Metapopulation Dynamics Following Habitat Loss and Recovery: Forest Herbs in Ancient and Recent Forests

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Many regions of Europe and eastern North America share broadly similar histories of land use over the past several centuries, with varying degrees of forest clearance followed by varying degrees of forest recovery. Here I use metapopulation models to explore the influence of the extent and timing of forest clearance and recovery on patch occupancy of slow-colonizing forest herbs in ancient and recent forests. If forest clearance exceeds the threshold for metapopulation persistence, extinction may require centuries to occur even when clearance is most severe. This suggests a heavy extinction debt for forest herbs in fragmented landscapes. The time between forest clearance and recovery (t_{c-r}) can have a strong influence on metapopulation dynamics. If t_{c-r} is short, patch occupancy in ancient forests (P_{AO}) will start out high, and exert a strong 'colonization pressure' on recent forests, increasing patch occupancy in recent forests (P_{RO}) above its equilibrium value before it ultimately declines towards equilibrium. If t_{c-r} is long, P_{AO} starts out low, and both P_{AO} and P_{RO} rise slowly towards equilibrium. The time required for P_{RO} to reach equilibrium is generally on the order of centuries, and increases with t_{c-r}. The results indicate that there may be long periods of time (decades to centuries) during which patch occupancy increases or decreases even in the absence of directional environmental change.

12.1 Introduction

In much of eastern North America, there have been two fairly distinct phases in the history of land use since European settlement. First was the widespread clearance of forest, largely during the 1800s, to create agricultural land. Forest cover was reduced during this phase from almost 100%, usually to less than 20%, depending on the particular region (Whitney, 1994). Not long after forest cover reached a minimum, sometime between the mid-19th and early 20th centuries, the second phase of land-use history was under way, during which time widespread abandonment of agricultural land allowed forest cover to increase; in some regions forest cover is now > 80% (Foster *et al.*, 1998).

In most of Europe, the history of intensive land use extends back in time for millennia rather than centuries, with the minimum forest cover < 5% in many regions (Kirby and Watkins, 1998). None the less, for many European regions it is possible to distinguish a relatively recent phase during which forest cover has increased (if only slightly) due to forest regrowth on former farmland (Honnay *et al.*, 2002a). Thus, many regions of Europe and eastern North America share broadly similar histories of forest-cover change over the past several centuries, with a phase of forest clearance followed by a phase of forest recovery. Forests that predate the earliest land-use maps in a given region are called 'ancient', and forests known to be growing on former agricultural land are called 'recent' (Rackham, 1980).

The influence of habitat loss and fragmentation on populations and communities has been the focus of a vast body of research in ecology and conservation biology. However, both theoretical and empirical studies have focused largely on the consequences of fragmentation for population dynamics in remnant habitat patches (Hanski, 1999; Haila, 2002), with little consideration of what happens when habitat recovers (but see Tilman *et al.*, 1997; Huxel and Hastings, 1999). This was recognized by Nee and May (1992), who stated that relative to habitat patch *removal*, 'the consequences of patch *addition* may be of more relevance to European ecology, if the farmland that is being removed from agriculture over the next decades is not simply paved over' (their italics). If remnant habitat patches provide the sources of colonists for recovered patches, it follows that the extent of habitat loss should influence re-establishment of populations and communities via the reduction of potential sources of colonists. In addition, for species with low rates of local colonization and extinction, such as many forest plants, there may be extended time lags between changes in landscape structure and changes in species distributions (Tilman *et al.*, 1994), such that we might expect not only the *extent* of habitat loss to be important, but also the relative *timing* of loss and recovery. In this chapter, I use metapopulation models to explore these issues for forest herbs in landscapes characterized by a history of forest clearance (i.e. habitat loss) and subsequent recovery.

During the past 20 years, an impressive body of knowledge has been accumulated concerning differences in plant community composition between ancient and recent forests in Europe (reviewed by Honnay *et al.*, 2002a) and eastern North America (Matlack, 1994; Singleton *et al.*, 2001; Bellemare *et al.*, 2002; Gerhardt and Foster, 2002). For forest herbs (i.e. herbaceous plant species whose distributions are restricted to forests), species diversity is generally lower in recent than in ancient stands. The relative paucity of forest herbs in recent stands can be explained by a combination of dispersal limitation and habitat limitation, although the bulk of the evidence appears to support dispersal limitation as the dominant process (Honnay *et al.*, 2002a). This points to an important aspect of forest herb ecology that is relevant to metapopulation modelling: rates of colonization of empty but suitable habitat patches are relatively low. In addition, because most forest herbs are long-lived perennials, rates of local extinction are also likely to be low.

Metapopulation models make predictions at the landscape scale. Dispersal-limited colonization suggests that landscapes with the lowest percent cover of ancient forest should show the most severe reduction in forest herb diversity in recent forests, due to limited sources of colonists. This prediction was supported by a comparison of two landscapes in Belgium, in which colonization of recent forest was slower in the landscape with less ancient forest (Honnay *et al.*, 2002b). A meta-analysis of data from the literature for ten regions of Europe and eastern North America was also consistent with this prediction (Vellend, 2003; Fig. 12.1). The proportion of the landscape occupied by ancient forest had a strong influence, and the proportion recent forest a relatively weak influence on relative species diversity of ancient forest herbs in recent stands (see Fig. 12.1). This pattern was mirrored by patch occupancy patterns derived from a metapopulation model parameterized for a relatively poor colonizing species (Vellend, 2003). Here I modify the metapopulation model used in Vellend (2003) to explore two questions:

1. How does the extent of forest clearance influence the time to extinction? In other words, how much time do we have after forest clearance before forest recovery becomes necessary to prevent regional extinction of species?
2. If ancient and recent forests provide habitat of equivalent suitability for forest herbs, how does the length of time between forest clearance and recovery influence the length of time it takes for patch occupancy in recent stands to reach equilibrium? In other words, independent of the *extent* of forest clearance and recovery, how does the *timing* of these events influence metapopulation dynamics?

12.2 Metapopulation Models

Levins (1969) introduced the metapopulation concept, and formulated a simple model for an infinite number of equally connected, identical habitat
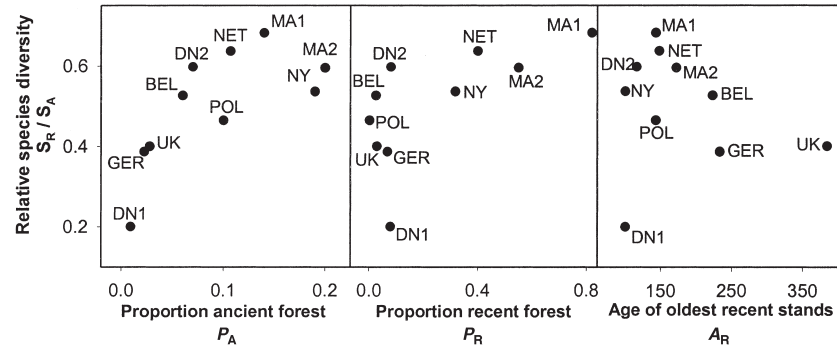
Fig. 12.1. Relationships among landscape variables in ten regions of Europe and eastern North America. Proportion ancient forest (P_A), proportion recent forest (P_R), and age of oldest recent stands (A_R) are plotted against the ratio of species diversity in recent versus ancient stands (S_R/S_A) for ten landscapes of Europe and eastern North America: Flanders, Belgium (BEL); Røsnaes, Denmark (DN1); Himmerland, Denmark (DN2); Lower Saxony, Germany (GER); Petersham, Massachusetts (MA1); Shelburne and Conway towns, Massachusetts (MA2); Twente region, The Netherlands (NET); Tompkins County, New York (NY); Western Carpathian Foothills, Poland (POL); and Lincolnshire, United Kingdom (UK). (Reprinted with permission from Vellend, 2003, where details of the analysis and references can be found.)

patches in which the proportion of patches occupied (i.e. patch occupancy) is determined by a balance between local rates of colonization and extinction. A large number of far more complicated metapopulation models have been devised (Hanski, 1999), but surprisingly, the simple Levins model provides a very close approximation to 'spatially realistic' models in which the size and isolation of a large number of individual patches are treated explicitly (Hanski and Ovaskainen, 2002; Ovaskainen and Hanski, 2002). Here I use modifications of the Levins model to include two types of habitat patch, ancient forest and recent forest. The models I use are not novel contributions to the theoretical literature (see Hanski, 1999 for a wide range of modifications to the Levins model), but are novel as applied to forest herbs in ancient and recent forests.

Two assumptions of metapopulation models require comment. The first assumption is that a landscape can be treated as consisting of suitable habitat patches in a matrix of entirely unsuitable habitat. As such, the models used here apply only to species whose distributions are restricted more-or-less entirely to forests. Secondly, metapopulation models assume an important role for local extinction and colonization events. The objection may be raised that it is inappropriate to use such models for a group of species in which extinction and colonization events are extremely infrequent, and thus have little influence on short-term dynamics. However, all populations have a non-zero probability of extinction in any given year, and for understanding *long-term* dynamics, colonization and extinction processes are critical. Forest herbs are of

particular interest in a conservation context precisely because of the slow rates at which these processes occur, and the resulting potential for extended time lags in response to landscape change.

12.2.1 Question 1: How does the extent of forest clearance influence time to extinction?

Following a modification of the Levins model that incorporates habitat loss (Hanski, 1999, p. 68 and references therein), the rate of change in patch occupancy in ancient forests (P_{AO}) can be modelled as follows:

$$\frac{dP_{AO}}{dt} = cP_A P_{AO}(1 - P_{AO}) - eP_{AO}$$

P_A is the proportion of the landscape that is forest after clearance ('A' denotes that this is ancient forest). The probability that the population in any given forest patch will go extinct per year is e, and the probability that any given empty patch will be colonized per year and per unit of occupied habitat is c. The definition of all symbols used in this chapter can be found in Table 12.1. Prior to forest clearance, the equilibrium patch occupancy is $P_{eq} = 1 - e/c$, whereas after clearance (and in the absence of any recovery) it is $P_{eq(clear)} = 1 - e/P_A c$. Therefore, if $P_A < e/c$ (i.e. the threshold for metapopulation persistence is crossed), the entire metapopulation will go extinct (Hanski, 1999). However, if e is low, the extinction process may be protracted, and a regional community may, for a long time, contain many species that are ultimately doomed to extinction. This phenomenon has been referred to as 'extinction debt' (Tilman *et al.*, 1994), and may be particularly pertinent for forest herbs due to their potential for long-term local persistence. Using values of c and e estimated approximately for a relatively slow-colonizing forest herb species (see below), I used this model to ask how the extent of forest clearance ($1 - P_A$) influences time to extinction. Since in this model extinction is never actually reached, but only approached asymptotically, I define extinction as having occurred when $P_{AO} < 0.01$. For simplicity, I also assume that patch occupancy is at equilibrium prior to forest clearance, and that forest clearance happens entirely at one point in time. All modelling analyses were coded and run using MATLAB version 6.0 (The MathWorks Inc., Natick, Massachusetts, USA).

12.2.2 Question 2: How does the timing of forest clearance and recovery influence metapopulation dynamics?

In the above-described model, patch occupancy will decline following forest clearance, either to a new equilibrium (if $P_A > e/c$) or to extinction (if $P_A < e/c$). If forest regenerates, and habitat that was once destroyed becomes suitable

Table 12.1.   Definitions of symbols.

P_A	The proportion of a landscape that is ancient forest
P_R	The proportion of a landscape that is recent forest
P_{AO}	The proportion of ancient forest patches that are occupied
P_{RO}	The proportion of recent forest patches that are occupied
$t_{c\text{-}r}$	The time in years between forest clearance and recovery
c	The colonization rate per occupied patch
e	The extinction rate
P_{eq}	The equilibrium patch occupancy prior to forest clearance (since all forests at this time are ancient, this is the equilibrium value of P_{AO})
$P_{eq(clear)}$	The equilibrium patch occupancy following forest clearance (again, all forests at this time are ancient, so this is the equilibrium value of P_{AO})
$P_{eq(rec)}$	The equilibrium patch occupancy following forest recovery (since ancient and recent forest patches are identical, this is the equilibrium value of both P_{AO} and P_{RO}, although P_{AO} and P_{RO} can take different values before equilibrium is reached)
S_R/S_A	The ratio of species diversity of ancient forest herbs in recent versus ancient stands

again, the overall equilibrium patch occupancy will rise. If we denote the proportion of the landscape that is recent forest as P_R, and assume that ancient and recent forests are equally suitable, the equilibrium patch occupancy following forest recovery is $P_{eq(rec)} = 1 - e/(P_A + P_R)c$. The proportion of recent patches that are occupied (P_{RO}) starts at zero following forest recovery, and the initial value of P_{AO} at the time of recovery (which is assumed to happen at one point in time) will depend on how much time has elapsed since forest clearance; both P_{RO} and P_{AO} will ultimately converge on $P_{eq(rec)}$. Thus, keeping track of patch occupancy in both recent (P_{RO}) and ancient (P_{AO}) patches, we can expect the dynamics to depend on the time between forest clearance and recovery. This may be relevant to understanding differences in metapopulation dynamics between European and North American landscapes, for which the differences in the times between forest clearance and recovery are large (long for Europe, short for North America).

To follow metapopulation dynamics in both recent and ancient forest patches requires solving the following two equations simultaneously.

$$\frac{dP_{AO}}{dt} = (cP_AP_{AO} + cP_RP_{RO})(1 - P_{AO}) - eP_{AO}$$

$$\frac{dP_{RO}}{dt} = (cP_AP_{AO} + cP_RP_{RO})(1 - P_{RO}) - eP_{RO}$$

I used this model to ask how the time between forest clearance and recovery influences the time it takes for patch occupancy in recent forest (P_{RO}) to reach equilibrium following recovery. I defined equilibrium as having been

reached when P_{RO} first comes within 5% of the value of $P_{eq(rec)}$ (i.e. when $|P_{RO} - P_{eq(rec)}| < 0.05$).

12.2.3 Model parameterization

I used values of e based on literature reports. Repeated surveys of vascular plants on islands or forest patches in Europe have resulted in estimates of e ranging from 0.002 to 0.01 (Nilsson and Nilsson, 1985; Gibson, 1986; Jerling, 1998; Roden, 1998). These values represent averages across species and sites, and estimate the probability of any given species going extinct in any given patch or island in any given year. Because forest herbs are generally long-lived perennials, e is unlikely to be higher than 0.01.

In Vellend (2003), I used a model similar to those described above, but with ancient forests treated as a mainland where $e = 0$, to estimate the value of c needed to explain the observed value of $P_{RO} = 0.4$ about 80 years after forest recovery for *Aster divaricatus*, a slowly colonizing forest herb in central New York (data from Singleton *et al.*, 2001). With $e = 0.05$, the estimated value was $c = 0.039$.

I have explored model output for a range of parameter values, but for the sake of brevity I report results here using only $c = 0.039$ and $e = 0.005$ or 0.01. For Question 2, I report results for $P_R = P_A = 0.15$. In general, changing parameter values alters dynamics quantitatively but not qualitatively. Forest herb species vary widely in their colonization and persistence ability, and are thus likely to vary widely in their values of c and e. I consider the parameter values used here representative of a long-lived, relatively slowly colonizing species.

12.3 Results and Discussion

12.3.1 Fragmentation and metapopulation (regional) extinction

If the rate of local extinction is relatively low, as expected for most perennial forest herbs, the time to metapopulation extinction can be very long. With $e = 0.01$, the time to metapopulation extinction is > 400 years, even when forest clearance is severe (i.e. when $P_A < 0.01$), and up to several thousand years when the extent of clearance is only slightly below the metapopulation persistence threshold, which occurs at $P_A = e/c = 0.256$ (Fig. 12.2). The time to metapopulation extinction is longer with $e = 0.005$, although the qualitative relationship with P_A is similar to that for $e = 0.01$, with a sharp increase in time to extinction close to the persistence threshold (Fig. 12.2). This is the same result as that reported by Hanski and Ovaskainen (2002), but with parameters chosen here to represent a long-lived and slowly colonizing forest herb. Essentially there are two thresholds that pertain to metapopulation extinction. First,
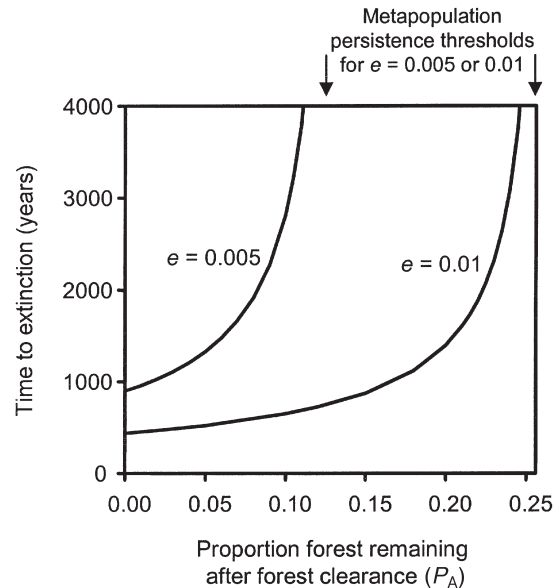
Fig. 12.2. Theoretical relationships between the proportion of forest remaining after fragmentation (P_A) and the time to metapopulation extinction when $c = 0.039$.

when $P_A < e/c$, extinction is certain but may take thousands of years to occur. When P_A is only slightly less than e/c, time to extinction shows a steep decline with P_A, and at $P_A \approx 0.8e/c$ (~0.1 for $e = 0.005$ and ~0.2 for $e = 0.01$) a second threshold is crossed below which further forest clearance has little influence on time to extinction.

A clear message from these results is that the extinction debt is likely to be substantial for forest herbs in many landscapes of Europe and eastern North America. Slow but steady decline in patch occupancy for many species may occur because of the slow crawl to extinction (or the slow decline to a positive patch occupancy equilibrium), even if the conditions for growth and reproduction within patches do not change. Because colonization and extinction rates vary among species, persistence thresholds for different species are likely to be crossed continually as forest clearance proceeds. However, even with only a small fraction of the landscape remaining as forest (e.g. $P_A < 0.01$), it may take centuries before many extinction events occur at the landscape scale. None the less, these extinctions are inevitable, at least theoretically, and the only ways they can be averted are if colonization rates are enhanced via seed or adult plant introductions, or if forests recover such that the proportion of forest in the landscape exceeds the persistence threshold. Because e is likely to be < 0.01 for many forest herbs, the conclusion that regional extinction will usually take centuries to occur, even with no changes to local habitat conditions, is likely quite robust.

12.3.2 Metapopulation dynamics and the time lag between forest clearance and recovery

Following forest clearance, patch occupancy declines from its initial equilibrium ($P_{eq} = 1 - e/c$) towards a new, lower equilibrium ($P_{eq(clear)} = 1 - e/P_Ac$). When forest recovery occurs, there is a new patch occupancy equilibrium ($P_{eq(rec)} = 1 - e/(P_A + P_R)c$), the value of which will be intermediate between the pre- and post-clearance values. In the unlikely case that the entire landscape becomes forested after recovery, it is possible that $P_{eq(rec)} = P_{eq}$. If recovery occurs shortly after forest clearance, it is likely that patch occupancy (P_{AO}) will initially be above $P_{eq(rec)}$, and so will continue to decline after recovery towards $P_{eq(rec)}$ (Fig. 12.3A, C). Patch occupancy in recent forest patches (P_{RO}) starts at zero, and if the initial P_{AO} is sufficiently high, P_{RO} may in fact first increase above $P_{eq(rec)}$ before converging on P_{AO} (Fig. 12.3C). P_{RO} and P_{AO} then decline together toward $P_{eq(rec)}$.

   If there is a long time period between forest clearance and recovery, P_{AO} at the time of recovery is likely to have declined below $P_{eq(rec)}$ (Fig. 12.3B, D).
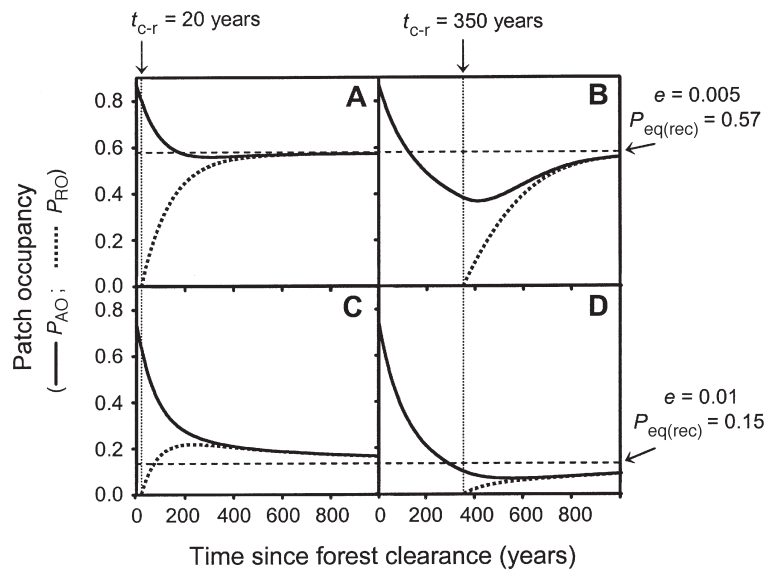

Fig. 12.3. Theoretical patch occupancy dynamics in ancient (solid curves) and recent (dotted curves) forests following forest clearance and recovery, with $e = 0.005$ (A, B) or $e = 0.01$ (C, D), and the time between clearance and recovery, $t_{c\text{-}r} = 20$ years (A, C) or $t_{c\text{-}r} = 350$ years (B, D). Forest clearance (occurring at time zero on the x-axis) and recovery were assumed to be instantaneous changes, with $P_A = P_R = 0.15$. Horizontal dashed lines indicate the equilibrium patch occupancy after recovery, $P_{eq(rec)}$, for the two extinction rates, and vertical dashed lines indicate $t_{c\text{-}r}$.

Interestingly, there may still be a period of 50+ years following forest recovery, during which P_{AO} continues to decline despite being below $P_{eq(rec)}$ (Fig. 12.3B, D). This is because the increase in forest cover due to recovery has little influence on overall patch occupancy until enough recent patches become occupied to act as significant sources of colonization. Once P_{RO} and P_{AO} converge, both increase towards $P_{eq(rec)}$.

The time it takes for P_{RO} to reach $P_{eq(rec)}$ increases with the time allowed to pass between forest clearance and recovery ($t_{c\text{-}r}$), though the shape and slope of the relationship depend strongly on the magnitudes of colonization and extinction rates (Fig. 12.4). The slope is much steeper when the extinction rate is relatively high ($e = 0.01$) than when the extinction rate is relatively low ($e = 0.005$; Fig. 12.4). The influence of $t_{c\text{-}r}$ on the time to equilibrium for P_{RO} is mediated by the initial value of P_{AO} at the time of forest recovery. When recovery follows quickly after forest clearance, P_{AO} starts out high and thus exerts considerable 'colonization pressure' on the initially empty recent patches, thereby increasing the rate of approach of P_{RO} towards $P_{eq(rec)}$.

These results have two important implications. First, the timing of forest clearance and recovery can have dramatic effects on metapopulation dynamics, independently of the effects of the extent of clearance and recovery. Recovery of forests sooner rather than later can accelerate the increase in recent forest patch occupancy, in addition to preventing otherwise inevitable extinctions. Secondly, there is tremendous potential for extended time lags in the dynamics of forest herb metapopulations in changing landscapes.
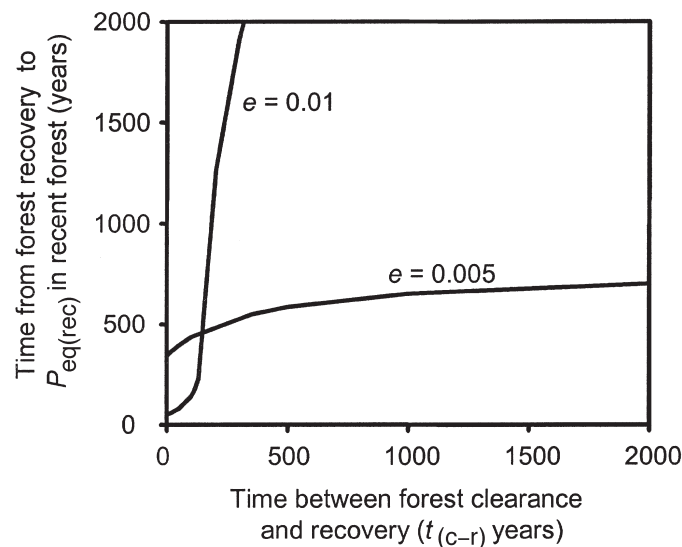
Fig. 12.4. Theoretical influence of the time between forest clearance and recovery ($t_{c\text{-}r}$) on the time from recovery to patch occupancy equilibrium in recent forests.

Centuries, or even millennia, may be required for the regional distributions of forest herb species to reach equilibrium with landscape properties. When directional trends in landscape-level species abundance patterns are observed, it may be tempting to assume that there must be underlying directional change in local environmental conditions, human-caused or otherwise. The results here warn against such interpretations. Due to slow rates of local colonization and extinction, patch occupancy can change directionally for decades to centuries in the absence of continued landscape change. The slow rate of colonization of recent forests is well appreciated (Honnay *et al.*, 2002a,b), but other kinds of time lags are possible as well. For example, there may be long periods of time during which patch occupancy in both ancient and recent forests either increases (Fig. 12.3B) or decreases (Fig. 12.3C), depending only on the timing of forest clearance and recovery.

12.3.3 Models and data

Theoretical models are simplified representations of nature. In the models used here, many aspects of real plants growing in real landscapes have been ignored. In particular, there was no explicit treatment of spatial structure, habitat heterogeneity, habitat quality, the rate of change in landscape structure, or deterministic local extinction. These factors and others may all be important in determining the regional distributions and dynamics of species. However, as mentioned in the introduction, qualitative predictions from simple metapopulation models are unlikely to change with the addition of complexities such as variable patch characteristics.

It is when confronted with empirical data that simple models may run into trouble. Landscapes that vary in the extent and timing of forest clearance and recovery (e.g. North America versus Europe) are also likely to vary in a suite of other characteristics. For example, the duration of arable land use (i.e. the time between forest clearance and recovery) can have a direct influence on local soil properties (Verheyen *et al.*, 1999), and therefore an indirect influence on vegetation. This may obscure any effect of the timing of clearance and recovery *per se* on patch occupancy patterns. Despite these limitations, models are indispensable in the present context because they represent one of the few tools available for exploring the consequences of large-scale landscape changes on long-term population dynamics, and for placing empirical observations in a coherent framework. In the remainder of this chapter, I briefly discuss one set of empirical observations in the light of theoretical predictions regarding extinction debt, and then some promising lines of enquiry for the future.

Hanski and Ovaskainen (2002) have recently pointed out that a transient excess of species with low patch occupancies is a signature of extinction debt. Testing for such a signature requires data either from several time periods before and after forest clearance within a given landscape, or from multiple

landscapes with different degrees of clearance. The expectation is that the excess of species with low patch occupancy would be greater where P_A is smaller. Since most studies report data for a single landscape, and the sampling regimes across studies are rarely identical, comparable data on multiple landscapes are few. However, Graae (2000) presented patch occupancy data for the same list of species in ancient forests in two landscapes in Denmark. In Himmerland and Hornsherred, the percentage of the landscape forested as of 1888 was 7% and 12%, respectively (Graae, 2000). Thus, we would predict a relative excess of rare species in Himmerland compared to Hornsherred, and this is exactly what was observed (Fig. 12.5). While recognizing that the extent of forest clearance is not the only variable that differs between the two landscapes (Graae, 2000), these data suggest a greater extinction debt in the landscape with less ancient forest. If we define rare species as $0 < P_{AO} < 0.1$, there were considerably more rare species in Himmerland (33) than in Hornsherred (22), despite very little difference in the number of forest plant species present in the two landscapes (91 in Himmerland, 88 in Hornsherred).

The extent and timing of forest clearance and recovery has varied greatly among different regions in the north-temperate zone (Whitney, 1994; Kirby and Watkins, 1998). For example, there has generally been more extensive clearance, longer periods of agricultural land use, and less recovery in Europe
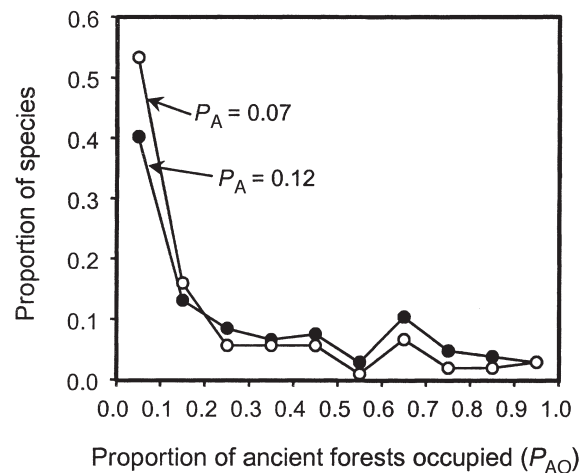
Fig. 12.5. The distribution of patch occupancies among species in two landscapes in Denmark [Himmerland (open circles), $P_A = 0.07$; and Hornsherred (closed circles), $P_A = 0.12$; data from Graae, 2000}. The proportion of species is presented in each of ten patch occupancy categories (0–0.1, > 0.1–0.2, etc.). There were significantly more rare species and fewer common species in Himmerland than in Hornsherred (Kolmogorov–Smirnov test, $P < 0.01$), regardless of whether or not absent species were included in the analysis (of 112 species searched for in both regions, 21 were absent in Himmerland and 24 in Hornsherred).

than in North America. Differences in soil characteristics between ancient and recent forest are also likely greater in Europe. As such, it is easy to predict that recolonization of forest plant species in recent forests should be far slower in Europe than in North America (Vellend, 2003), but much more difficult to pinpoint which particular aspects of landscape history drive such a pattern. When more comparable data become available for regional comparisons, the construction of more complex models may aid in distinguishing among historical hypotheses.

Two approaches to testing landscape-scale predictions in the future may prove particularly promising. There is now a wealth of data from many regions of Europe and North America derived from censuses of plant species in forest patches varying in age, area, isolation and environmental characteristics. If raw data are archived in an accessible format, with explicit information on geographic locations and sampling methods, researchers in the coming decades will be able to estimate extinction and colonization rates directly. Repeated surveys are available for a few individual sites (e.g. Gibson, 1986; Harmer *et al.*, 2001), but the potential exists for such valuable information to be collected in a range of different landscapes. Secondly, there is now the potential for direct comparisons among different landscapes. This requires careful selection of comparable landscapes, and statistically controlling for variation in multiple landscape characteristics, but these hurdles are surmountable, and this approach has already yielded some important insights concerning the long-term influence of habitat loss and fragmentation (Honnay *et al.*, 2002b; Vellend, 2003). Synthesis of results across regions and continents holds great potential for improving our understanding of how forest vegetation responds to continual landscape change.

Acknowledgements

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