresholds at a site. Site-level experimental tests and adaptive management are tools to identify specific barriers to ecosystem recovery and to decide if management interventions can reverse their effects (Chapter 18). Two additional considerations are important here. First, it is possible that a system is so altered that the totality of thresholds acting at the site cannot be easily identified. For these highly degraded landscapes, bet-hedging management that employs an array of approaches may be the most effective strategy. Second, the social and economic costs as well as the ecological consequences of intervention can determine whether in practice the threshold is actually reversible, or whether the ecosystem is or should be managed as a novel ecosystem (further described in Section 3.6.1 and Chapter 18).

Ecological and social barriers can interact in a variety of ways. First, social and ecological drivers can combine to create novel ecosystems. Earlier we described suppressed fire frequency as a site-level driver that could be reversed to prevent a hybrid ecosystem from becoming novel. Fire suppression, however, is often due to social pressure to prevent fires near human habitation: housing growth around natural areas may in practice turn ecologically reversible factors into irreversible drivers of ecosystem change (Radeloff et al. 2010). Importantly, as described in Chapter 5, ecosystems are composed of individuals that move independently of one another and in response to their environment. Humans are no exception to this individualistic concept; rather, people and societies are capable of adapting to and valuing aspects of ecosystem change. The value humans derive from some aspects of novel ecosystems may form a social threshold that cannot, and possibly should not, be reversed (Marris 2011).

The notion of an irreversible threshold is therefore a multidimensional one that includes ecological and social components. In reality, it may often be theoretically possible to reverse many thresholds but not practical due to knowledge, social or resource constraints. At times, new methods or approaches may shift perceptions of whether the same threshold is reversible or not. These themes are expanded on in Section 3.6.2 and in Chapter 18. Once an irreversible threshold has been identified, however, managers know they have a novel ecosystem and are faced with decisions of how to manage it. If there is no going back, what is next? We suggest that a consideration of function in novel ecosystems can aid in setting goals related to both biodiversity conservation and ecosystem services.

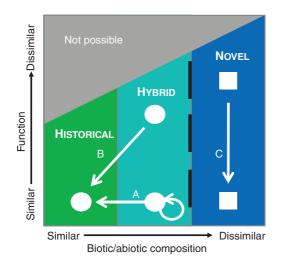
3.3 FUNCTION AS A MANAGEMENT GOAL

An underlying assumption in much of environmental management is that maintaining or restoring a historical species assemblage is the best approach to achieve a suite of other common goals from biodiversity conservation to ecosystem service provisioning. As anthropogenic change increases, this assumption becomes less defensible (Hobbs et al. 2011). As described earlier, escalating change may push an increasing number of ecosystems past thresholds such that they cannot be returned to their historical states. Rather than abandoning restoration or persisting with futile efforts, these systems may require a shift in evaluation metrics. Are there specific conservation goals or ecosystem services that can be provided through further management?

The idea of 'function' in ecology is used in three main ways that are relevant to the management of novel ecosystems (Jax 2005). First, function can refer to interactions between species or between a species and its environment. To understand function at the species level we ask, how does a species affect its environment, and how is it affected by its environment (Naeem 2002)? Second, function can refer to the collective effect of a complex set of interactions on the processes that sustain the functioning of the whole ecosystem. This meaning of ecosystem function is broad in scope and so prompts a different set of questions, for example, what do individual species or groups of species contribute to particular ecosystem functions? How do individual functions sum to affect the functioning of the whole ecosystem (Grime 1998)? Third, when ecosystem functions are considered in relation to human well-being, they become ecosystem services. Ecosystem services can take a variety of forms from regulatory (e.g. climate regulation and pollination) and supporting (e.g. nutrient cycling) services to provisioning (e.g. food and water) and cultural services (Millennium Ecosystem Assessment 2005).

An explicit focus on function provides metrics to set management goals in novel ecosystems. Novel ecosystems by definition differ from historical ecosystems in their biotic and/or abiotic characteristics, but functional similarities between past and present species can potentially mitigate the effects these changes have on ecosystem functions (Benayas et al. 2009). Environmental filtering can cause trait compositions to converge even while species compositions diverge (Fukami et al. 2005), and consequently novel ecosystems with altered biotic composition may still function like their historical ecosystems.

Figure 3.3 illustrates the space of possible relationships between historical, hybrid and novel ecosystems and their functional similarity to the historical system. For both historical systems and functionally similar hybrid systems, interventions may be a low priority



Restoration threshold

Figure 3.3 A state-space of functional similarity to the historical ecosystem in relation to abiotic and biotic novelty. Depending on management goals, functional similarity in this context may refer to habitat provision, ecosystem service provision or diversity maintenance. Compositionally similar but functionally dissimilar ecosystems are unlikely to occur and are labeled 'not possible'. Circles represent ecosystems that have not crossed a threshold into a novel state; squares represent ecosystems that have. Three pathways are considered in order of management preference: (A) when possible, functionally similar historical or hybrid ecosystems should be managed to prevent threshold shifts into a novel state; (B) functionally dissimilar hybrid ecosystems should be prioritized for restoration to their historical state; and (C) novel ecosystems should be managed to maintain or restore functional similarity to the historical state.

with one exception: managers may aim to understand possible threshold points in the system and at times intervene to prevent an irreversible threshold from being crossed (Fig. 3.3, pathway A). For novel ecosystems with high functional similarity to historical systems, intervention may similarly be a lower priority. Alternatively, for both hybrid and novel ecosystems in which key functions are lost, interventions to restore those functions may be a priority. For hybrid systems this can be achieved by returning the ecosystem to its historical state (Fig. 3.3, pathway B). For novel ecosystems, however, interventions to restore functions may be more successful if they are not restricted to promoting the historical species pool (Fig. 3.3, pathway C).

3.4 SCALES OF ECOSYSTEM FUNCTIONING

Conservation of single species, as in the case of rare and endangered species, requires consideration of the functional traits and relationships of the species of concern. Managers should aim for a novel ecosystem to provide the focal species with functionally similar habitat to the historical ecosystem. As in the case of the Rodrigues fody, these relationships are often capitalized on for bird conservation. In the British Isles, for example, native blue tits began to feed upon non-native gall wasps hosted by the non-native Turkey oak after a decline in native oak and caterpillar populations (Stone et al. 2008; Hobbs et al. 2009). Similarly, removal of non-native pines outside of Perth, Australia was recently slowed when it was recognized that pine seeds had become an important food source of the endangered Carnaby's black cockatoo (Valentine and Stock 2008). Other examples of novel ecosystems providing habitat for bird species (Gleditsch and Carlo 2011) led one editorialist to answer the question 'do native birds care whether their berries are native or exotic?' with a simple 'no' (Davis 2011). While birds are a wellstudied taxa for these questions, there is evidence the same principles hold true more broadly from the seeddisperser requirements of trees (Dungan et al. 2002) to the habitat requirements of beetles (Pawson et al. 2008).

To achieve other goals, a focus on ecosystem-level functions and services may become important. Increasingly, managers look to enhance ecosystem services as well as maintain key species. For some regulatory and supporting services, the origin of the species may matter very little; rather, they may depend on whether specific functional groups are present (Mascaro et al. 2012). Although an extreme example of ecosystem change, mine-site reclamation illustrates this well. Vegetation removal prior to mining results in a need to quickly re-stabilize soils once mining is complete. As a consequence, managers often plant fast-growing or deep-rooted plants regardless of their origin to ensure that this supporting service is restored (Richardson et al. 2010). At the landscape level, the well-reputed Working for Water program in South Africa partners

with local communities to remove invasive species based not on the origin of species, but rather on how species affect ecosystem function. In working landscapes in the United States, range managers employ a range-assessment protocol that evaluates soil stability, hydrology and biotic integrity without considering species identity (Pyke et al. 2002). Finally, cultural ecosystem services are not necessarily tied to historical species assemblage. This is particularly evident in urban landscapes, in which novel ecosystems can reflect people's preference for nature that may not include historical ecosystems (Chapter 38).

3.5 PUTTING IT TOGETHER: MULTIPLE FUNCTIONS AND FUNCTIONAL TRADE-OFFS

Although specific functions may be similar between novel and historical ecosystems, no two species are exactly alike or functionally redundant. As a consequence, it is unlikely that a novel ecosystem will be similar to its historical analog for all functions. Rather, goals based on function require managers to choose specific functional relationships, conservation priorities and ecosystem services to focus on. Literature is rapidly growing on when and where ecosystem services can be bundled versus when there are trade-offs between services, but our understanding is still limited as to how services interact (Nelson et al. 2009; Lavorel et al. 2011). Similarly, there is often uncertainty about whether specific functions in a novel ecosystem will be retained over time. Ecosystem functions can shift with environmental variability, and there is growing evidence that multiple species are needed to maintain the same ecosystem function over time (Isbell et al. 2011). As a consequence, in many cases managers will be willing to consider ecosystem processes in tandem but not in place of biodiversity or native species diversity (Thompson and Starzomski 2007; Duffy 2009). Threshold effects may limit the feasibility of restoring native diversity to novel ecosystems but, to the extent that restoring native species is possible, synergies and tradeoffs may similarly exist between this goal and goals based on species conservation and ecosystem services.

These decisions are context-dependent, but the following examples illustrate the range of trade-offs and choices faced by managers.

• Management for species conservation may not translate to ecosystem conservation. Kirtland's warbler (Setophaga

kirtlandii) is a rare bird with very specific habitat requirements, spending its winters in the Bahamas and summers in jack pine (*Pinus banksiana*) barrens in Michigan. Historically the jack pine barrens ecosystem was maintained by fire, but fire suppression around human population centers has reduced this ecosystem type. Strategic logging in jack pine plantations provides a habitat analog for the warbler and has been viewed as a good choice for conservation (Houseman and Anderson 2002). However, logging fails to replicate vegetation diversity and stand structure (Spaulding and Rothstein 2009).

• Synergies and trade-offs between cultural services, ecosystem function and biodiversity. Indirect human effects on wetlands near human habitation, such as altered hydrological regimes and nutrient levels, and direct human effects such as recreation can result in major compositional and structural change. In urban wetlands in New Jersey, Ehrenfeld (2004) found that increased human use of wetlands resulted in both emerging ecosystem functions as well as trade-offs among ecological and social functions. For example, increased potential to store flood waters was associated with an increase in plant diversity but a decrease in the presence of vertebrates. Low water levels were associated with more vertebrates but also with increased disturbance from humans, such as trash dumping. Different again, areas with a lot of human recreational use also had low plant diversity (Ehrenfeld 2004).

These examples highlight that understanding the synergies and trade-offs in achieving different conservation goals and ecosystem services is a key aspect of novel ecosystem management. At times this may entail tough value judgments to set realistic goals for ecosystem management. In other cases, such as the example of urban wetlands, a landscape perspective may be required to achieve multiple goals across several sites. Often, complementarity between species that provide different ecosystem functions may allow managers to augment management interventions to achieve a core goal while also achieving additional functions and services. For example, to guide restoration decisions aimed at controlling post-fire invasion of cheatgrass (Bromus tectorum), Wainger et al. (2010) developed an optimization model that focused on several ecosystem services (antelope hunting, property protection from fire, sage-grouse habitat and forage production) and incorporated cost-effectiveness ratios of restoration options. They found that if managers selected sites to optimize multiple services and utilized treatments with

the greatest cost-effectiveness ratios (often the lowest intensity treatment), service benefits would increase three-fold. In this example and in general, practical and cost considerations shape ecosystem management. These constraints are expanded upon in the following sections.

3.6 FROM GOALS TO IMPLEMENTATION: PRACTICAL CONSIDERATIONS AND NOVEL METHODS

3.6.1 Practical considerations

Considering the functional relationships of species and ecosystem services helps provide goals for interventions in novel ecosystems. Practical constraints may however have an effect on when it is appropriate to intervene in novel ecosystems.

First, consideration should be given to temporal factors that may affect how long interventions are likely to persist in the system. In ecosystems characterized by frequent or intense disturbances, the effects of management may be superseded by subsequent disturbance. In tropical forests, for example, secondary succession following anthropogenic disturbance and natural disturbances such as hurricanes can routinely result in the assembly of new species combinations (Chazdon 2003). As a consequence, attempts to manage for specific species assemblages in these ecosystems are often futile. Over longer timescales, management with disturbance may also become unnecessary due to the self-organizing capacity of ecosystems. For example, Thompson et al. (2007) suggest that hurricane disturbance in the Luquillo Mountains of Puerto Rico serve as a check on species unable to tolerate infrequent but intense disturbance. In other situations, however, reducing the frequency of a disturbance may be the chief intervention necessary to achieve management goals. Increased fire frequency in the Amazon, for example, can result in large shifts in forest structure. Policies to control fire disturbance are therefore an important management response to prevent large shifts in ecosystem function (Nepstad et al. 2001).

Second, spatial factors will matter for the scale of management action required and its likelihood of success. For example, the location of a site in relation to source populations can largely influence the longterm success of interventions. Working along the

Sacramento River, Holl and Crone (2004) found that plant restoration was more successful near remnant forests. Limited evidence exists on how local and landscape factors dictate restoration and management success, but the need to consider these factors is of growing research and management interest (Brudvig 2011). Further, while novel species assemblages can provide site-level conservation benefits and ecosystem services, they may also have wider landscape-level effects. Novel ecosystems near sites with a more exclusive management focus on historical assemblages, such as national parks or 'museum-style' conservation sites, might undermine those management efforts. Having local management projects out of sync with other patches at the regional or landscape scale may lead to the failure of restoration projects at one or both sites: at the very least, it may alter important localregional relationships that structure local diversity (Ricklefs 1987; Starzomski et al. 2008). Thus, the net value of novel ecosystems may matter in relation to landscape factors.

Third, intervention in novel ecosystems should be based on an understanding of costs as well as benefits. Miller and Hobbs (2007) emphasize that in ecosystem management costs generally do not scale linearly with benefits. For some management objectives, initial conservation goals may be achieved with a minimal initial cost while achieving subsequent improvements becomes disproportionately costly. For example, when assessing habitat restoration options for grassland birds in suburban Chicago, Snyder et al. (2007) found that large areas distant from urban development could be restored relatively inexpensively whereas the costs of both restoration and land acquisition increased greatly for land parcels nearer to urban areas. On the other hand, large initial costs may be necessary to achieve initial benefits. For example, native plant restoration efforts in the Gulf Islands of British Columbia. Canada, were stymied by herbivores including introduced fallow deer (Dama dama) and Canada geese (Branta canadensis). These herbivores have negative effects on local vegetation because they facilitate competitively superior non-native grasses (Best and Arcese 2008) by increasing nutrient loading in conjunction with non-native species propagule supply and herbivory (Best 2008; Gonzales and Arcese 2008). Consequently, the Parks Canada Agency has found it necessary to invest additional funds to fence an entire island within the park (Eagle Island) to achieve their goal of restoring native plants.

Further, and especially in relation to novel ecosystems, it is important to consider the inadvertent impacts of management interventions to functions already maintained within an ecosystem. Herbicide application, for example, can deleteriously affect desired species populations as well as curb populations of non-desired species. Removal of non-native species may create 'weed-shaped holes' (Buckley et al. 2007) that without additional management expense will simply be refilled, sometimes with invasive species that can cause even greater changes to the desired species composition (Jäger et al. 2009). Lastly, when non-native species naturalize in an ecosystem they can form facilitative relationships with existing species and provide valued (though not necessarily historical) ecosystem functions. In Puerto Rico, for example, the invasive tree Leucaena leucocephala serves as a nurse plant for native species and also reduces risks of fire damage by decreasing fuel loads (Santiago-Garcia et al. 2008). Decisions on whether to remove a species should therefore include consideration of the costs required to replace the ecosystem functions it provides.

While many of these constraints would suggest higher tolerance of novel assemblages and non-native species, the greater uncertainty associated with novel assemblages also suggests that precaution is an important element of novel ecosystem management. Many invasive species go through low-abundance lapse phases before becoming highly abundant. In Germany, for example, 51% of the 184 woody weed species had a lapse phase longer than 200 years before they became invasive (Kowarik 1995). In southeastern USA, Kudzu (Puerarua montana) was planted widely in the early 1900s because it reduced soil erosion in drought years. Since that time it has become highly invasive, covering over 3 million hectares in the eastern USA (Forseth and Innis 2004). Humans have long managed ecosystems for specific functions and the approach we advocate here is no different, but the history of Kudzu in the USA emphasizes the need to temper a focus on ecosystem function with caution for an uncertain future.

3.6.2 Novel methods

In the framework we have presented, a novel ecosystem paradigm shifts management concerns from the specific goal of maintaining historical ecosystems toward an admittedly more qualitative consideration of how the ecosystem functions to provide species habitat and

ecosystem services. As a consequence, many management decisions focus on what to value and when to intervene in these ecosystems. Valuing some novel species interactions, however, also introduces new approaches for how to manage ecosystems (Seastedt et al. 2008). Traditional management responses to species invasions facilitated by novel drivers often include removing or reversing the driver and targeting the invasive species to restore native assemblages. These approaches implicitly assume that successional trajectories can be predicted and that removing drivers of change is sufficient to reverse change (Hobbs and Norton 1996). A growing body of research on priority effects (Belyea and Lancaster 1999; Starzomski et al. 2008) and alternative stable states (Froend et al. 1997; Suding et al. 2004) suggests that these assumptions are not always true (Firn et al. 2010). Further, in a world of global climate change and shifting nutrient cycles, many drivers of ecosystem change are playing out at a scale beyond the control of site managers. To achieve many conservation goals, new approaches become necessary.

These new approaches tend to take two forms. First, new species interactions can mitigate the effects of novel drivers, even if those drivers cannot be reversed. Grazing as a management tool is often used in this context, from mimicking the effects of now-suppressed fire regimes (Seastedt et al. 2008) to mitigating the effects of shifting nutrient cycles (Weiss 1999; Box 3.2) and even curbing the dominance of species whose initial invasion was facilitated by grazing (Firn et al. 2010).

Second, when a system has been degraded through multiple pathways, it can be difficult to isolate and account for all possible thresholds that pose barriers to restoration. Uncertainty about the identity of all thresholds need not be an excuse for inaction, however. For plant restoration, Seastedt et al. (2008) suggest seeding species with a wider range of functional traits and environmental tolerances than present in the historical community. In areas where seed source is not limited, this provides a cost-effective way to increase the likelihood that some desired species establish at the site. For example, in an attempt to restore a mined gravel pit that was once tallgrass prairie, Cherwin et al. (2009) seeded grasses with moisture requirements spanning a wide (500 mm) rainfall gradient. This resulted in a mixed-grass community that, while different from the historical community, was able to persist and provided many of the same ecosystem functions (Seastedt et al. 2008; Cherwin et al. 2009).

Box 3.2 A novel management technique to restore species diversity in California serpentine grasslands

Covering only 1% of California's landscapes, serpentine grasslands contain 10% of California's endemic plant species (Safford et al. 2005). These endemics include Lasthenia californica, which in the spring lives up to its common name of goldfields, and Plantago erecta, which serves as the key host plant for the well-studied highly endangered Bay Area checkerspot butterfly. In short, California serpentine grasslands are prime for management focused on native species diversity. Historically, little intervention was necessary to achieve this goal. The high level of endemic serpentine plant species is due their adaptation to harsh low-nutrient soil conditions that characterize serpentine soils. These same soil characteristics have also historically restricted the establishment of non-native Mediterranean grasses that have successfully invaded most other California grasslands. More recently, however, nitrogen deposition from automobiles has provided a release which allows non-native annual grasses to invade serpentine systems (Weiss 1999). When these tall thatchforming annual grasses become dominant in serpentine systems, they dramatically reduce many native species abundances (Weiss 1999). Removing nitrogen from the system or slowing rates of deposition are outside of the control of site managers. Cattle grazing however serves to remove much of the biomass of non-native species from the serpentine, and cattle trampling reduces the accumulation of non-native thatch that suppresses native species (Weiss 1999). Consequently, cattle grazing constitutes a novel management technique to mitigate the effects of a novel and, from a species conservation perspective, deleterious driver of change.

3.7 WHEN DOES A NOVEL STATE BECOME THE REFERENCE?

Throughout this chapter we have retained the assumption that the historical ecosystem is an appropriate ref-

erence (if not always for species composition, then for key species interactions and ecosystem function). It is worth tempering this assumption with a consideration of ecological history. First, ecosystems are constantly in flux and the time point which we designate 'historical' will be different relative to past time points. Natural climate change coupled with other environmental changes and contingencies have generated no-analog species combinations throughout ecological history (Jackson et al. 2009). Second, a growing body of literature indicates that human societies have long altered ecosystems to suit their needs (Mann 2005; Gammage 2011). This literature both challenges notions of what is natural and suggests that long-past human actions may leave legacies that continue to shape ecosystems. Consequently, a consideration of history provides justification for modern societies to accept some ecosystem change and intervene in ways that promote biodiversity and ecosystem services (Jackson and Hobbs 2009). As species assemblages shift and adapt to anthropogenic change, there may be instances in which novel ecosystems are preferable to any historical ecosystem. This is either because they provide functions that would be lost in the attempt at traditional restoration, or because emergent assemblages are better able to respond to ongoing environmental change. This is the rationale behind efforts to increase connectivity for species to adapt to climate change, and also behind more extreme management suggestions such as assisted colonization (Loss et al. 2011). While these management questions are largely outside of the scope of this chapter, the reasons they are considered highlight the importance of assessing what species and functions an ecosystem currently maintains before attempting to alter it.

3.8 CONCLUDING NOTES

We live in a world shaped by widespread and escalating human activity. As long as anthropogenic change exists, other species will continue to respond to it. This basic premise of the novel ecosystem framework is the foundation for both realistic and optimistic conservation actions. Attempts to restore historical assemblages that do not consider the costs, long-term probabilities of success and ecological consequences of these actions are likely to have unexpected and often unwanted results. Trying to understand when to value emerging species assemblages and interactions, in contrast, provides new opportunities for biodiversity conservation. Acknowledging the dynamism inherent in ecosystems should underpin research and theory as we move toward a robust framework for managing ecosystems in a world of rapid change.

ACKNOWLEDGEMENTS

We thank Keith Bowers, Jack Ewel, Tom Jones, Karen Keenleyside and Tim Seastedt for discussions that developed ideas in this chapter and Steve Jackson, Ariel Lugo and Cara Nelson for helpful comments on earlier drafts.

REFERENCES

- Anderson, R.C., Schwegman, J.E. and Anderson, M.R. (2000) Micro-scale restoration: A 25-year history of a southern Illinois barrens. *Restoration Ecology*, 8, 296–306.
- Belyea, L.R. and Lancaster, J. (1999) Assembly rules within a contingent ecology. *Oikos*, **86**, 402–416.
- Benayas, J.M.R., Newton, A.C., Diaz, A. and Bullock, J.M. (2009) Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* (Washington), **325**, 1121–1124.
- Best, R.J. (2008) Exotic grasses and feces deposition by an exotic herbivore combine to reduce the relative abundance of native forbs. *Oecologia*, **158**, 319–327.
- Best, R.J. and Arcese, P. (2008) Exotic herbivores directly facilitate the exotic grasses they graze: mechanisms for an unexpected positive feedback between invaders. *Oecologia*, **159**, 139–150.
- Bestelmeyer, B.T. (2006) Threshold concepts and their use in rangeland management and restoration: The good, the bad, and the insidious. *Restoration Ecology*, **14**, 325–329.
- Bestelmeyer, B.T., Goolsby, D.P. and Archer, S.R. (2011) Spatial perspectives in state–and–transition models: a missing link to land management? *Journal of Applied Ecology*, **48**, 746–757.
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L. and De Vries, W. (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications*, 20, 30–59.
- Brudvig, L.A. (2011) The restoration of biodiversity: where has research been and where does it need to go? *American Journal of Botany*, **98**, 549–558.
- Buckley, Y.M., Bolker, B.M. and Rees, M. (2007) Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. *Ecology Letters*, **10**, 809–817.

- Chazdon, R.L. (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology Evolution and Systematics*, 6, 51–71.
- Cherwin, K.L., Seastedt, T.R. and Suding, K.N. (2009) Effects of nutrient manipulations and grass removal on cover, species composition, and invasibility of a novel grassland in Colorado. *Restoration Ecology*, **17**, 818–826.
- Cramer, V.A. and Hobbs, R.J. (2002) Ecological consequences of altered hydrological regimes in fragmented ecosystems in southern Australia: Impacts and possible management responses. *Austral Ecology*, **27**, 546–564.
- Davis, M. (2011) Do native birds care whether their berries are native or exotic? No. *Bioscience*, **61**, 501–502.
- Duffy, J.E. (2009) Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, 7, 437–444.
- Dungan, R.J., O'Cain, M.J., Lopez, M.L. and Norton, D.A. (2002) Contribution by possums to seed rain and subsequent seed germination in successional vegetation, Canterbury, New Zealand. New Zealand Journal of Ecology, 26, 121–127.
- Ehrenfeld, J.G. (2004) The expression of multiple functions in urban forested wetlands. *Wetlands*, **24**, 719–733.
- Firn, J., House, A.P.N. and Buckley, Y.M. (2010) Alternative states models provide an effective framework for invasive species control and restoration of native communities. *Journal of Applied Ecology*, **47**, 96–105.
- Forseth, I.N. and Innis, A.F. (2004) Kudzu (Pueraria montana): History, physiology, and ecology combine to make a major ecosystem threat. *Critical Reviews in Plant Sciences*, 23, 401–413.
- Fox, D. (2003) Using exotics as temporary habitat: an accidental experiment on Rodrigues Island. *Conservation*, 4, 32–37.
- Froend, R.H., Halse, S.A. and Storey, A.W. (1997) Planning for the recovery of Lake Toolibin, Western Australia. *Wetlands Ecology and Management*, 5, 73–85.
- Fukami, T., Bezemer, T.M., Mortimer, S.R. and Van Der Putten, W.H. (2005) Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, 8, 1283–1290.
- Funk, J.L., Cleland, E.E., Suding, K.N. and Zavaleta, E.S. (2008) Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology & Evolution*, 23, 695–703.
- Gaertner, M., Den Breeyen, A., Hui, C. and Richardson, D.M. (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Pro*gress in Physical Geography, **33**, 319–338.
- Gammage, B. (2011) The Biggest Estate on Earth: How Aborigines Made Australia. Allen & Unwin, Crows Nest, NSW.
- Gleditsch, J.M. and Carlo, T.A. (2011) Fruit quantity of invasive shrubs predicts the abundance of common native avian frugivores in central Pennsylvania. *Diversity and Distributions*, **17**, 244–253.

- Gonzales, E.K. and Arcese, P. (2008) Herbivory more limiting than competition on early and established native plants in an invaded meadow. *Ecology*, **89**, 3282–3289.
- Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, 86, 902–910.
- Hamann, O. (1975) Vegetational changes in the Galapagos Islands during the period 1966–1973. *Biological Conservation*, 7, 37–59.
- Hamann, O. (1985) The El Niño influence on the Galápagos vegetation, in El Niño in the Galápagos Islands: The 1982– 1983 Event (eds G. Robinson and E. Del Pino), Charles Darwin Foundation, Quito, Ecuador, 299–330.
- Hastings, A. and Wysham, D.B. (2010) Regime shifts in ecological systems can occur with no warning. *Ecology Letters*, 13, 464–472.
- Hobbs, R.J. and Norton, D.A. (1996) Towards a conceptual framework for restoration ecology. *Restoration Ecology*, **4**, 93–110.
- Hobbs, R.J. and Norton, D.A. (2004) Ecological filters, thresholds and gradients in resistance to ecosystem reassembly, in Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice (eds V.M. Temperton, R.J. Hobbs, T. Nuttle and S. Halle), Island Press, Washington, DC, 72–95.
- Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vila, M., Zamora, R. and Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.
- Hobbs, R.J., Higgs, E. and Harris, J.A. (2009) Novel ecosystems: implications for conservation and restoration. *Trends* in Ecology & Evolution, **24**, 599–605.
- Hobbs, R.J., Hallett, L.M., Ehrlich, P.R. and Mooney, H.A. (2011) Intervention ecology: Applying ecological science in the twenty-first century. *Bioscience*, **61**, 442–450.
- Holl, K.D. and Crone, E.E. (2004) Applicability of landscape and island biogeography theory to restoration of riparian understorey plants. *Journal of Applied Ecology*, **41**, 922– 933.
- Houseman, G.R. and Anderson, R.C. (2002) Effects of jack pine plantation management on barrens flora and potential Kirtland's warbler nest habitat. *Restoration Ecology*, **10**, 27–36.
- Impey, A.J., Cote, I.M. and Jones, C.G. (2002) Population recovery of the threatened endemic Rodrigues fody (Foudia flavicans) (Aves, Ploceidae) following reforestation. *Biological Conservation*, **107**, 299–305.
- Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer–Lorenzen, M., Schmid, B., Tilman, D., Van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S. and Loreau, M. (2011) High plant diversity is needed to maintain ecosystem services. *Nature*, **477**, 199–202.

- Jäger, H. and Kowarik, I. (2010) Resilience of native plant community following manual control of invasive Cinchona pubescens in Galapagos. *Restoration Ecology*, 18, 103–112.
- Jäger, H., Kowarik, I. and Tye, A. (2009) Destruction without extinction: long-term impacts of an invasive tree species on Galápagos highland vegetation. *Journal of Ecology*, 97, 1252–1263.
- Jackson, S.T. and Hobbs, R.J. (2009) Ecological restoration in the light of ecological history. *Science*, **325**, 567–569.
- Jackson, S.T., Betancourt, J.L., Booth, R.K. and Gray, S.T. (2009) Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proceedings* of the National Academy of Sciences of the United States of America, **106**, 19685–19692.
- Jax, K. (2005) Function and 'functioning' in ecology: what does it mean? Oikos, 111, 641–648.
- Kowarik, I. (1995) Time lags in biological invasions with regard to the success and failure of alien species, in *Plant Invasions: General Aspects and Special Problems* (P. Pysek, K. Prach, M. Rejmanke and M. Wade, eds), SPB Academic Publishing, Amsterdam, pp. 15–38.
- Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.–P., Garden, D., Girel, J., Pellet, G. and Douzet, R. (2011) Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology*, **99**, 135–147.
- Loss, S.R., Terwilliger, L.A. and Peterson, A.C. (2011) Assisted colonization: Integrating conservation strategies in the face of climate change. *Biological Conservation*, **144**, 92–100.
- Mann, C.C. (2005) 1491: New Revelations of the Americas before Columbus. Alfred A. Knopf, New York.
- Marris, E. (2011) Rambunctious Garden: Saving Nature in a Post-wild World. Bloomsbury, New York, NY.
- Mascaro, J., Hughes, R.F. and Schnitzer, S.A. (2012) Novel forests maintain ecosystem processes after the decline of native tree species. *Ecological Monographs*, 82, 221–238.
- Millennium Ecosystem Assessment. (2005) Ecosystems and Human Well-being. Synthesis. Island Press, Washington, DC.
- Miller, J.R. and Hobbs, R.J. (2007) Habitat restoration: Do we know what we're doing? *Restoration Ecology*, 15, 382–390.
- Naeem, S. (2002) Ecosystem consequences of biodiversity loss: The evolution of a paradigm. *Ecology*, 83, 1537– 1552.
- Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D.R., Chan, K.M.A., Daily, G.C., Goldstein, J., Kareiva, P.M., Lonsdorf, E., Naidoo, R., Ricketts, T.H. and Shaw, M.R. (2009) Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Frontiers in Ecology and the Environment*, 7, 4–11.
- Nepstad, D., Carvalho, G., Barros, A.C., Alencar, A., Capobianco, J.P., Bishop, J., Moutinho, P., Lefebvre, P., Silva, U.L. and Prins, E. (2001) Road paving, fire regime feedbacks,

and the future of Amazon forests. *Forest Ecology and Management*, **154**, 395–407.

- Pawson, S.M., Brockerhoff, E.G., Meenken, E.D. and Didham, R.K. (2008) Non–native plantation forests as alternative habitat for native forest beetles in a heavily modified landscape. *Biodiversity and Conservation*, **17**, 1127–1148.
- Polasky, S., Carpenter, S.R., Folke, C. and Keeler, B. (2011) Decision–making under great uncertainty: environmental management in an era of global change. *Trends in Ecology* & *Evolution*, **26**, 398–404.
- Pyke, D.A., Herrick, J.E., Shaver, P. and Pellant, M. (2002) Rangeland health attributes and indicators for qualitative assessment. *Journal of Range Management*, 55, 584–597.
- Radeloff, V.C., Stewart, S.I., Hawbaker, T.J., Gimmi, U., Pidgeon, A.M., Flather, C.H., Hammer, R.B. and Helmers, D.P. (2010) Housing growth in and near United States protected areas limits their conservation value. *Proceedings* of the National Academy of Sciences of the United States of America, **107**, 940–945.
- Richardson, P.J., Lundholm, J.T. and Larson, D.W. (2010) Natural analogues of degraded ecosystems enhance conservation and reconstruction in extreme environments. *Ecological Applications*, **20**, 728–740.
- Ricklefs, R.E. (1987) Community diversity: Relative roles of local and regional processes. *Science*, **235**, 167–171.
- Rossiter, N.A., Setterfield, S.A., Douglas, M.M. and Hutley, L.B. (2003) Testing the grass–fire cycle: alien grass invasions in the tropical savannas of Northern Australia. *Diversity and Distributions*, **9**, 169–176.
- Rumpff, L., Duncan, D.H., Vesk, P.A., Keith, D.A. and Wintle, B.A. (2011) State-and-transition modelling for Adaptive Management of native woodlands. *Biological Conservation*, 144, 1224–1236.
- Safford, H.D., Viers, J.H. and Harrison, S.P. (2005) Serpentine endemism in the California flora: a database of serpentine affinity. *Madroño*, **52**, 222–257.
- Santiago-Garcia, R.J., Colon, S.M., Sollins, P. and Van Bloem, S.J. (2008) The role of nurse trees in mitigating fire effects on tropical dry forest restoration: A case study. *Ambio*, **37**, 604–608.
- Sax, D.F. and Gaines, S.D. (2008) Species invasions and extinction: The future of native biodiversity on islands. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11490–11497.
- Seastedt, T.R., Hobbs, R.J. and Suding, K.N. (2008) Management of novel ecosystems: are novel approaches required? *Frontiers in Ecology and the Environment*, 6, 547–553.
- Snyder, S.A., Miller, J.R., Skibbe, A.M. and Haight, R.G. (2007) Habitat acquisition strategies for grassland birds in an urbanizing landscape. *Environmental Management*, **40**, 981–992.
- Spaulding, S.E. and Rothstein, D.E. (2009) How well does Kirtland's warbler management emulate the effects of

natural disturbance on stand structure in Michigan jack pine forests? *Forest Ecology and Management*, **258**, 2609–2618.

- Standish, R.J., Robertson, A.W. and Williams, P.A. (2001) The impact of an invasive weed Tradescantia fluminensis on native forest regeneration. *Journal of Applied Ecology*, 38, 1253–1263.
- Starzomski, B.M., Parker, R.L. and Srivastava, D.S. (2008) On the relationship between regional and local species richness: a test of saturation theory. *Ecology*, **89**, 1921– 1930.
- Stone, G.N., Van Der Ham, R.W.J.M. and Brewer, J.G. (2008) Fossil oak galls preserve ancient multitrophic interactions. *Proceedings of the Royal Society B: Biological Sciences*, 275, 2213–2219.
- Suding, K.N. and Hobbs, R.J. (2009) Threshold models in restoration and conservation: a developing framework. *Trends* in Ecology & Evolution, 24, 271–279.
- Suding, K.N., Gross, K.L. and Houseman, G.R. (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, **19**, 46–53.
- Thompson, J., Lugo, A.E. and Thomlinson, J. (2007) Land use history, hurricane disturbance, and the fate of introduced species in a subtropical wet forest in Puerto Rico. *Plant Ecology*, **192**, 289–301.
- Thompson, R. and Starzomski, B.M. (2007) What does biodiversity actually do? A review for managers and policy makers. *Biodiversity and Conservation*, 16, 1359–1378.
- Valentine, L.E. and Stock, W. (2008) Food resources of Carnaby's black cockatoo (*Calyptorhynchus latirostris*) in the Gnangara sustainability strategy study area. Report to Forest Products Commission, Perth, Australia.
- Wainger, L.A., King, D.M., Mack, R.N., Price, E.W. and Maslin, T. (2010) Can the concept of ecosystem services be practically applied to improve natural resource management decisions? *Ecological Economics*, **69**, 978–987.
- Wallace, K.J. (2003) Lake Toolibin: working together. Pacific Conservation Biology, 9, 51–57.
- Watson, J., Trueman, M., Tufet, M., Henderson, S. and Atkinson, R. (2009) Mapping terrestrial anthropogenic degradation on the inhabited islands of the Galápagos archipelago. *Oryx*, **44**, 79–82.
- Weiss, S.B. (1999) Cars, cows, and checkerspot butterflies: Nitrogen deposition and management of nutrient-poor grasslands for a threatened species. *Conservation Biology*, 13, 1476–1486.
- Westoby, M., Walker, B. and Noymeir, I. (1989) Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, **42**, 266–274.
- Wilkinson, S.R., Naeth, M.A. and Schmiegelow, F.K.A. (2005) Tropical forest restoration within Galapagos National Park: Application of a state-transition model. *Ecology and Society*, **10**, 28–43.