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18.1 Introduction

Landscape ecologists and conservation biologists usually assume a causal relation between the observed current landscape pattern and the species distribution pattern. This assumption may not always be correct, because species distribution patterns can reflect past as well as present landscape conditions (Figure 18.1).

Time delays in the reaction of biodiversity to changed circumstances are of major importance because they may determine how much extinction or other ecosystem change is awaiting us. Habitat destruction is generally seen as the dominant threat to biodiversity (e.g., Pimm et al. 1995; Pimm 1998). Recorded species extinction, however, is much less than expected theoretically (Heywood and Stuart 1992; Whitmore 1997). Some authors therefore reason that the predictions are too pessimistic (e.g., Budiansky 1994). Others argue that extinction takes place with a delay and that many extant species are doomed (e.g., Heywood et al. 1994; Whitmore 1997; Pimm 1998). Hence, it is extremely important to investigate the extent and mechanisms of time-delayed biodiversity changes.

In this chapter we focus on the role of metapopulation dynamics in delayed responses to landscape changes. Note, however, that other processes, like succession, range expansion, and evolution, can also be responsible for time lags. We first introduce the principles of metapopulation lags, explain relevant concepts, and discuss recent work. We continue with principles for application, identify major theoretical and empirical knowledge voids, and end with suggesting protocols for filling those voids.

Figure 18.1. Illustration of the time-lag phenomenon. The landscape can be constant over time (a, right part of b) or gradually changing (c, d). The (meta)population may appear to be in equilibrium with the landscape (a, c) or lagging behind. In (b), the population responds to an earlier sudden landscape change; in (d), the population response is lagging behind a gradual landscape change. The landscape feature may be, for example, area or percentage of habitat, or number or average size of habitat patches. The (meta)population feature may be, for example, population size, range, or patch occupation.

18.2 Concepts, Principles and Emerging Ideas

18.2.1 Principles of Time Lags in Metapopulation Dynamics

A *metapopulation* is a system of discrete subpopulations, with some turnover, linked by dispersal. Of N habitable patches per unit area, only n are occupied at any given moment. *Metapopulation dynamics* (the course of *occupancy* [n] over time) is determined by the turnover processes of local extinction and colonization. The metapopulation equilibrium (n^*) is achieved when these turnover processes balance. This equilibrium is decreased by a lower colonization rate or a higher local extinction rate. Metapopulation dynamics may take place on a long time scale, simply because of the probabilistic nature of the basic processes. Local extinction and (re)colonization rates, expressed as probability per year, often are in the order of 10^{-2} - 10^{-1} (e.g., Verboom et al. 1991). For an extinction rate of $e = 0.01$, the mean time to local population extinction equals $1/e = 100$ years. A subpopulation may persist for tens or even hundreds of years without alarming conservation managers. A similar reasoning applies to colonization. Because the dynamics of the whole

metapopulation is driven by colonization and extinction, effects of landscape change can go unnoticed for long periods.

Time lags in metapopulation response may be encountered in the following cases: (1) following a relatively fast landscape change that decreases n^* , the metapopulation may linger near the old equilibrium for a while (Figure 18.1b); (2) following a landscape change that increases the metapopulation equilibrium, the metapopulation may expand slowly. Intuitively, the first case should be due to a low local extinction rate, and the second case to a low colonization rate. We show below, however, that what really matters is the size of the *difference* between colonisation and extinction. A special case of (1) is where the landscape has deteriorated so much that the new equilibrium is metapopulation extinction. Cases related to (2) include the invasion of an alien species, and metapopulation recovery after a catastrophe or cessation of persecution.

18.2.2 Concepts Relevant to Time Lags in Metapopulation Response

Delays in the response of biodiversity to landscape degradation have been discussed by Tilman et al. (1994). For a community of species that hierarchically competed for the same habitat, they found an *extinction debt*--the loss of species following a delay after landscape degradation. Time delays, however, are a robust metapopulation phenomenon not dependent on the competitive interactions assumed by Tilman et al. (1994). The other side of the coin is a *colonization credit*, which is the slow reappearance of species after landscape restoration. The *return time* is the time the metapopulation needs to return to equilibrium after perturbation. It is used as a measure of the time lag.

Relaxation applies to communities of species in isolated areas like islands, mountain tops, and forest fragments. It is the progressive local loss of species caused by an excess of extinction over colonization, after a decline in area due to factors like sea level rise, climate change, or habitat destruction (reviewed by Diamond 1984).

Ghosts of the landscape past appear when the distribution of a species is better explained by a prior landscape configuration than by the current one. *Living dead* are (meta)populations that will certainly go extinct because they have become non-viable. An obvious example is the last individual of a Galapagos giant turtle subspecies (Caccone et al. 1999) but more subtle cases may escape our attention. Hanski and Kuussaari (1995) estimate that in Finland 10 of 94 resident butterflies are represented by non-equilibrium metapopulations heading for extinction.

18.3 Recent Applications

18.3.1 The Lack of On-the-Ground Applications

We failed to find a single explicit field application of the time-lag concept in relation to metapopulation dynamics, though we consulted many colleagues and systematically searched the Web and all relevant literature data bases we could think of. The extinction

debt concept has been used to predict future species loss from current landscapes (e.g., Brooks, Pimm and Collar 1997; Cowlshaw 1999), but not in an explicit metapopulation context. This absence of applications did not come as a surprise, because the concepts, principles and emerging ideas are all quite recent. For example, the general discussion about extinction debts just began in 1994. Moreover, no general principles for applying the concepts have been published and the theory is still far from complete. The focus of both conservation managers and researchers tends to be on short-term processes rather than long-term transient dynamics. Rather than discussing actual on-the-ground applications of the concepts of section 18.2, we discuss how the concepts have been involved in research contexts. We present recent evidence for time lags in metapopulation responses to landscape change (18.3.2) as well as theoretical models of these phenomena. The latter will address time lags in the Levins metapopulation model and mainland-island model (18.3.3), time lags in a model assuming evolved dispersal (18.3.4), the role of stochasticity in small networks (18.3.5), time lags in spatially explicit models (18.3.6), and time lags in mosaic landscapes with multi-species communities (18.3.7).

18.3.2 Evidence for Time Lags in Metapopulation Responses to Landscape Change

There are several examples of metapopulations expanding with a time lag. The number of patches occupied by the butterfly *Hesperia comma*, which depends on heavily grazed habitat, expanded slowly in Britain after rabbit mortality by myxomatosis subsided (Thomas and Jones 1993). The butterfly *Proclissiana eunomia* slowly increased its occupation of a habitat network after reintroduction in central France (Neve et al. 1996). The range of the sea otter (*Enhydra lutis*) in North America is expanding steadily since the cessation of persecution (Estes 1990). After decimation due to extreme conditions in wintering habitat, marshland birds in The Netherlands recovered quickly in less fragmented habitat, but recovery in more fragmented habitat had not yet taken place after eight years (Foppen et al. 1999). There is a body of literature about sluggish expansion following introduction of alien species. For example, the zebra mussel *Dreissena polymorpha* is only slowly spreading into isolated inland waters in the USA, whereas it quickly expanded over interconnected waters (Johnson and Padilla 1996). The other side of the time-lag coin, metapopulations declining with a lag after landscape degradation, has been documented for carabid beetles (De Vries 1996; Petit and Burel 1998).

Whether declining fragmented populations still are metapopulations, that is, whether (re)colonization of patches still occurs, is often unclear. Declining species will often mimic a metapopulation without being one (Simberloff 1997). For example, on isolated Spanish dunes, Obeso and Aedo (1992) found only extinctions of plant species and no colonizations.

Metapopulation dynamics arises from colonization and extinction. The evidence for lags in these basic processes, which will translate into metapopulation delays, is much more abundant than for lags in metapopulations. There is much evidence (reviewed by Diamond 1984 and Pimm 1991) of relaxation on islands or mountain tops. Relaxation in habitats fragmented by humans is exemplified by the extinction of mammals in Tanzanian and

North American reserves (Newmark 1995, 1996), small mammals in Californian shrub fragments (Bolger et al. 1997), and many organisms in tropical forest fragments (Corlett and Turner 1997). Other possible evidence for a time lag in extinction is that Java and other long-settled islands have a remarkably poor lowland bird fauna (Van Balen 1999), whereas recently deforested islands nearby have lost few species as yet (Brooks, Pimm and Collar 1997). Low colonization rates also are often reported. There are many examples of plants colonizing newly available areas at very low rates (Peterken and Game 1984; Eriksson 1996; Grashof-Bokdam 1997). For many European plant species modern human landscapes and practices seem to be especially detrimental to dispersal (Poschlod and Bonn 1998). Tropical inner-forest trees can be very slow in colonizing adjacent secondary forests, especially when their seed dispersers have disappeared (Corlett and Turner 1997). Saproxylic insects characteristic of old forests also colonize very slowly (Warren and Key 1991).

Examples of ghosts of the landscape past are given for carabid beetles by Petit and Burel (1998), and for forest plants by Van Ruremonde and Kalkhoven (1991) and Grashof-Bokdam and Geertsema (1998). Grashof-Bokdam and Geertsema (1998) showed that present occurrence of forest plant species was significantly related to the amount of currently occupied forest that was already present nearby about 150 years ago, but not to the contemporary amount of occupied adjacent forest.

18.3.3 Time Lags in Simple Metapopulation and Mainland-Island Models

In real landscapes patches generally differ in size and connectivity. However, for creating general insights, it is useful to study simple models that ignore those differences. We consider the Levins metapopulation model (Levins 1969) and the related mainland-island model (MacArthur and Wilson 1967). In both models, all patches are equal, but the latter model differs from the former in that the colonization rate for an “island” is constant, whereas in the Levins model patch colonization rate is proportional to the number of patches occupied. Real-life metapopulations may lie in between these two extreme cases, because colonization may occur both from within the metapopulation and from outside.

The Levins model has the form

$$\frac{dn(t)}{dt} = cn(t)(N - n(t)) - en(t), \quad (1)$$

where occupancy $n(t)$ is the density (or number) of occupied patches at time t , N is the total density (or number) of patches, c is the colonization rate per occupied patch and per empty patch, and e is the extinction rate per occupied patch. The equilibrium densities are

$$n^* = N - \frac{e}{c} \quad (cN > e) \quad (2a)$$

and

$$n^* = 0 \quad (cN \leq e). \quad (2b)$$

Hence, when $cN > e$ the metapopulation is viable.

We define T_{50} as the time it takes to reduce a deviation from an equilibrium value by 50%. For this measure of return time, we find that for a viable metapopulation (F. van den Bosch, unpublished results)

$$T_{50} = \frac{\ln 2}{cN - e} \quad (n^* = N - \frac{e}{c}), \quad (3a)$$

and for a non-viable metapopulation

$$T_{50} = \frac{\ln 2}{e - cN} \quad (n^* = 0). \quad (3b)$$

Strictly, these equations are only true for small deviations but they give a reasonable approximation. Clearly, when a metapopulation is viable, the return time increases with increasing patch extinction rate (e), decreasing colonization rate (c), and decreasing number of patches (N). For non-viable metapopulations, the dependence of return time on the parameters is reversed. Figure 18.2a shows that return times are especially large for parameter combinations where the equilibrium is close to the viability boundary, $p = 0$, where p is the proportion of occupied patches ($= n^*/N$) at equilibrium (see also Figure 18.3).

When most colonizations of several smaller patches take place from a large “mainland”, a more appropriate model is the mainland-island model,

$$\frac{dn(t)}{dt} = c'(N - n(t)) - en(t), \quad (4)$$

where c' is the number of colonizations per empty patch per time unit. The equilibrium for this model is $n^* = c'N/(c' + e)$, and the metapopulation is now always viable, because there will always be colonization from the mainland. The return time becomes

$$T_{50} = \frac{\ln 2}{c' + e} \quad (5)$$

From Figure 18.2b we see that return times are small when the colonization and extinction rates are large. Speed is determined by the sum of the colonization and extinction

Figure 18.2. The return time in years (T_{50} , dotted lines) and the equilibrium fraction of occupied patches ($p = n^*/N$, solid lines) as functions of the colonization parameters (cN or c') (year^{-1}) and extinction rate (e) (year^{-1}) of the Levins model (a) and the mainland-island model (b).

parameters. This contrasts with Levins metapopulations for which it is the difference between the parameters e and cN that determines return time. For comparable rates of colonization (per empty patch; hence c' vs. cn) and extinction, the mainland-island model always reacts faster than the Levins model.

Landscape degradation can occur by a decrease in the amount of habitat N , an increase in the local extinction rate e (e.g., an increase in disturbance rate) or an increase in landscape resistance to dispersal that decreases c . To compare different kinds of degradation we investigate return times for impacts that result in equal changes in n^* and hence are of the same size. For the Levins case, habitat destruction and an increase in e do not differ in speed of reaction, but reaction to an increase in dispersal resistance is much slower (Figure 18.3). Note, however, that increases in e have, compared to decreases in N or in c , no obvious natural maximum, hence reaction to increased disturbance can become very fast. In all cases return times are highest near the viability border, as predicted by Eq. 3a and 3b. In the mainland-island model, an increase in dispersal resistance also produces a slower reaction than a change in e , but changes in N never produce out-of-equilibrium situations.

18.3.4 Time Lags Assuming Evolved Dispersal

From Eqs. 3a and 3b we can predict return time from the parameters, and for example, investigate the influence of differences in e on delay length, while keeping c constant. However, we often do not know both e and c . Fortunately, e and c may not be independent. Data show that, generally, species from unstable habitats are also good dispersers (Hanski 1999). Supporting this, evolutionary theory predicts that dispersal will be molded by natural

Figure 18.3. Comparison of the influences of three types of landscape degradation on the return time of a metapopulation according to the Levins model. The size of the impact is defined as the reduction in the equilibrium number of occupied patches, n^* (i.e., $n_p^* - n_d^*$). Negative values of n_d^* are virtual results obtained by using Eq. 18.2a for non viable metapopulations, necessary to assess the size of impacts resulting in extinction. The parameter values for the pristine landscape are $N = 10$, $e = 0.04$ and $c = 0.02$, resulting in $n_p^* = 8$. Impact size for habitat destruction is bounded (vertical line m). Left of m the curves for habitat destruction and increased disturbance coincide.

selection in response to the local extinction rate (Comins, Hamilton and May 1980; Ferriere, Dieckmann and Couvet, in press). To incorporate this we use the simple evolutionary relationship that the optimal rate of dispersal d^* is equal to the extinction rate e (Van Valen 1971). Further, we translate dispersal rate d into c with a scaling factor α , hence, $c = \alpha e$. The value of α will depend on such factors as fecundity and dispersal ability. An assumption is that evolution is slow compared to landscape change, and that, therefore, the dispersal rate which evolved in the pristine landscape does not change during landscape deterioration. Hence, to be clear, we do *not* investigate evolutionary reactions to degradation, but study the consequences of earlier parameter evolution.

We can now investigate how this evolutionary dependency between e and c influences the reaction to landscape change. Return time and equilibrium for a viable metapopulation are now given by

$$T_{50} = \frac{\ln 2}{e(\alpha N - 1)} \quad , \quad n^* = N - \frac{1}{\alpha} \quad , \quad (6a)$$

and for a doomed metapopulation by

$$T_{50} = \frac{\ln 2}{e(1 - \alpha N)} \quad , \quad n^* = 0. \quad (6b)$$

We put e equal to the habitat disturbance rate and compare species from habitats that differ in stability. Other causes of local extinction, for example small population size, have the same effect as high habitat disturbance.

First we investigate habitat destruction (decreasing N). Table 18.1 and Eqs. 3a and 3b show that, when disregarding evolved dispersal, we would conclude that, after a fatal decline in the amount of habitat, species from habitats with a high disturbance rate go extinct faster (shorter return time) than do species of more stable habitats. However, when the endpoint is not extinction but a new positive equilibrium, the return time increases with local extinction rate. Including evolved dispersal changes our predictions markedly. As long as the amount of available habitat does not differ between species, return times will always *decrease* with increasing e . Species from habitats with a high (low) disturbance rate, will react rapidly (slowly) to changes in the amount of habitat, irrespective of the endpoint. These outcomes are intuitively more appealing than are the results using independent rates. For example, we expect weeds to react speedily to increased opportunities. Clearly, there are “slow” species and “fast” species, and evolution ensures that reaction speed correlates positively with the disturbance rate of the habitat. Slow species live in relatively stable habitats and react with a long lag to changes in the amount of habitat, whereas fast species live in often-disturbed habitat and react with a short lag.

We now consider effects of increasing the disturbance rate, e . The model without evolved dispersal predicts that, after a given increase in disturbance rate, a species facing extinction fades out slower when the pristine disturbance rate was low. Incorporating evolved dispersal again brings new insights. The velocity with which doomed species approach extinction now *decreases* with increasing pristine disturbance rate, contrary to the effect of habitat destruction. The added disturbance causes the originally slow species to become the faster ones. This implies that species from originally relatively stable habitats go extinct sooner. The reason is that their evolved low colonization rate is easily swamped by an increase in local extinction rate.

For increased resistance to dispersal, the results are comparable to those of habitat destruction.

Table 18.1. The influence of evolved dispersal on predictions about reaction speeds of metapopulations under the Levins model, as influenced by the (pristine) disturbance frequency e_p (assumed to be equal to the local extinction rate). The dispersal rate has evolved in the pristine landscape and does not change after landscape degradation. The effects of several landscape degradation types are shown. n^* : equilibrium occupancy, c : colonization rate, α : evolutionary relationship between c and e_p ; subscripts p: pristine state, d: degraded state; + and - : effect of larger e_p on reaction speed; a '+' means that species with high e_p have a faster reaction (shorter time lag), compared to species with low e_p (C. J. Nagelkerke unpublished). Results are given for both viable ($n^* > 0$) and non-viable ($n^* = 0$) metapopulations.

Degradation type		Without evolved dispersal (c independent of e)	With evolved dispersal ($c_p = \alpha e_p$)
Pristine landscape	($n^* > 0$)	-	+
	($n^* = 0$)	+	+
Habitat destruction	($n_d^* > 0$)	-	+
	($n_d^* = 0$)	+	+
Increased disturbance	($n_d^* > 0$)	-	+
	($n_d = 0$)	+	-
Increased dispersal resistance	($n_d^* > 0$)	-	+
	($n_d^* = 0$)	+	+

18.3.5. Time Lags in Simple Stochastic Models

The Levins model is deterministic, but in reality metapopulations will show stochastic fluctuations in occupancy n , which means that small metapopulations can go extinct by chance, hence after a variable delay, even when their deterministic n^* is positive. Gurney and Nisbet (1978) gave the following approximation for the expected time to metapopulation extinction (T_M) in small networks:

$$T_M = \frac{1}{e} \exp \left[\frac{n^{*2}}{2(N - n^*)} \right] \quad (7)$$

Realised time to extinction can, however, be extremely variable (Lehman and Tilman 1997). Eq. 7 means that for a given n^* the delay to stochastic extinction T_M will be shorter

when N is larger and hence p is smaller and e and cN nearly balance. This is because fluctuations are more violent when only a small proportion of a network is occupied. See Hanski, Moilanen and Gyllenberg (1996) and Hanski (1999) for a further discussion of stochastic extinction in small networks. One point raised by these authors is that T_M will be shorter when there is spatially correlated environmental stochasticity.

18.3.6 Time Lags in Spatially Explicit Models

In spatially explicit models, patches can differ in size and connectivity. The equilibrium occupancy, n^* , now depends upon the exact configuration of patches and the dispersal structure of the metapopulation (Hanski 1999). Time lags may become longer as the spatial structure becomes more heterogeneous. We discuss two case studies.

Hanski's incidence function model (Hanski 1994, 1997, 1998) includes both patch size and configuration. Hanski and co-workers (Hanski, Moilanen and Gyllenberg 1996; Hanski 1998) found that after habitat destruction, the lag in this model was much longer when the endpoint was metapopulation extinction than it was when the endpoint was a lower positive equilibrium. Hanski, Moilanen and Gyllenberg (1996) suggested that this occurred because when extinction was the endpoint, local extinction occurs last in the largest patches with the lowest extinction rates, and their demise may take a long (and very unpredictable!) time. Metapopulation shrinkage to a lower equilibrium is caused mainly by local extinction in small patches with a high e , and should go faster. It is clear that in habitat networks with unequal patch size, mean extinction and colonization rates may change during the shrinkage process, and such rate changes may have important consequences, including a long delay to final metapopulation extinction.

In the second case study, Van de Wolfshaar (1999) analyzed landscapes for time lags with a spatially explicit deterministic model. Landscape structure and inter-patch dispersal rate estimates were taken to apply to the butterfly *Melitaea cinxia* in Finland or to the European badger (*Meles meles*) in The Netherlands. Eliminating connectivity variance decreased the time lags with a factor 2 – 100. No variance corresponds to the assumption used in 18.3.3 and 18.3.4 that all patches are equally accessible from all other patches. Hence, simple models might underestimate the time lag.

See Hanski, Moilanen and Gyllenberg (1996) and Hanski (1998, 1999) for a discussion of the expected time to stochastic extinction in small spatially realistic networks.

18.3.7 Time Lags in Mosaic Landscapes with Multi-Species Communities

When we understand the reactions of the individual species, it is possible to predict the reaction of a whole assembly of species when a landscape degrades or is allowed to recover. As an example we present simulations using the models with evolved dispersal from 18.3.4 but adding some immigration from outside the landscape. Landscapes can be

Figure 18.4. The landscape as a mosaic of habitats that vary in disturbance rate. (a) Pristine landscape, (b) degraded landscape.

seen as a mosaic of different habitats that vary in disturbance rate (Figure 18.4). Each species faces the patch extinction rate specific for the habitat it uses.

We first investigate the effect of changes in the relative amounts of the different habitats. A pristine landscape will be dominated by relatively stable habitats, whereas a degraded landscape will have more habitat that is often disturbed (Figure 18.4). After degradation, species from more stable habitats will decline or go extinct, because their habitat diminishes, whereas species from often disturbed habitats profit. However, the increase of the fast, disturbance-dependent species will occur at a higher pace than the decline of the slow species from the more stable habitats. This results in a temporary increase in diversity (Figure 18.5a), by immigration, before the number of species settles at its new lower equilibrium. Because many species from more stable habitats will disappear only after a delay, there is an extinction debt. In contrast, after restoration, a colonization credit appears (Figure 18.5b). Biodiversity then decreases temporarily before rebounding to its pristine level--the fast species quickly react to the decline in their habitat, whereas the slow species only return after a delay. Clearly, there is a strong asymmetry between degradation and recovery.

Figure 18.5. Examples of simulation results for total number of species over time in a mosaic landscape after different types of landscape degradation and restoration. There are 20 habitats with pristine disturbance rates ranging from 0.005 to 0.1 per year. Every species has a metapopulation in its own habitat network. There is only one species for every habitat, and species do not interact. Landscape changes are applied suddenly and some immigration from outside is allowed. (a) Changing the relative amounts of the different habitats toward habitats with a high disturbance rate (e.g., from Figure 18.4a to Figure 18.4b). (b) Restoring the original habitat distribution. (c) Applying a general increase (of 0.06 per year) in disturbance rates. (d) Restoring the original disturbance rates. C. J. Nagelkerke (unpublished).

A general increase in the disturbance rate causes declines in occupancy for all species. Species from the originally most stable habitats suffer the most and, contrary to the effect of habitat destruction, they are also the ones that decline the fastest. There are now no temporary increases or decreases in the number of species (Figures 18.5c and 18.5d) and there is little asymmetry between degradation and recovery. Whereas (formerly) slow species are now the first to disappear, they also are the last to reappear when the disturbance rate returns to the pristine value.

18.4 Principles for Applying Landscape Ecology

The most important message is that time lags do matter. Many metapopulations may be living dead, and protection of the current landscape may not guarantee long-term survival. In subsections 18.4.1 - 18.4.3 we provide general, tentative application principles based on the simple mathematical models presented in 18.3 and on empirical findings.

18.4.1 When to expect time lags and why they are important

Delays can occur both during metapopulation decline and expansion. In response to degradation, a slow metapopulation decline, or even a temporary increase in biodiversity, may lead to unjustified optimism when monitoring short-term change. Such delays in decline may mask the fate of a large part of biodiversity. On the positive side, delays can provide a buffer. They may enable species to persist during a period of pollution or habitat destruction until better times return (Kellman 1996). For example, longevity may have helped the Golden Eagle (*Aquila chrysaetos*) in western Scotland to maintain its breeding density through the 1960s despite reproductive failure due to organochlorine pollution (Newton 1998). When properly identified, a time lag also gives us time for action before it is too late. Slow recovery after restoration or after a disaster may lead to unjustified pessimism, especially so when a temporary biodiversity decline occurs. Delays in recovery also increase the possibility of stochastic metapopulation extinction. Further, slow expansion of a nonindigenous species can lead to underestimation of its potential impact but also provides time for countermeasures.

Time lags other than those caused by pure metapopulation dynamics may also be important. Species may change over time due to evolution or behavioral adjustment, allowing them to cope with the environmental change. Also, communities may take time to reorganize (Kellman, Tackaberry and Meave 1996), after which they may be more resistant to stresses of the new situation and be able to maintain many species, albeit in new structures and combinations (Kellman 1996). For example, the deterioration of new tropical forest fragments may not be representative of the longer-term condition (Brokaw 1998).

18.4.2 Time Lags Depend on Habitat, Type of Degradation, Landscape, Species, and Ecological Setting.

Being able to estimate time lag length helps to interpret the present, to predict the future, and to devise appropriate actions. When lags are long, it may be difficult, or at least take a long time, to observe the effect of harmful environmental changes or of conservation measures taken to improve persistence. Establishing causality will often be near impossible. Remedial action is less urgent, but slow declines should not conceal that drastic measures can be ultimately needed. When lags are short, conservation measures have extra urgency. Below we discuss factors influencing time lags length.

(a) Pristine habitat stability and type of degradation determine which species are fast or slow.

In 18.3 we showed that pristine local extinction rate e (and hence disturbance frequency) and type of degradation are important determinants of reaction speed. Species from stable habitat such as old growth forests will react slower to changes in the amount of habitat or in dispersal resistance than will species from often-disturbed habitat, such as river banks. One consequence is that after habitat destruction, we expect in the more stable habitats a higher prevalence of walking ghost species. When the disturbance rate is increased, however, species from originally stable habitats disappear fast, but recover slowly after eventual

restoration. In this case there can then be large differences in time scales between decline and recovery.

(b) A balance of colonization and extinction parameters curbs speed.

In the Levins model, speed is set by the difference between the colonization and extinction parameters cN and e . When parameters are nearly equal, and, hence, metapopulations are on the brink of viability, metapopulation dynamics may give rise to long lags between landscape change and biotic response. In small networks, stochastic fluctuations may then become important and cause fast extinction.

(c) Reaction speed differs between types of degradation.

Reaction to impacts of similar size (see 18.3.3) will be equally fast for habitat destruction and increased disturbance, but slower for increases in dispersal resistance. Reaction speed to increases in disturbance can be very fast however.

(d) Landscape configuration is important.

Lags will be long, assuming disturbance remains the same, if patches are large and isolated (Hanski 1997) because then e and c will both be low. The effects of heterogeneity between patches in size or connectivity remain to be elucidated fully (see 18.3.5).

Principles (a) - (d) are based on the classical Levins model. When there is a mainland-island configuration, speed depends on the sum of the parameters and reactions are faster, possibly much faster. Species from stable habitats are always slower in a mainland-island situation. Habitat destruction (of the islands) produces no time lags, but reaction to increased dispersal resistance is slower than reaction to increased disturbance, as in the Levins model. Degradation of the mainland source has the same effect as increased dispersal resistance.

(e) Lag times will differ among species, taxonomic groups and ecological settings.

Habitat stability is not the only factor in local extinction. Small local populations may also die out from, for example, demographic stochasticity. Hence, attributes like density, longevity and other life history characteristics are important (reviewed by Pimm 1991). Therefore, lag times will differ among species that share the same habitat. Fragments of temperate old forests seem to lose their characteristic carabid beetles much faster (< 100 years, Gruttke 1997) than they lose their plants (hundreds of years, Peterken and Game 1984; Dzwonko and Loster 1989). In temperate areas, butterflies decline much faster than their food plants (Erhardt and Thomas 1991; Erhardt 1995). In tropical forest remnants plants also respond slower than animals (Corlett and Turner 1997). This, apparently general, slower reaction of plants may be due to their long life time or seed banks (Eriksson 1996), small individual area requirements, or (in the case of expansion) low rate of colonization (Peterken and Game 1984; Eriksson 1996; Grashof-Bokdam 1997). Among plants in tropical forest fragments, trees and ferns have a lower rate of loss than orchids (Corlett and Turner 1997). In all of these cases, however, it is not known whether the

differences concern only the speed of decline or also the endpoint. More specific are Brooks, Pimm and Oyugi (1999) who claim for birds in tropical forest fragments a return time T_{50} of approximately 50 years. The survival of much tropical tree diversity during repeated glacial forest contractions points to persistence time scales longer than 10.000 - 20.000 years (Kellman, Tackaberry and Meave 1996).

Lags will be most prominent when both (1) species have low e and c , and hence are slow, and (2) dispersal resistance is increased. In that case, short-term persistence will be the most misleading. Forest plants provide an example--they have low e and c and their dispersal is easily impaired. Forest plants indeed seem to be especially slow. This seems true also for saproxylic insects from old forests, as 18th Century parks where the habitat seems good still have an impoverished saproxylic fauna (Warren and Key 1991).

In general, low local extinction rates occur in species with large or stable local population size, due to small individual area requirements, long individual life span, low sensitivity to environmental stochasticity, low patch disturbance rate, large patch size, or large within-patch heterogeneity. Low colonization rate occurs in species that have low dispersal rate (high site fidelity), short dispersal distances, inefficient dispersal behavior, or small establishment chance, combined with large inter-patch distance, large between-patch resistance, or both.

18.4.3 Manage Time Lags in Preferred Directions

Perhaps the only universal principle for preserving species in the face of time lags is that we should decrease local extinction and enhance colonization. When temporary, such measures slow or reverse the speed of decline or speed up recovery. In the first case they increase the time window for more fundamental measures (or for an unmanaged return of better times). Speeding up recovery decreases the possibility of stochastic metapopulation extinction and other deleterious effects of small population size. The fastest way to accelerate recovery may be by boosting colonization. When more permanent, such measures also increase the equilibrium, but their effect on return time can then be counterintuitive. For example, in declining but viable metapopulations, countermeasures *reduce* the time needed to reach an equilibrium. Local extinction risk can be decreased by, for example, (1) increasing patch carrying capacity by increasing patch size, or managing habitat quality, (2) increasing population growth rate by managing habitat quality or decreasing human-induced mortality such as traffic mortality, hunting, and poaching, and (3) interfering in cases of extreme downward fluctuations in numbers, by feeding when food is scarce, vaccination, predator control, and special conservation measures such as temporarily closing down roads (Goodman 1987). Measures for promoting colonization include translocating individuals, sowing, reintroduction programs, creating corridors, and situating habitat restoration projects adjacent to occupied existing habitat.

When communities need reorganization, for example the formation of protective edges around fragments, we can help them to do so, especially when degradation has proceeded too rapidly for spontaneous restructuring (Kellman, Tackaberry and Rigg 1998).

However, we must be vigilant for possible unwanted side effects of management measures, such as pollution of the gene pool, introduction of predators, pests, diseases or parasites, and effects on other species. Furthermore, we must be prepared for surprises as stochastic events take place, species adapt to their new environment, or communities reorganize.

18. 5 Theoretical and Empirical Knowledge Gaps

Here, we identify the major gaps preventing application of the concept of time lags in metapopulation responses to landscape change. Theoretical knowledge is still far from complete (cf. Simberloff 1992) and empirical knowledge is almost non-existent. Prediction is made difficult by (1) lack of knowledge about basic metapopulation processes and the evolutionary plasticity of species, and (2) the nascent state of a multifaceted theory that needs to incorporate models that are spatially more realistic. The lack of empirical knowledge about time lags makes it hard to test theory.

18.5.1 Theoretical Voids

Models can be an important help for interpreting empirical results, searching for generalities, and (especially important for time-lag research) extrapolating over time. There is a need for a multifaceted theory. We need simple general rules for recognizing situations where time lags are expected and for guessing their order of magnitude, and we need complex models that yield specific estimates of the expected time length of the lags. Most work has been done on simple deterministic spatially implicit models, and the most important void concerns spatially explicit, realistic, stochastic models, because these potentially can produce markedly different predictions. Major factors influencing time lags that should be investigated are: heterogeneity in patch size, quality and connectivity; stochastic fluctuations in small networks; environmental correlation among patches; influence of dispersal on local population dynamics; source/sink dynamics; and life-history characteristics such as individual life span. Further voids concern: more comprehensive evolutionary models that take, for example, habitat amount and dispersal distance into account; and how landscape dynamics, such as ecological succession, and evolutionary dynamics add their own time lags to those associated with metapopulation dynamics.

18.5.2 Empirical Voids

There is a need for records of time lags classified according to species characteristics (e.g., longevity, dispersal characteristics) and landscape characteristics (e.g., pace, type and severity of degradation). Accurate records of changes over time in the landscape as well as in species distributions are needed. Information about long lags is particularly important, as is the untangling of natural and anthropogenic causes of non-equilibrium situations.

Other empirical voids concern the basic processes of local extinction and, especially, colonization (and hence dispersal, cf. Opdam 1990). Knowledge about the rates of the basic

processes is essential to predict time lags, and deterioration of these rates can be an important component of environmental degradation. How do species-specific characteristics (e.g., longevity, social structure), landscape characteristics (e.g., reserve size, heterogeneity, habitat dynamics) and interspecific interactions (e.g., competition and predation) influence local extinction rate? Is there still a functioning metapopulation with local extinction accompanied by recolonization, or will absence of colonization result in regional extinction? Especially relevant questions concerning dispersal are: what is the occurrence of rare long-distance dispersal events, often crucial for colonization (Cain, Damman and Muir 1998)? what is the role of interactions such as zoochorous seed dispersal? and to what extent is dispersal compromised in modern landscapes?

The last void concerns evolution. How and how fast do characteristics relevant to metapopulation dynamics adapt to the landscape? For example, species of traditionally stable habitats such as late-successional stages are thought to have evolved into poor colonizers, but this needs more testing. Possible tradeoffs between different aspects of colonization ability and persistence ability also deserve significant study. Many species seem to have adapted to traditional cultural landscapes (e.g., Thomas and Morris 1995). But how widespread and important is this? Are generation time and genetic heterogeneity crucial factors? Can evolutionary changes also compromise metapopulation survival (“evolutionary suicide”, e.g., Leimar and Norberg 1997)?

18.6 Research Protocols

First, a general point applicable to both theoretical and empirical research should be made. Species-specific characteristics *and* landscape features together determine time lags. Therefore, the concept of ecologically scaled landscape indices developed by Vos et al. (in press) can be of particular use. This approach involves looking at landscapes “from a species’ perspective” and reducing parameter space from landscape statistics and life-history characteristics to scaled indices such as “local carrying capacity” and “connectivity”, which capture the essentials of both species and landscape.

18.6.1 Protocols for Theoretical Research

The effects of the major factors mentioned in section 18.5.1 should be investigated using a series of models, ranging from simple, strategic models (May 1973) to spatially explicit, stochastic and/or individual-based models. See Durrett and Levin (1994), Hanski and Gilpin (1997), Hanski (1999), and Holyoak and Ray (1999) for guidance on general spatial models. A promising middle ground between cumbersome and untransparent spatially explicit and/or individual-based models on the one hand, and unrealistic simple models on the other hand, is the “mesoscale” approach advocated by Casagrandi and Gatto (1999) which uses statistical distributions of abundance per patch. For prediction of the fate of specific metapopulations, PVA software such as ALEX, VORTEX, and RAMAS/metapop is available. For references and a comparison of five PVA software packages see Brook et al. (1997). Such packages enable the user to add demographic and environmental stochasticity, inbreeding (in some) and other details. The more realistic models can be used for impact

assessment, and the simpler ones, such as the Levins model, can be used to gain a better general understanding. Simple models provide no concrete answers for specific problems, but detailed PVA software provides no general understanding, results are often very sensitive to the parameter values chosen, and there is a severe risk of introducing errors. For basic modeling strategy and guidance for how to deal with these pitfalls of modeling, we refer researchers to Burgman, Ferson and Akçakaya (1993). See Ferriere, Dieckmann and Couvet (in press) for approaches to modeling evolutionary dynamics, and see Remmert (1991) and Stelter et al. (1997) for methods to model landscape dynamics.

18.6.2 Protocols for Empirical Research

Specific protocols are not easy to supply because as yet there is no experience with empirical research on time lags, and many empirical voids require application of general ecological methods. However, some guidance can be given.

To obtain records of time lags we can learn a lot from natural and human-induced catastrophes such as hurricanes and oil spills, and from gradual landscape changes involving habitat loss, habitat fragmentation and habitat-quality degradation; Restoration projects also provide opportunities. We must monitor both landscape changes and effects upon biodiversity closely. To have controls in both space and time, the best research protocol is BACI (Before, After, Control, Impact) (Green 1979). This will usually be possible only in cases of planned impacts. We should especially pay attention to differences among taxa, habitats, landscapes, ecosystems and impacts. The populations of a selected group of indicator species should be monitored on the basis of habitat patches that cover if possible a complete habitat network or at least a comprehensive part of the landscape (Opdam et al. 1993). Getting insight in the turnover processes is an important aim. Monitoring for numbers or densities is preferable, but determining presence and absence can provide insight too (cf., Kareiva, Skelly, and Ruckelshaus 1997). Until now, research has concentrated on species with “fast” metapopulations, like birds and butterflies, and on habitat destruction. Researchers need to pay more attention to “slow” species and to dispersal impairment, where metapopulation decline may be less apparent but in the long term more severe.

Just as the impact of ongoing change of landscapes and land use may be visible only in the future, the patterns in species distributions witnessed today may reflect landscapes and land use in the past. We can study the latter by “ghost hunting” (searching for ghosts of the landscape past) with historical maps and records to look for bygone landscape features that correlate with current biodiversity patterns (e.g., Grashof-Bokdam and Geertsema 1998). This is also an approach to obtain information about long time lags. Other ways to study long delays are trying to find comparable systems where the history of the focal impact is much longer, or searching for natural analogs of impacted systems (e.g., Kellman, Tackaberry and Meave 1996). Such study of long-term historical effects can help to predict robustness of present systems. We also stress the importance of developing long-term monitoring programs. The difference in time scale between time lags and the opportunities of studying them is now a major constraint.

Dispersal is hard to investigate, one of the reasons being that in many species effective dispersal from one patch to another is rare. As a consequence, deterioration of dispersal is much more difficult to measure than habitat destruction or increased disturbance. Techniques and specific research protocols for studying dispersal can be found in Turchin (1998) and the references therein.

When colonization and extinction processes cannot be observed directly, species distribution data and their turnover in time can be analyzed using logistic regression. An example of this approach is application of the incidence function model” (Verboom et al. 1991; Hanski 1994, 1997, 1999). Such methods, however, imply deriving processes from patterns, and a major drawback is that by disregarding time lags one may get seriously over-optimistic predictions for non-equilibrium (declining) metapopulations (Ter Braak, Hanski and Verboom 1998).

See Dieckmann, O'Hara, and Weisser (1999) and Ferriere, Dieckmann and Couvet (in press) for the emerging field of research in evolutionary conservation. Research should concentrate on how habitat use (e.g., Van Balen 1999) and dispersal-related traits (e.g., Hill, Thomas and Lewis 1999) evolve in response to landscape change.

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