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Invoking the Ghosts of Landscapes Past to Understand the Landscape Ecology of the Present . . . and the Future

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Abstract. Most landscapes bear the imprint of past human land use that in some cases dates back centuries or even millennia. Land use has the potential to create strong legacy effects on biotic communities that may persist for decades or centuries, even after the landscape has been abandoned and seemingly restored to its natural pre-settlement state. Current species distributions may thus better reflect historical than contemporary landscape configurations, owing to the lagged response of species to landscape change. These "ghosts of landscapes past" have been found to haunt the biota of both terrestrial and aquatic systems. This chapter examines several case studies that illustrate the magnitude of human land-use legacies, and considers the types of species and landscape scenarios for which lagged responses to landscape change are especially likely, in the hopes that we can better detect delayed responses to land use, should we ever wish to attempt to exorcise the ghosts of landscapes past. Ignoring the ghosts of landscapes past is potentially risky from a conservation or land-management perspective. Past land use may incur an extinction debt, especially in landscapes that have undergone rapid transformation and if the remaining habitat lies below the extinction threshold for many species. Because time lags to landscape change are expected to be especially long at the extinction threshold, we may be seriously underestimating extinction risk and the impact of past land use on biological communities. Thus, knowledge of current landscape structure may not be the best basis for assessing extinction risk, or for predicting the response of species to future landscape change, in the absence of information on landscape history. The ultimate value of adopting a historical perspective, however, is a better understanding of the temporal dynamics of landscapes, which not only provide a frame of reference for evaluating the impact of past human land-use activities within an ecological context, but may also contribute to the development of land-management systems that are more in tune with the dynamic landscape systems they are designed to manage.

3.1. Introduction

In many parts of the world, humans have emerged as the primary drivers of landscape change, ushering in an era of widespread habitat transformation, rapid

climate change, and diminished biological diversity. Never before has there been a greater need—or urgency—for understanding the impact of human land-use activities on landscape structure and hence on the ecology of human-modified landscapes. Given that 50–80% of the Earth's land surface has been transformed, altered, or influenced by human activities (Vitousek et al., 1997; Sanderson et al., 2002), nearly all landscapes can be considered human-modified, at least at some point in human history. Habitat transformation driven by human land use represents the single greatest threat to biodiversity, followed by the threat posed by invasive species (Wilcove et al., 1998; Hilton-Taylor, 2000). Land transformation contributes to the outright loss, fragmentation, and degradation of habitat and may also facilitate invasion by non-native species, creating a positive feedback that further enhances land transformation (Hobbs, 2000; With, 2002).

Little wonder, then, that conservationists and landscape ecologists tend to focus on the spatial dimensions of landscape change, particularly in terms of identifying how much habitat is enough to avert extinction or to mitigate fragmentation effects on biodiversity and invasive spread (Fahrig, 2001, 2003; With, 2004). Even studies that purport to examine the effect of "habitat loss" on biodiversity, which implies an analysis of landscape change, generally have assayed only the effect of "habitat difference" among contemporary landscapes that vary in the amount of habitat (Schrott et al., 2005a). Such studies make a space-for-time substitution (Hargrove and Pickering, 1992) by analyzing landscapes that are replicated in space rather than time. For this approach to be valid, one must assume either that all landscapes lie on the same trajectory of change (Fig. 3.1a), or that landscape history—the rate and process by which landscapes have achieved their current state—is not important.

Ignoring the temporal dimensions of landscape change is potentially risky from a conservation or management standpoint. Clearly there is an urgent need to recognize landscapes that are currently undergoing broad-scale transformation at unprecedented rates (e.g., humid tropical forests in Southeast Asia; Achard et al., 2002), but landscape history increasingly is seen as integral to sound environmental science and for providing the proper context and guidance for ecosystem management (Swetnam et al., 1999; Foster et al., 2003). Partly this stems from: (1) the growing recognition among natural resource and land managers that landscapes are inherently dynamic systems, with important ecosystem processes and disturbance regimes operating over many different scales in space and time, spanning decades, centuries, or even millennia; (2) that human land-use activities may lie outside the range of natural variability for the system; and (3) that adopting a historical perspective may enable managers to set goals with a better chance of maintaining and protecting ecosystems while continuing to meet societal demands for the goods and services provided by those systems (Landres et al., 1999; Parsons et al., 1999). The reconstruction of historical landscapes thus provides a frame of reference for assessing how past environmental changes have driven changes in biodiversity through time (Delcourt and Delcourt, 1998; Swetnam et al., 1999), as a means of documenting how these changes may have been altered by human
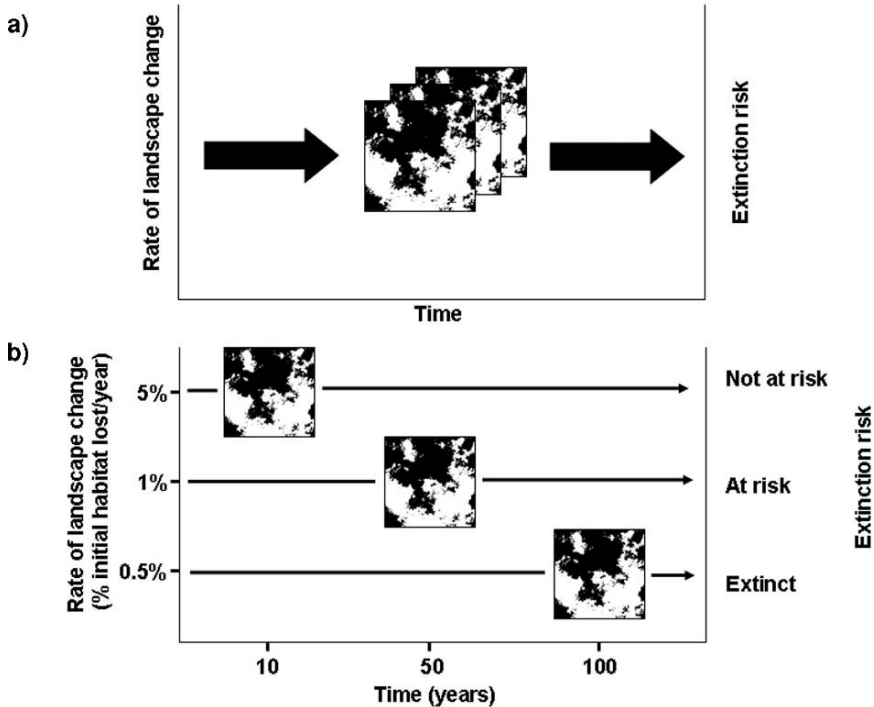
FIGURE 3.1. The importance of landscape history for assessing a species' risk of extinction from habitat loss and fragmentation. Most studies ignore landscape history and assume that all landscapes lie on the same trajectory of change: (a) Extinction risk is thus assessed probabilistically for populations on landscapes for a given amount and distribution of habitat (e.g., 50%). If these landscapes achieved their current state at very different rates, however, then assessment of extinction risk will be dependent on this aspect of landscape history; (b) Populations may be variously assessed as "not at risk," "at risk," or "extinct," depending upon how long the landscape has been subjected to human land use. In particular, extinction risk may be underestimated in landscapes undergoing rapid rates of change because of demographic lags. (based on results of Schrott et al. 2005a).

activities that have transformed more natural landscapes into more cultural ones (Delcourt and Delcourt, 1988, 2005).

The cultural footprint left on landscapes is typically large, deep, and long-lasting. Some landscapes have a long history of human land-use spanning many centuries or millennia, and the modern landscape may still bear the imprint of ancient land-use activities produced by clearing, plowing, draining, or terracing (Dupouey et al. 2002; Foster et al., 2003; Davidson and Simpson, 2005). Land use creates a strong legacy effect on biotic communities that may persist for decades or centuries, even after the landscape has been abandoned and seemingly restored to its "natural" pre-settlement state (Swetnam et al., 1999; Foster et al., 2003). Such appearances may be deceiving, however, because the recovered post-settlement landscape may

only superficially resemble its pre-settled state or a comparable landscape that had never been disturbed by such land use. Thus, present-day communities may better reflect past landscape states than current ones, especially if species exhibit lagged responses to landscape change.

In this chapter, I present several case studies that illustrate the enduring legacy of land use on populations and communities. In particular, I review the potential for lagged responses to landscape change to occur, in which the decline or extirpation of species may not happen for many decades and may continue long after the initial period of human-induced disturbance has ceased and the landscape appears to have recovered. Because past land use may incur an *extinction debt* (*sensu* Tilman et al., 1994), knowledge of current landscape structure may not be the best basis for understanding species–habitat relationships or for predicting the response of species to future landscape change in the absence of information on landscape history.

3.2. Legacy Effects of Landscape Change

The "ghosts of landscapes past" have been found to haunt the biota of both terrestrial and aquatic systems. Land-use legacies on vegetation communities are especially prevalent and well documented. In central Massachusetts (USA), for example, the legacy of past agricultural land-use from the 18th century is still reflected in the vegetation of today's forests. This landscape has undergone a complete transformation during the past three centuries: from a primarily forested region that was largely cleared for timber and agriculture by the mid-1800s following European settlement, to a now mostly forested region once again as industrialization during the latter half of the 19th century led to farm abandonment and migration to urban centers, thus allowing for natural reforestation over the past 100–150 years in spite of a steadily increasing human population (Foster et al., 1998). Despite the return to forest, the structure and composition of these forests have been dramatically—and perhaps permanently—altered by this relatively brief but intense period of deforestation and agricultural land use, such that current landscapes are much more homogeneous across the region than during Colonial times. Forests are now dominated by trees such as paper birch (*Betula papyrifera*), red maple (*Acer rubrum*) and white pine (*Pinus strobum*) that were relatively uncommon in Colonial forests, but which are essentially "pioneer species" that were capable of broad-scale dispersal and rapid establishment following severe disturbance wrought by clearing, cutting, and cultivation of the region (Foster et al., 1998). In contrast, species such as eastern hemlock (*Tsuga canadensis*) and beech (*Fagus grandifolia*), which are long-lived and poor dispersers, have yet to recover their former abundance or extent.

Looking past the trees, the forest contains other land-use legacies from America's Colonial period. The current impoverishment of forest herbs is also thought to be a legacy of 18th-century forest clearing. The understory flora of woodlands that had been cleared and plowed, but which were allowed to reforest naturally following agricultural abandonment, still bear the signature of past cultivation: they contain more weedy species and fewer ericaceous shrubs (e.g., wintergreen,

Gaultheria procumbens; huckleberry, *Gaylussacia baccata*; wild raisin, *Viburnum cassinoides*) than woodlands that escaped the plow (Foster et al., 2003). Many forest herbs have low seed production, lack persistent seed banks, and are dispersal-limited (i.e., their seeds are ant-dispersed or lack morphological structures for long-distance dispersal) because they are adapted to relatively stable forest ecosystems that are characterized by fine-scale patch disturbances (Bellemare et al., 2002). These species have not exhibited rapid recovery and recolonization following their extirpation from areas that had been cleared and cultivated. In a modeling study of land-use change over a 300-year period, Matlack (2005) showed that seed dispersal ability was critical to the regional survival of forest herb species. Further, the model predicted that the legacy effects of agricultural land-use would likely persist for at least another century. Given the spatial and temporal scale of human land-use, slow-migrating species and those lacking gap-crossing abilities are most at risk of regional extinction, raising the possibility of an extinction debt for herbaceous species in these forests. Additionally, past land-use may affect nitrogen cycling and the spatial heterogeneity of soil resources (Fraterrigo et al., 2005), which could produce effects that persist for many decades, resulting in a fundamental shift in the composition and diversity of these forested ecosystems. If true, it may not be possible to recover historical vegetation even if dispersal limitation is eventually overcome in time (see also Dupouey et al., 2002).

Past land use also influences the biological diversity of aquatic systems. Aquatic systems have a strong dependence on the surrounding landscape, and land-use practices throughout the watershed may affect a wide range of conditions, such as hydrology, organic inputs, temperature, and water chemistry, and are thus capable of contributing to strong legacy effects (Allan et al., 1997). For example, patterns of fish and invertebrate diversity within streams draining two watersheds in the southern Appalachians were best explained not by current land use, but by the intensity of agricultural land use some 40 years earlier (Harding et al., 1998). Although some streams currently flow through watersheds that are mostly forested, their complement of fish and invertebrate species more closely resembled those found in agricultural streams. Significantly, these "anomalous" forested streams were in watersheds that had formerly experienced a high degree (∼40%) of deforestation and agriculture in the 1950s. Reforestation over the past half-century has thus resulted in little effective recovery of these stream communities. As in terrestrial systems, the recovery of aquatic biota from high-impact disturbances such as deforestation or agriculture—even though seemingly removed from the stream or lake in question—can still take decades to achieve.

It comes as no surprise that landscape transformation has such profound effects on biological communities; rather, the surprise is that these effects are so persistent even after human activities have ceased and vegetation has been allowed to recover (however illusory that recovery may be). Even if transformation was not complete or particularly extensive, human land use can still have other more subtle effects on landscape structure, which may have no less a dramatic effect on patterns of diversity. For example, a seemingly trivial loss of habitat at a critical point can effectively disrupt the habitat connectivity of the entire landscape, which may have consequences for biodiversity that far exceed the actual amount of habitat lost (e.g.,

nonlinear or critical threshold responses; With and Crist, 1995). A disruption of landscape connectivity can reduce dispersal or colonization success and enhance species extinction risk (With and King, 1999a,b), even when local conditions are not directly affected by land-use activities. As with landscape transformation, a disruption of connectivity has the potential to produce strong legacy effects in diversity patterns. For example, high plant species diversity within the small remaining patches of semi-natural grassland in Sweden is a relic of a formerly connected open farming landscape that existed nearly a century ago (Lindborg and Eriksson, 2004). These grasslands have declined more than 90% during the past 80 years, such that historical grasslands had much higher connectivity than present-day remnants. Subsequently, these grasslands have maintained a higher diversity of plants than might otherwise be expected based on the current amount and distribution of habitat. Similarly, historical habitat connectivity still exerts an influence on the distribution of carabid beetles within hedgerow networks of France (Burel, 1992; Petit and Burel, 1998). Hedgerows have been declining since the 1950s as a result of a shift from traditional to modern farming practices, resulting in increased isolation of beetle populations. It may take many decades, however, before beetle populations disappear from isolated hedgerows. Beetle distributions thus exhibit a 'memory' of past landscape structure, with the result that current carabid beetle assemblages better reflect the historical landscape structure of a half-century ago than the present-day hedgerow network. It is worth noting, then, that land-use legacies are not always negative (e.g., depauperate herb or fish communities in reforested landscapes following agricultural abandonment), but may actually appear to be positive (a retention of native species, such as carabids or grassland plants, in spite of past land clearing), at least in the short term.

3.3. Of Time Lags and Extinction Debts

As these examples illustrate, legacy effects of past land-use are ultimately produced by lags in species' responses to landscape change, which leads to a decoupling of landscape pattern and species distributions. Despite the severity of the impact, the response by the biological community to human land use is usually not immediate. Instead, communities may undergo a slow hemorrhaging, with some species eventually going extinct many decades or centuries even after the initial disturbance has ceased. *Extinction debt* is an extreme manifestation of a lagged response to past landscape change (Tilman et al., 1994). Time lags are expected to be especially long near the extinction threshold—the critical amount of habitat required for species persistence (Hanski and Ovaskainen, 2002). As habitat loss and fragmentation push the metapopulation closer to its extinction threshold, theory predicts increasingly longer delays in the time required for the metapopulation to achieve a new equilibrium in the changed landscape (extinction, in this case). In other words, extinction debts are likely in landscapes that exceed the extinction threshold for many species. If so, then we may be seriously underestimating the threat posed by past land-use to current biodiversity. For example, the rich diversity of

freshwater mussels in the Midwestern United States has undergone a precipitous decline following a century of landscape conversion to agriculture that entailed draining almost all (>90%) of the wetland habitat (Poole and Downing, 2004). In Iowa, nearly half of the stream mussel species that had ever been recorded in the state were extinct by 1985. Freshwater mussels have the dubious distinction of suffering the highest extinction rates of any taxonomic group, terrestrial or aquatic, but then such a dire statistic is hardly surprising given the scale of habitat loss and degradation. Over the ensuing decade (1985–1998), however, mussel species continued to go extinct and had totally vanished from half the streams surveyed, an alarming discovery given that land use has changed little over the past several decades (Poole and Downing, 2004). The extinction debt incurred by near total habitat transformation more than a century ago continues to pay out, and is greatest where historically habitat destruction had been the most complete (i.e., watersheds that had the most habitat converted to farmland suffered the greatest loss of species). As grave as the present situation appears to be for freshwater mussels, the future may be far bleaker than previously imagined as these lagged extinctions play out. Nor are these land-use effects on mussels a relatively recent phenomenon. An analysis of prehistoric shell middens revealed declines in freshwater mussels that are coincident with the advent of broad-scale maize agriculture by Native Americans throughout the eastern half of the Mississippi River basin some 1,000 years ago (Peacock et al., 2005). Prehistoric land use was thus capable of exacting a toll on biological communities that was similar—if less acute—than that exerted by modern societies.

An extinction debt also has been inferred for primates inhabiting the forests of Africa (Cowlishaw, 1999). Nearly half of all primate species are threatened with extinction, yet none has gone extinct since 1600, suggesting there may be a long extinction lag. Cowlishaw (1999) developed species-area relationships based on past deforestation levels to quantify the magnitude of the extinction debt. Forest loss over the past 50 years should have resulted in the extinction of several forest primates, yet none has yet occurred. In most countries, the debt is estimated to comprise over 30% of the forest primates (a debt of 4–8 species), with Cameroon and Nigeria having the largest extinction debts. Extinction debts for forest primates may thus take thousands of years to pay out. Historical deforestation poses a grave threat to forest primates, but this extinction debt is only exacerbated by the rapid rate at which forests are currently being lost in Africa (e.g., Achard et al., 2002).

The problem, then, lies with rapidly changing landscapes and slow-changing populations, a situation which may describe the plight of Neotropical migratory songbirds, which have demonstrated widespread declines in North America over the past 30 years or so. Using a spatially structured avian demographic model, Schrott et al. (2005a) showed how extinction risk in songbirds could be underestimated in populations on landscapes undergoing rapid habitat loss, relative to landscapes where populations were subjected to low-level chronic disturbance over a long time period. In the former scenario, the rate of landscape change exceeded the response time of the population (Fig. 3.2a). That is, there was not sufficient time for the demographic consequences of habitat loss and fragmentation, such as
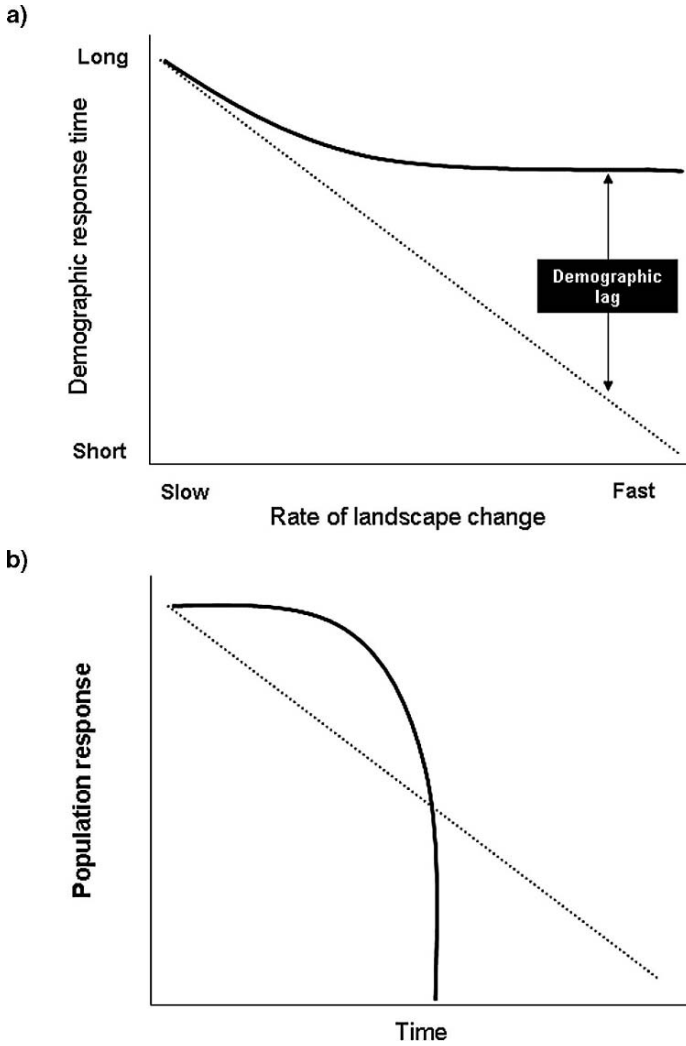
a)

b)

FIGURE 3.2. Demographic lags may produce discordant responses to landscape change. Species incapable of rapid response to landscape change tend to be found in more stable landscapes subjected to infrequent or low levels of disturbance (diagonal line, a). In landscapes undergoing rapid rates of change owing to human conversion, however, such species will exhibit delayed population responses to landscape change as a consequence of demographic lags, such as initially high survivorship or longevity (a). Even if habitat loss and fragmentation have a negative effect on fecundity or survivorship, it may take awhile before these demographic consequences are translated into obvious population responses such as negative exponential growth (b). At that point, populations may suddenly undergo rapid declines (i.e., a nonlinear or threshold response). Such threshold responses may come as a surprise if landscape history is not taken into consideration.

reduced nesting success and fledgling production, to be reflected in population-wide measures of viability such as intrinsic growth rate (λ) that are used to assess extinction risk. As a consequence, the population may not be assessed as "at risk" in these landscapes undergoing rapid habitat loss, and yet the population ultimately goes extinct, often abruptly with little apparent warning (Fig. 3.2b). There thus appears to be a scaling mismatch between the temporal scale of landscape change relative to the temporal scaling of the species' demographic response (Fig. 3.2). The past history of landscape change—such as the rate of habitat loss—is thus important for evaluating extinction risk in current landscapes.

In assessing a species' risk of extinction from habitat loss and fragmentation, the time it has taken a landscape to achieve its present state may be just as important as the amount of habitat lost or how fragmented the current landscape has become. For example, three landscapes may have similar amounts of habitat (e.g., 50%) and levels of fragmentation, but depending upon the rate at which habitat was destroyed and thus how quickly these landscapes achieved their current state, populations on these landscapes may be variously assessed as either (l) locally extinct (habitat lost at a rate of 0.5%/year over 100 years), (2) at risk for extinction (habitat lost at a rate of 1.0%/year over 50 years), or (3) not at risk of extinction (habitat lost at a rate of 5%/year over 10 years; Fig. 1b). In the latter case, extinction risk is underestimated because the landscape has changed more rapidly than the demographic potential of the population, resulting in a lagged response of the population to habitat loss and fragmentation as discussed previously. Such lagged responses to landscape change may also have implications for recovery of songbird populations through habitat restoration (Schrott et al., 2005b). Although it is generally assumed that populations will recover once habitat has been restored (either naturally or through human intervention), demographic lags to landscape change—even positive changes—can also affect the potential for recovery. Although populations may have declined in response to habitat loss and fragmentation (they are habitat-sensitive), recovery of these populations may no longer be limited by the amount of the habitat on the landscape. For example, populations subjected to chronic low-level disturbance over a long time period may suffer demographic erosion (e.g., reproductive success and fecundity decline as habitat continues to be lost and fragmented), such that complete habitat restoration will not be sufficient to offset mortality and recover the population (Schrott et al., 2005b). Recovery for these species is considered to be more demographically limited than habitat-limited. In such cases, conservation efforts would need to focus on measures capable of boosting fecundity and/or survivorship (e.g., improve quality of nesting habitat, control nest predators) to rescue such species, in addition to restoring habitat (see Bissonette, Chapter 1, this volume).

3.4. Management and Conservation Implications of Landscape Ghosts

If most landscapes bear the legacy of past land use, which in some cases dates back centuries, then many extant species may be relics of a bygone landscape that no longer exists, or at least, has been significantly altered. This raises some

important practical—as well as ethical—considerations regarding the management and conservation of such species. If the species are associated with the native habitat and have persisted in spite of human land-use activities, then the concern might be whether these are the collateral of an extinction debt that has yet to be fully paid. If population declines lag well behind the loss and fragmentation of habitat, then extinction risk could be greatly underestimated, especially if habitat transformation occurred rapidly relative to the species' generation time (Schrott et al., 2005a). Most assessments of extinction risk ignore landscape history and are based only on the current landscape configuration, or use this as a baseline for evaluating the effect of future land-use change. This approach may not be valid if the manner by which the landscape achieved its current state affects the population trajectory (Fig. 1b).

Alternatively, if a species' presence is a legacy of the past land use (e.g., "weedy" or early successional species associated with cultivated or grazed habitats), then is their decline following the abandonment and subsequent recovery of the landscape a concern for conservation? Or, are these non-native and potentially invasive species that should be actively expunged from the landscape? What if these early-successional species are now globally rare because they were maintained historically by land-use activities such as grazing that no longer occur? Do biological assemblages that have developed as a consequence of past human activity have value, and if so, should we actively manage to preserve these cultural landscapes (Landres et al., 1999)?

Such a case has been made for the flora associated with the grasslands, heathlands, and shrublands of coastal New England, which support the highest concentration of rare and uncommon species in the Northeast. Despite the common belief that these habitats were native and had been widespread in the pre-European landscape, these open-land habitats are apparently anthropogenic, having been created and maintained by farming practices such as plowing, prescribed burning, and grazing by sheep following European settlement and clearing of the region in the 17th century (Motzkin and Foster, 2002). These open habitats are in fact a cultural artifact, which have been dwindling in the face of widespread reforestation of the region, such that the early-successional species associated with these habitats now are rare and considered a high priority for conservation. Many of these species have continued to decline in spite of active management involving prescribed burning and mowing, which has not been entirely successful in halting the encroachment of woody vegetation and the return to forest. Motzkin and Foster (2002) recommend a return to traditional grazing practices to recover these plants, despite the fact these species are relics of a bygone—and cultural—landscape. They still represent a unique and important component of regional biodiversity.

Clearly, then, not all ghosts of landscapes past are necessarily unwelcome or even undesirable. Humans inevitably bring a cultural bias to the problem of which species or habitats to conserve. Throughout Europe, for example, where landscapes have had a more pronounced history of human occupation and alteration, environmental legislation puts high conservation value on numerous habitat types

and species communities that resulted from traditional land-use practices, and are now at risk from abandonment of these practices (e.g., semi-natural grasslands; European Union Habitats Directive 92/43/EEC; Redecker et al., 2002).

3.5. Ghost-Busting and the Exorcism of Landscapes

In cases where land-use legacies have an undesirable effect on biodiversity, however, we are faced with the dual problem of detecting (or anticipating) lagged effects, as well as potentially exorcising these ghosts of landscapes past. By definition, a lagged response to landscape change means that the effects of land use will not be immediately apparent. Short of a séance, then, how can we detect such lagged effects? What types of species are most likely to exhibit lagged responses to landscape change? When are time lags to landscape change to be expected? Can we ever hope to exorcise the ghosts of landscapes past?

3.5.1. How Can We Detect Lagged Responses to Land Use?

As illustrated by the case studies in this chapter, time lags may be revealed through "ghost hunting" (Nagelkerke et al., 2002), which reveals whether current species distributions match a historical landscape configuration better than the current landscape (e.g., Petit and Burel, 1998; Lindborg and Eriksson, 2004), or through statistical analyses that demonstrate a significant relationship between the species present (or lost) and the type or intensity of past land use (e.g., Harding et al., 1998; Poole and Downing, 2004). Alternatively, it may be possible to quantify the magnitude of the extinction debt by developing species–area relationships based on past habitat amounts or relative to some type of "reference landscape" (e.g., Cowlishaw, 1999). Modeling approaches may also be used to predict extinction debt, to assess extinction risk, or to forecast population trends based on simulations of past landscape change (e.g., Tilman et al., 1994; Hanski and Ovaskainen, 2002; Nagelkerke et al., 2002; Schrott et al., 2005a).

3.5.2. What Types of Species Are Most Likely to Exhibit Lagged Responses to Landscape Change?

The types of species most likely to exhibit lagged responses to landscape change are species with poor colonization abilities; species with large or stable local population sizes; species with long individual lifespans or seed banks; species with low turnover or population growth rates; and species with low sensitivity to environmental fluctuations (Nagelkerke et al., 2002; Lindborg and Eriksson, 2004). For example, Lindborg and Eriksson (2004) have suggested that short-lived or highly mobile organisms (such as insects or birds, respectively) may not be as sensitive to landscape history as, say, long-lived plants. As the case studies in this chapter have illustrated, however, even carabid beetles (Burel, 1992; Petit and

Burel, 1998) and songbirds (Schrott et al., 2005a,b) may show legacy effects or lagged population responses to landscape change. Time lags are thus determined by the interaction between species' life-history attributes and landscape dynamics (e.g., rate of habitat change).

3.5.3. When are Time Lags to Landscape Change to be Expected?

The ghosts of landscape past are most likely to haunt habitats that historically have been relatively stable (e.g., old growth forests), where species tend to react slower and exhibit greater lags (Nagelkerke et al., 2002; Fig. 3.2). For example, the high diversity of crustose lichens within recently isolated remnants of old-growth boreal forest in northern Sweden—relative to naturally fragmented forest patches that have been isolated for millennia—suggests an extinction debt incurred by logging (Berglund and Jonsson, 2005). Such old-growth species are also expected to recover slowly, producing a large difference between the timing of decline and recovery. Time lags may be particularly long in landscapes where the amount of remaining habitat is near a species' extinction threshold (Hanski and Ovaskainen, 2002).

No habitat type is immune to the effects of land-use legacies, especially if the disturbance is novel within the context of the system (as human land-use activities often are), and exceeds the extent, intensity, or frequency of natural disturbances that have shaped the landscape historically. Lagged responses are likely following a relatively fast landscape change that exceeds the demographic potential (or response time) of the population, leading to delayed local extinction that may contribute to an extinction debt (Nagelkerke et al., 2002; Schrott et al., 2005a). Conversely, there is also the potential for a lag in recovery following landscape restoration due to a "colonization credit", which is the slow reappearance of species owing to low colonization rates (Nagelkerke et al., 2002; Matlack, 2005). Slow recovery is not limited to just poor colonizers, however. Populations may also be demographically limited in their ability to respond to habitat restoration, such as when habitat fragmentation decreases fecundity or survivorship of individuals in habitat remnants (Schrott et al., 2005b).

3.5.4. Can we Ever Hope to Exorcise the Ghosts of Landscapes Past?

Because biological communities bear the legacy of past environmental change, the real issue here concerns the extent to which we will be able to reverse or prevent the negative impacts of human-driven landscape change on biodiversity. This is obviously the mission of conservation biology, but adopting a historical perspective provides the necessary vista from which to gauge what direction we should be heading given where we have been.

Clearly, the protection of the current landscape is unlikely to be sufficient to guarantee the long-term survival of species impacted by past land use (Nagelkerke et al., 2002), but is restoration of the historical landscape absolutely necessary in order to rescue these species? Given that dispersal limitation characterizes many species that exhibit lagged responses, increasing connectivity of the remaining habitat should at least increase colonization rates and help to mitigate extinction risk. For example, Cowlishaw (1999) recommended constructing habitat corridors between remaining forests as a means of averting extinction in some forest primates, thus canceling part of the debt. Turning a negative into a positive, it might even be possible to exploit time lags because such lags in species' responses to landscape change also give time for action before it is too late (Nagelkerke et al., 2002).

Nevertheless, we should anticipate that recovery from past land use may be slow, owing to demographic lags (Schrott et al., 2005b) and colonization credits (Nagelkerke et al., 2002), which predict that species may also lag in response to habitat restoration. In addition, the amount of habitat required for population recovery (the restoration threshold) may be far greater than that leading to the species' extirpation from the initial landscape (extinction threshold). That is, restoring just the minimum amount of habitat that was initially required to avert extinction (i.e., slightly above the species' extinction threshold) may no longer be sufficient to recover populations on landscapes that have fallen below the species' extinction threshold. It is sobering to realize that the impact of some past land-use activities may well be irreversible, having set the landscape on a different trajectory such that it may no longer be possible to recover the historical conditions that once favored certain species. For example, past cultivation may greatly alter soil carbon and nitrogen levels, causing long-lasting and sometimes permanent changes in productivity and plant species composition (e.g., Foster et al., 2003; Davidson and Simpson, 2005). In such cases, it is important to recognize the limitations of habitat restoration as a management tool for species recovery (e.g., Schrott et al., 2005b) to avoid wasting valuable time and resources that could be better applied elsewhere.

To conclude, the ghosts of landscapes past are omnipresent and will continue to haunt the ecology of landscapes future. The ultimate value of adopting a historical perspective is a better understanding of the temporal as well as spatial dynamics of landscapes. This provides not only a frame of reference for evaluating the impact of past human land-use activities within an ecological context, but may also contribute to the development of management systems that are more in tune with the management of these dynamic landscape systems (Landres et al., 1999; Swetnam et al., 1999).

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