CHAPTER 10

Biodiversity as spatial insurance: the effects of habitat fragmentation and dispersal on ecosystem functioning

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10.1 Introduction

Anthropogenic habitat destruction (e.g. strip mining or clear cutting of forests), conversion to agriculture (e.g. conversion of grasslands to croplands or rangelands, or conversion of forests to plantations), and fragmentation (e.g. dividing ecosystems inhabited by native species into parcels that are separated by inhospitable terrain) are generally considered the dominant drivers of biodiversity loss. The loss of inhabitable area is the predominant cause of population (Hughes *et al.* 1997) and species extinctions (Pimm *et al.* 1995). Isolation of fragments of habitat and edge effects associated with such fragmentation can cause further declines in both the number of species, changes in their relative abundance, and other aspects of biodiversity within remnant habitat patches (e.g. Andrén 1994, Fahrig 2003, Ewers and Didham 2006). Although other anthropogenic drivers (e.g. climate change, overexploitation, and the spread of non-indigenous species that adversely affect indigenous species) are growing in importance, it is clear that their impacts will be felt within the context of ongoing habitat loss. Indeed, strong synergies between habitat fragmentation and climate change are expected (Holt 1990, Travis 2003) and will likely compound the loss of biodiversity at local and regional scales.

The threat of widespread and rapid loss of biodiversity across most regions has prompted two decades of research on the impacts of biodiversity loss on ecosystem functioning and services. A number of controlled experiments have established that reduced levels of species diversity can impact community processes, such as biomass production and nutrient uptake (Cardinale *et al.* 2007), although data from unmanipulated plant communities suggest that these effects may be weaker or masked by other covarying factors in the environment (Grace *et al.* 2007, Hector *et al.* 2007). Overall, the beneficial effects of biodiversity in experimental conditions have been shown to saturate at relatively low to moderate levels, even when several functions are considered simultaneously (Hector and Bagchi 2007). The relevance of results from biodiversity and ecosystem function experiments, given the rapid saturation of biodiversity effects, has questioned their utility as a case for conservation biology and has led to calls for a broadening of empirical and theoretical perspectives within the field (Gonzalez and Chaneton 2002, Srivastava 2003, Srivastava and Velland 2005, Lawlor *et al* 2002).

Biodiversity effects on ecosystem functioning (BEF), though small or sometimes negligible in small-scale studies, may nevertheless be more significant at larger spatial and temporal scales (Yachi and Loreau 1999, Loreau *et al.* 2003, Cardinale *et al.* 2004). Typically, experimental BEF studies have been performed over small spatial and temporal scales, relative to the size, mean habitat range, and generation times of the organisms involved. Although these limitations are most acutely associated with studies of terrestrial plant and tree communities, experiments with aquatic systems can also have similar limitations. The results of BEF experiments, whether terrestrial or aquatic, although clearly valuable for establishing the effect of varying local biodiversity, cannot provide a complete understanding of the spatial processes affecting the relationship between biodiversity and ecosystem functioning at landscape (e.g. more than one ecosystem), regional, or global scales (Gonzalez and Chaneton 2002, Rantalainen *et al.* 2005, Srivastava and Velland 2005, Dobson *et al.* 2006).

The loss of biodiversity in fragmented landscapes has underscored the importance of viewing communities as 'open' structures dependent upon spatial fluxes from the surrounding communities in the region (Kareiva and Wennergren 1995, Leibold *et al.* 2004). Although the importance of dispersal for the maintenance of biodiversity is relatively well understood (e.g. MacArthur and Wilson 1967, Schmida and Wilson 1985; Loreau and Mouquet 1999, Amarasekare 2004, Holyoak *et al.* 2005, Mouquet et al. 2005) its importance to ecosystem functioning remains relatively unexplored (Kareiva and Wennergren 1995). For example, weak flows of individuals between habitats may have significant impacts on population production (Holt and Loreau 2002, Mouquet *et al.* 2002, Ives *et al.* 2004) and community stability (Huxel and McCann 1998, Loreau *et al.* 2003). From this perspective, a more complete understanding of the impacts of biodiversity loss on local ecosystem functioning requires a fuller understanding of dispersal-dependent mechanisms of biodiversity. At the regional, or metacommunity scales, the spatial components of diversity – both spatial variance in diversity among habitats or patches and turnover in composition from habitat to habitat or patch to patch – are significant determinants of ecosystem functioning at scales greater than the habitat or patch (Fukami *et al.* 2001, Bond and Chase 2002, Gonzalez and Chaneton 2002, Loreau *et al.* 2003a,b, Cardinale *et al.* 2004, Leibold and Norberg 2004). A framework for understanding how spatial processes mediate biodiversity-ecosystem functioning relationship is needed to improve our understanding and ability to predict the ecosystem consequences of biodiversity loss at larger scales.

In this chapter we will review several concepts that allow us to link local and regional scales of the biodiversity and ecosystem functioning relationship. First we will consider how the species–area relationship can link loss of habitat to delayed loss of diversity and ecosystem functioning in remnant fragments. Second, we will then show how spatial variance in biodiversity can affect estimates of regional functioning by non-linear averaging (Benedetti-Cecchi 2005). Finally we will use a metacommunity framework to formalize the *spatial insurance hypothesis* (Loreau *et al.* 2003). Throughout we will consider how each of these perspectives informs our understanding of the impacts of habitat destruction and fragmentation on biodiversity and ecosystem functioning and stability. We will conclude that our understanding of the relationship between biodiversity and ecosystem functioning is substantially altered when we incorporate the spatial processes required to link local and regional scales.

10.2 Fragmentation, species loss and functioning debts

Habitat destruction is not a uniform process and the end result is typically a mosaic of remnant fragments of habitat containing a subsample of the flora and fauna that occupied the formerly continuous habitat (Fahrig 2003, Ewers and Didham 2006). The loss of habitable area, increased isolation and increased edge effects associated with fragmentation collectively initiate a process of community disassembly (Diamond 1972), involving declines in both species abundance and diversity within remnant habitat fragments. Community disassembly following habitat fragmentation can be simplified to two processes operating at different time-scales: the first a relatively rapid sampling of the original diversity as habitat is lost and the second a longer-term process of decay or 'relaxation' in residual diversity from the remaining fragments. Ecologists have sought to calculate the extent of future species loss due to habitat destruction and fragmentation, but little attention has been paid to estimating the functional (i.e. biogeochemical or ecosystem process) effects of community disassembly in fragmented landscapes (e.g. Laurence *et al.* 1997, Larsen *et al.* 2005, Rantalainen *et al.* 2005)

Most experiments relating ecosystem function to changes in species diversity have so far adopted a 'static' approach. Ecosystem variables are usually measured across gradients of spatially interspersed diversity treatments, consisting of communities assembled at random from a given species pool (e.g. Tilman *et al.* 1997; Hector *et al.* 1999). Although these designs are useful for revealing diversity effects independent of species composition, they might not reveal the ecosystem changes that accompany diversity loss in fragmented habitats, where extinction is a non-random process dominated by non-equilibrium dynamics. In particular, the identity of species extinctions (e.g. rare versus dominant) and the timing of their occurrence may be variable and delayed (e.g. the *extinction debt* described by Tilman *et al.* 1994, Gonzalez 2000, Vellend *et al.* 2006). The functional effects of extinction debts in fragmented landscapes are unobservable in experiments if they use spatially structured gradients of fixed diversity levels as a surrogate for species loss following fragmentation.

Delayed losses of diversity due to habitat fragmentation should also generate a *functioning debt* – *i.e.* a delayed alteration in ecosystem attributes driven by the delayed decline and extirpation of species persisting in remnant patches (Gonzalez and Chaneton 2002). The possibility that extinction debts may be associated with functioning debts has received little attention to date. This is in part because the static and local approach of current experimental protocols precludes the study of these dynamic aspects of diversity loss. Although recent studies have addressed the problem of species loss as a non-random process through theoretical (Ives and Cardinale 2005) and statistical means (Solan *et al.* 2004) they have not the addressed the more complex dynamical issues arising from habitat fragmentation (Fahrig 2003). Extinction debts are threshold phenomena (Ovaskainen and Hanski 2002) that arise because species persistence depends upon the spatial configuration of the landscape; fragmentation affects landscape connectivity that alters local and regional colonization and extinction rates. The challenge now is to understand how this phenomenon of diversity loss affects ecosystem functioning.

For a long time the species–area relationship has been used to estimate the extent of species loss due to destruction and relaxation (the slow approach to a new equilibrium in species richness within the landscape, e.g. Brooks *et al.* 1999). The method involves increasing the exponent (z) of the species–area relationship to account for the disproportionate loss of species from small areas of habitat. If the original habitat area A_o, is reduced to A_n, we do not simply expect the original number of species to decline to S_n, but rather to S_n estimated with a new higher value of z. Here we use this approach to examine how habitat fragmentation will affect local ecosystem functioning.

Figure 10.1 depicts our conceptual model. We begin with the familiar species–area relationship, $S = cA^z$, which describes how diversity S scales with area A raised to the power z, where z ranges from about 0.15 for continuous tracts of continental habitat to about 0.25 for habitat islands. Two species–area curves can be drawn corresponding to 'before' and 'after' fragmentation. These curves can be used to estimate how many species there are in a given area before fragmentation by interpolating along the 'before' fragmentation curve ($z = 0.15$). The eventual loss of species from a fragment because of isolation (i.e. due to relaxation) can be estimated by switching to the lower, but steeper, species–area curve ($z = 0.25$). These changes in species richness can then be mapped onto the generally saturating function (Cardinale *et al.* 2006) describing the relationship between species richness and ecosystem functioning (e.g. productivity) to produce estimates of Δf, the delayed change in ecosystem functioning in a fragment due to the delayed species loss. This approach predicts that the smaller the fragment, the larger the reduction in ecosystem functioning (functioning debt) due to delayed species loss (Fig. 10.1).

Few data exist to test the validity of this approach for natural landscapes. A good starting point would be to use data from experimental model systems (e.g. Wardle *et al.* 2003b). Gonzalez and Chaneton (2002) noted the existence of a functioning debt following the delayed loss of species in experimental fragments of a bryophyte-based microecosystem, but they did not try to predict the extent of the functioning debt from the observed species loss. Although it may take considerable time for local extinction to occur, certainly experiments could be conducted in a grassland

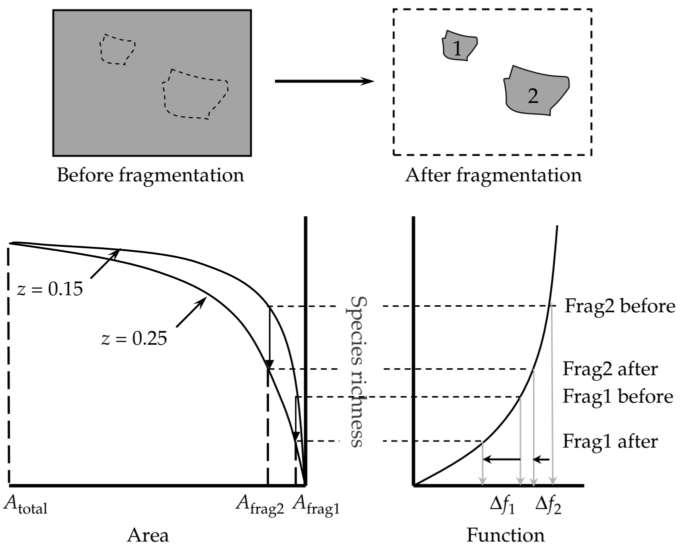

Figure 10.1 Predicting the delayed effects of habitat loss and isolation on local ecosystem functioning. The upper panel shows two fragments of differing area before and after habitat destruction (habitat is represented in grey). The lower left graph shows the two species–area relationships corresponding to before ($z = 0.15$) and after ($z = 0.25$) fragment isolation. The lower right graph shows a typical relationship between species richness and ecosystem functioning. The loss of species richness due to isolation is predicted by the increase in the slope of the species–area relation. This change in species richness due to isolation and community disassembly (frag 1 or 2 before) can be mapped onto the species richness-functioning relation (frag 1 or 2 after) to estimate the delayed change in function (Δf, the *functioning debt*).

setting to estimate the functional impacts of community isolation from the surrounding landscape (e.g. Robinson *et al.* 1992). Experiments in tractable systems, such as microbial microcosms, would be able to evaluate the different effects of fragmentation (e.g. isolation, edge effects, loss of area), and directly address how these causes of local extinction affect ecosystem functioning, although the laboratory context of microcosms often limits their utility for predicting phenomena in larger, more complex, less environmentally controlled ecosystems like grasslands or forests.

Others have recently pointed out the utility of the species–area relationship to address other impacts of area loss on ecosystem functioning (Tilman 1999a, Naelsund and Norberg 2006, Dobson *et al.* 2006), but have not used the approach to estimate the functional impacts of extinction debts. Dobson *et al.* (2006) pointed out that some functional groups (e.g. body size) and higher trophic levels are expected to have greater values for the exponent z, and thus differential sensitivity to area loss. An important consequence of this is that species loss due to habitat destruction should involve the top-down collapse of food webs (Holt *et al.* 1999). Although the evidence for this is equivocal (Mikkelson 1994, Holyoak 2000, Gonzalez and Chaneton 2002, Rantalainen *et al.* 2005), the functional consequences of such trophic collapse are likely to be great (e.g. Duffy 2003, Rantalainen *et al.* 2005, Rooney *et al.* 2006). Habitat destruction and fragmentation are the major causes of species loss in terrestrial ecosystems and more work is needed to establish how it affects ecosystem functioning (Kareiva and Wennergren 1995).

10.3 Spatial variance of biodiversity in fragmented landscapes

We noted that habitat fragmentation creates landscapes with many remnant fragments of variable size and species richness (Fahrig 2003). In the previous section we raised the problem of estimating the longer-term functional impacts of species loss within a given fragment. Here we address the problem of estimating the mean change in functioning across a set of fragments of variable size and species richness.

Within fragmented landscapes distributions of fragment size are often skewed with relatively few large patches distributed within a network of a large number of small patches (e.g. Keitt *et al*. 1997). This variation in fragment area translates into spatial variation in species diversity that may be exacerbated by a mix of deterministic and stochastic patterns of extinction and colonization across fragments (Wright *et al.* 2007). What are the consequences of spatial variance in diversity from fragment to fragment for estimating the change in mean ecosystem functioning at the landscape level? The answer involves spatial averaging. Benedetti-Cecchi (2005) recently pointed out that spatial variation in local diversity could significantly reduce estimates of mean ecosystem functioning in a fragmented landscape if the non-linear relationship between biodiversity and ecosystem functioning was not taken in account. This reasoning is based on Jensen's inequality (Jensen 1906, Ruel and Ayres 1999), the well known property that the expected value of a concave down function typical of biodiversity-functioning relationships, is lower than the function of the expected value: $E(f(X)) < f(E(X))$. Thus spatial variation in diversity (between communities) would, as a result of non-linear averaging across patches, produce lower than expected levels of ecosystem functioning. Drawing upon data from recent terrestrial plant experiments Benedetti-Cecchi (2005) found that, depending on the level of variance he assumed around the mean, Jensen's inequality could result in a 5–45% reduction in biomass production when compared to the case where spatial homogeneity in diversity was assumed. Although the range of this effect is large, it has generally been statistically significant.

Few biodiversity-functioning experiments have been conducted at the appropriate spatial scale to verify the importance of community-to-community variation in diversity due to non-linear averaging. In Fig. 10.2 we provide an example of how Jensen's inequality may lower the estimate of mean community production in landscapes with different distributions of habitat fragment size. Although we obtain a reduction in mean functioning due to Jensen's inequality, the effect is modest and corresponds to the low end of Benedetti-Cecchi's (2005) range. This is due in part because our use of the species–area relationship constrains the range of variation in species richness across fragments. However, Benedetti-Cecchi (2005) also used a larger range of variation (spatial variance) in species richness that may not be entirely realistic at the scale of local communities (Crawley and Harral 2001).

Our example raises empirical issues that merit further study. We assumed that the form of the BEF function is constant across the region of interest and thus the same function can be used to map diversity to function for any given community. Although this assumption probably breaks down across larger regions (e.g. Hector *et al.* 1999) we know remarkably little about spatial variation in BEF relationships at regional scales. We also assumed that the species–area relationship could be used as a first approximation to map the distribution of fragment size to the spatial variance in biodiversity. The general nature of non-linear averaging and the potential for large changes in spatial variation in diversity in disturbed landscapes suggest that this effect is likely to be sufficiently great that future studies should estimate it. Finally, we note that similar arguments can be made when estimating variation in mean ecosystem functioning when species diversity varies through time (Ruel and Ayres 1999), as it will in any fragmented landscape undergoing relaxation (Brooks *et al.* 1999, Gonzalez 2002).

10.4 Linking local to regional: the spatial insurance hypothesis

In the previous sections we have ignored dispersal and its role in driving spatial patterns of diversity and ecosystem process. The loss of biodiversity in fragmented landscapes forces a perspective that communities are 'open' structures dependent upon dispersal from the surrounding communities in the region (Kareiva and Wennergren 1995, Tilman and Kareiva 1997, Leibold *et al.* 2004). However, the way in which dispersal mediates the effects of diversity on ecosystem functioning has only recently been investigated theoretically (Holt and Loreau 2002, Mouquet and Loreau 2002, Loreau

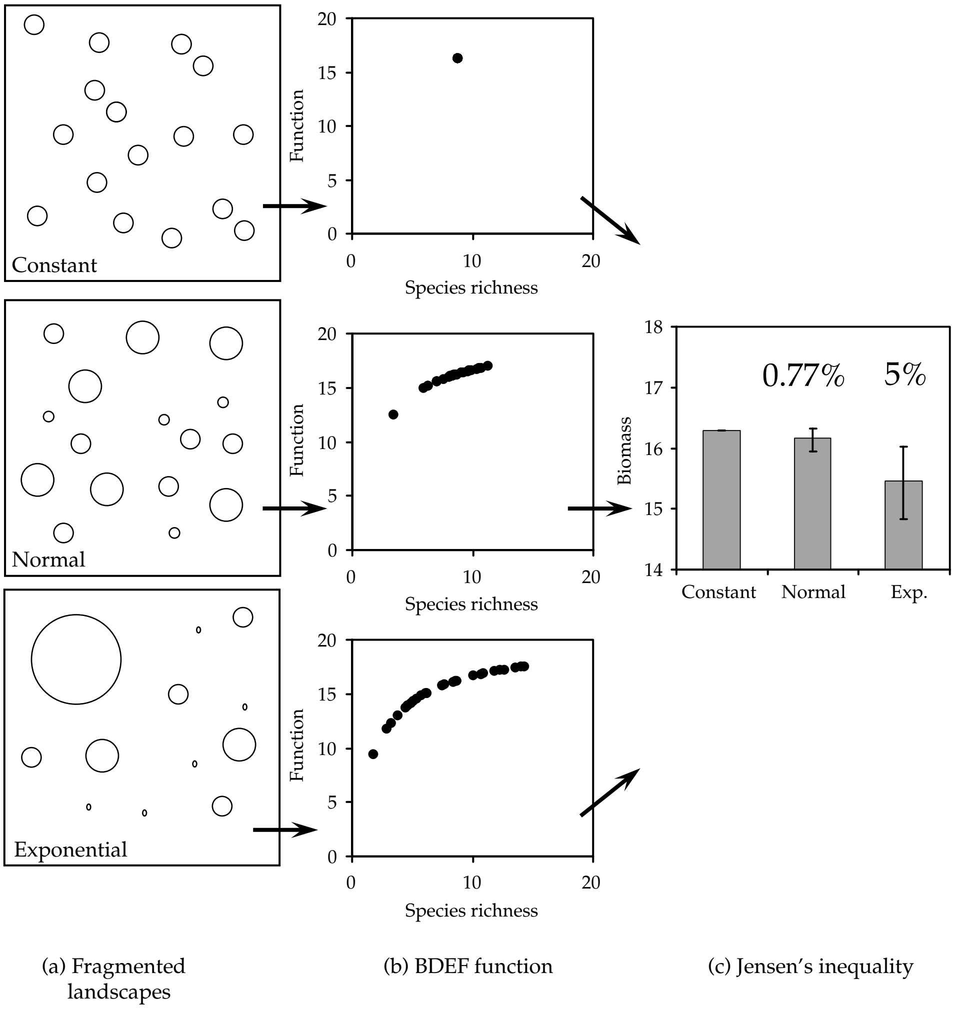

Figure 10.2 Spatial variation in species richness due to variation in fragment area across three different landscapes demonstrates the effect of Jensen's inequality. To calculate Jensens's inequality we assumed a nonlinear biodiversity-functioning relationship (a) of the form $aS/(S + b)$ where $S =$ species richness, $a = 20$, and $b = 2$. We then generated three types of landscape of 30 fragments each with equal total fragment area. In the first landscape every fragment has a constant area ($A = 5$ units), in the second each fragment area was drawn from a normal distribution ($\mu = 5$, $\sigma = 2$), and in the third the fragment area was drawn from an exponential distribution ($\mu = 5$). The fragments drawn here are for illustration only and are not to scale. We used the species–area relationship ($S = cA^z$, where $z = 0.3$) to generate species richness for each fragment in the three landscapes. Here we assume that the extinction debt has been paid and that z is at its equilibrium. (b) Values of species richness were then used to generate values for ecosystem function for each fragment (black dot for each fragment). We then compared mean biomass production per fragment (± 95% CI generated by Monte Carlo randomization, 1,000 iterations) for each landscape (c). The difference between the three landscapes defines the level of Jensen's inequality.

et al. 2003a and Loreau *et al.* 2003b, Mouquet and Loreau 2003, Cardinale *et al.* 2004, Leibold and Norberg 2004) and experimentally (Gonzalez and Chaneton 2002, Matthiesen and Hillebrand 2005, France and Duffy 2006b, Venail *et al.* 2008). We recently formalized the idea that dispersal mediates the effects of diversity of ecosystem functioning both directly and indirectly, an effect we have called the *spatial insurance hypothesis* (Loreau *et al.* 2003a).

The spatial insurance hypothesis is based on two mechanisms: (1) compensatory fluctuations between species (or functional groups) in the presence of spatio-temporal environmental heterogeneity, and (2) dispersal-driven spatial averaging of environmental heterogeneity. Under the first mechanism dispersal maintains biodiversity, which buffers ecosystem functioning against environmental fluctuations because functional compensations among species (or phenotypes) provide enhanced and more predictable aggregate ecosystem properties. Under the second mechanism dispersal directly buffers growth rates and inflates mean biomass production. This effect is based on the well-known principle that in the presence of dispersal, spatial variability in population growth averages arithmetically whilst in the absence of dispersal variability in growth averages geometrically (e.g. Ives *et al.* 2004). In general, the arithmetic mean will be greater than the geometric mean and this will translate into greater mean population biomass in the presence of dispersal. The extent to which spatial averaging due to dispersal translates into greater mean biomass will depend upon the extent of the increase in population growth rate and the strength of density dependence (Ives *et al.* 2004). Previous theoretical results suggest that the relationship between dispersal and mean biomass is unimodal with a peak at low to intermediate rates of dispersal (Holt 1993, Holt *et al.* 2005).

10.4.1 A source–sink metacommunity model: 'contemporaneous disequilibrium'

We reanalyze the source–sink metacommunity model of Loreau *et al.* (2003) with more species and by varying the input of nutrients within the metacommunity. We begin with a fragmented (patchy) landscape composed of a number of communities each experiencing variation in habitat quality (e.g. fluctuating temperature). We assume that each community experiences sinusoidal variation in the environment which varies out-of-phase across communities. We assume a set of species competing for a single resource and that species show dissimilar responses to the environment. Because they have different environmental optima each species will be the best competitor (defined by the rate at which they take up resource) in any given local community at different times. All species are assumed to be identical in all other aspects of their ecology (e.g. equal death and dispersal rates). Coexistence is not driven by temporal variation (i.e. resource partitioning through time) but is dependent on a spatial storage effect (Snyder and Chesson 2004), whereby dispersal allows species to persist by tracking spatio-temporal variation in environmental quality. In the absence of dispersal resource competition ensures that only a single species will persist with variable abundance in each community. Thus dispersal ensures local coexistence and environmental niche partitioning ensures regional coexistence (Mouquet and Loreau 2002).

The equations governing the metacommunity read:

$$\begin{aligned}\frac{dN_{ij}(t)}{dt} &= [e_{ij}c_{ij}(t)R_j(t) - m_{ij}]N_{ij}(t)\\ &\quad + \frac{a}{M-1}\sum_{k\neq j}^{M} N_{ik}(t) - aN_{ij}(t)\\ \frac{dR_j(t)}{dt} &= I_j - l_jR_j(t) - R_j(t)\sum_{i}^{S} c_{ij}(t)N_{ij}(t)\end{aligned}$$

$N_{ij}(t)$ is the biomass of species i (e.g. a plant) and $R_j(t)$ is the amount of limiting resource (e.g. a nutrient such as nitrogen) in community j at time t. The metacommunity consists of M communities and S species in total. Species i consumes the resource at a rate $c_{ij}(t)$, converts it into new biomass with efficiency e_{ij}, and dies at rate m_{ij} in community j. We assume that the resource is renewed locally through a constant input flux I_j, and is lost at a rate l_j. Species disperse at a rate a, dispersal is global, and propagules are redistributed uniformly across the landscape but do not return from the community they come from. We further assume that the consumption rates $c_{ij}(t)$ reflect the match between species traits and local environmental conditions as in Mouquet *et al.* (2002). Let the constant trait value of species i be H_i, which may be interpreted as its niche optimum along an environmental gradient, and the fluctuating environmental value of community j be $E_j(t)$. We assume that both species traits and environmental values vary between 0 and 1, and that a species' consumption rate is highest when the environmental value matches its niche optimum as measured by its trait value. Specifically, consumption rates are given by:

$$c_{ij}(t) = \frac{1.5 - |H_i - E_j(t)|}{10}$$

Ecosystem productivity at time t is the production of new biomass per unit time, average metacommunity productivity is thus:

$$\Phi(t) = \frac{\sum_{i=1}^{S}\sum_{j=1}^{M} e_{ij}c_{ij}(t)R_j(t)N_{ij}(t)}{M}$$

Here we study a metacommunity made up of 20 communities. Because various community properties (e.g. local and regional diversity and stability) are known to vary with rate of resource input we also examined the effect of varying the rate of resource input (system fertility) on metacommunity production and stability. In our simulations, we considered the following parameters: $e_{ij} = 0.2$; $m_{ij} = 0.2$; $I_j = (110 \text{ or } 165)$; $\ell_j = 10$;. Environmental fluctuations follow a sinusoid with period T:

$$E_j(t) = \frac{1}{2}\left[sin\left(Einit_j + \frac{2\pi t}{T}\right) + 1\right]$$

In contrast to our previous analysis (Loreau *et al.* 2003) we do not force the initial environmental conditions in each community so that each species is the best competitor in a different community: the $Einit_j$ were chosen randomly from a uniform distribution between ± 2π resulting in $E_j(0)$ being random between 0 and 1. This more realistic assumption results in fewer species having source communities, and demonstrates the robustness of our results to variation in initial conditions. We started the simulation with 20 species ($H_1 = 1$ and $H_i = H_{i-1} - 1/20$ for $i = 2$ to 20). Simulations at each dispersal value were repeated 50 times with different initial environmental conditions and results were averaged over the 50 repetitions. Each simulation lasted 800,000 iterations (Euler approximation with $\Delta t = 0.08$) with the period T chosen to be large enough ($T = 40{,}000$) so that there was rapid competitive exclusion in the absence of dispersal. Temporal mean diversity (local and regional) and temporal mean productivity and its coefficient of variation (CV) were calculated over the last 200,000 iterations.

10.4.2 Metacommunity dynamics

The dynamics of the metacommunity are strongly dependent upon the rate of dispersal. Dispersal permits local coexistence. Increasing dispersal, and resource input increases the level at which diversity is maintained both locally and regionally (Figs. 10.3 (a) and (b)). Local diversity attains a maximum value of seven species for $a = 0.07$, whilst regional diversity declines to a minimum for $a = 0.004$ and then returns to its maximum for $a = 0.1$. For values of dispersal greater than 0.1, local and regional diversity declines linearly. Species best adapted to the average environmental conditions at the metacommunity scale now prevail; recall that because the environment varies out of phase across the metacommunity the average condition is $E = 0.5$ to which intermediate species are best adapted. Species adapted to the extremes of environmental variation contribute progressively less to community productivity and eventually go extinct locally and regionally. Local and regional diversity are now at their lowest levels and the metacommunity has now been reduced to a metapopulation of a single species. Overall, increasing dispersal has strongly non-linear effects on the diversity of the source–sink metacommunity. Although diversity is causally dependent upon the rate of dispersal in this metacommunity it is useful to study the change in local and regional dynamics as a function of variation in species richness and as a function of dispersal rate.

10.4.3 Metacommunity productivity

Mean temporal productivity (the rate of biomass production per unit time averaged over the last 200,000 iterations) was affected by dispersal and attained its lowest level when dispersal was absent. Increasing dispersal resulted in a unimodal response in mean ecosystem productivity that peaked at dispersal rates of 0.01 (Fig. 10.3(c)). The position of this peak was not affected by the rate of

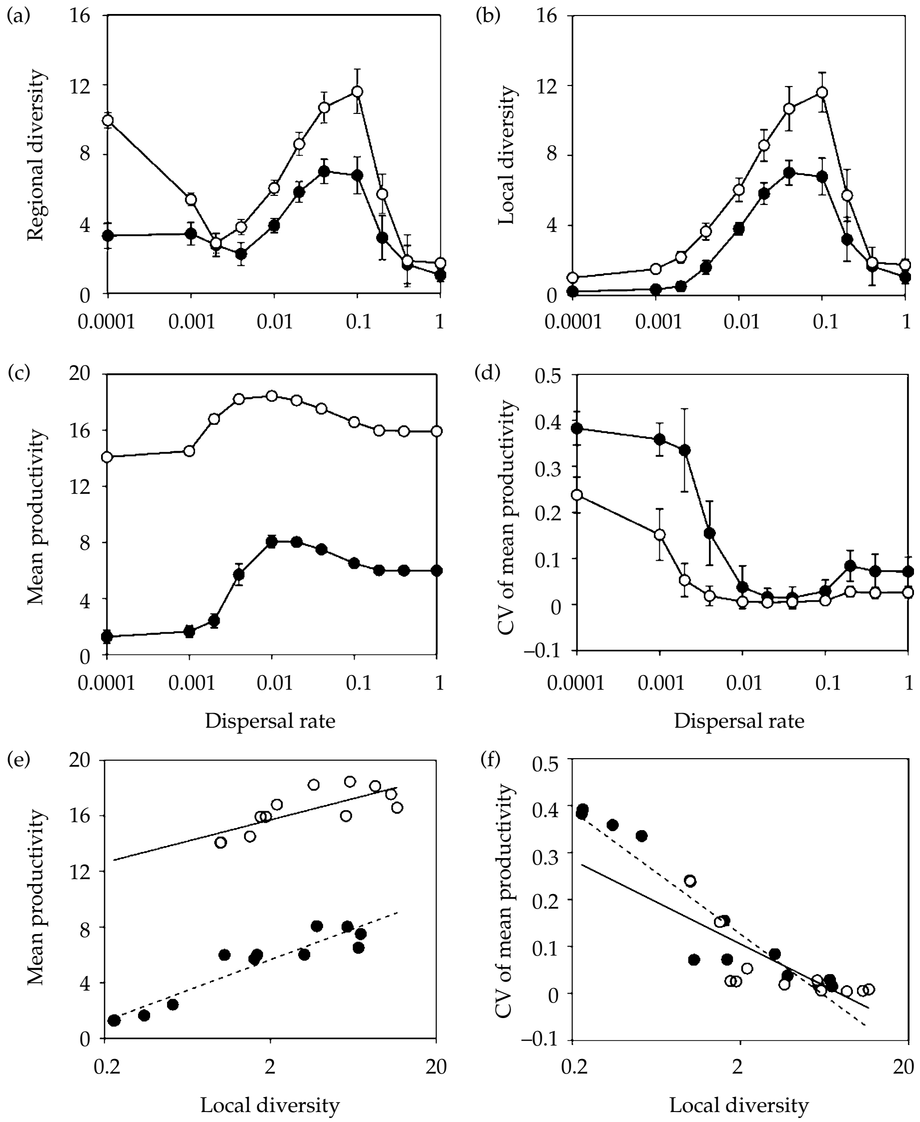

Figure 10.3 Mean regional (gamma) diversity (a), mean local (alpha) diversity (b), mean temporal productivity (c), and the mean temporal CV of mean productivity as a function of dispersal rate averaged over 50 simulations. Mean ecosystem productivity (e) and the mean temporal CV of mean productivity (f) as a function of dispersal rate. Variation between simulations is shown with standard error (a, b, c) and standard deviation (d). The symbols in each plot indicate different rates of resource input: filled circles $I = 110$; empty circles $I = 165$. All other parameter values are given in the text.

resource input, although average productivity increased significantly with increasing resource input, both in the presence and absence of dispersal. When productivity was plotted against local species richness (Fig. 10.3(e)) we obtained an increasing log-linear function that resembles the concave down relationship observed in many biodiversity-ecosystem functioning experiments. Increasing resource flow did not greatly alter the form of the richness–productivity relation; for a given level of species richness local productivity was increased roughly two-fold.

Increasing dispersal also enhances the productivity of each species directly through the

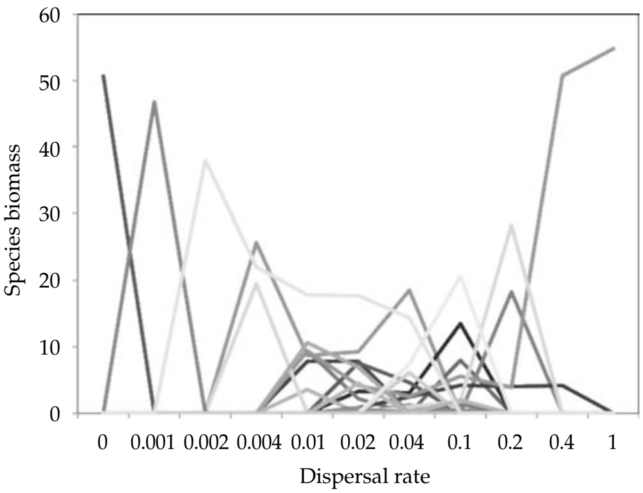

Figure 10.4 Example of how spatial averaging produces species-specific biomass peaks at different dispersal rates. We have averaged individual species biomasses over the last 250,000 time steps within a single community. We give values for different dispersal rates (each species is represented by a different grey line). Each species has a distinct mode, indicating the rate of dispersal at which each is most productive within this particular community. Parameter values are given in the text with $l = 140$.

phenomenon of spatial averaging. The effect of dispersal rate on productivity can be seen for all species in Fig. 10.4. The figure shows species-specific responses to increasing dispersal whereby the level of dispersal that maximizes mean productivity due to spatial averaging differs among species.

10.4.4 Metacommunity stability

We summarized the stability of ecosystem productivity with the coefficient of variation (CV = standard deviation/mean, e.g. Tilman 1999a, Hughes and Ives 2002). As local species richness increases the CV declines non-linearly (Fig. 10.3(f)). Increasing resource flow rate enhances this stabilizing effect of species richness (Fig. 10.3(f)). The CV shows a very different relation with increasing dispersal rate (Fig. 10.3(d)). Here we see an inverse unimodal relationship with the minimum CV obtained for intermediate dispersal ($a = 0.02$–0.1). Ecosystem productivity is strongly stabilized by dispersal and is very stable at intermediate levels of dispersal. Stability is still greater at high rates of dispersal than at very low rates, and this is again due to spatial averaging. Increasing resource flow further improves stability and reduces the CV across all levels of dispersal, but especially at the lowest rates.

Stability arises because of compensatory species dynamics within local communities (not shown). This insurance effect of diversity is obtained at low levels of dispersal that maximize diversity. As above, spatial averaging also contributes to ecosystem stability by enhancing mean productivity (the denominator in the CV). However, low dispersal is not great enough to synchronize biomass growth across the metacommunity and eliminate compensation. This contrasts with the dynamics at high levels of dispersal ($a = 0.4$) where the dominant species is strongly synchronized across the community and spatial averaging dampens biomass fluctuations.

10.4.5 Discussion

The results of our metacommunity model reveal the importance of dispersal as a key process affecting the structure and function of patchy or fragmented landscapes. Two types of insurance effect were observed: an increase in the temporal mean of ecosystem productivity within and between communities, and a decrease in temporal variability. Dispersal rate mediates the strength of these insurance effects and links the diversity and functioning of communities from local to regional scales. Importantly our model allowed us to quantify and compare the indirect and direct roles of dispersal underlying the spatial insurance hypothesis: (1) dispersal indirectly affects the insurance effects of diversity by maintaining diversity in heterogeneous environments, and this effect is complemented by (2) the direct functional effects of dispersal due to spatial averaging. Furthermore, increasing the rate of resource flow enhances these effects. The relative importance of these two processes in fragmented landscapes will depend upon the type of coexistence mechanisms (dispersal-dependent or independent) and the degree of spatio-temporal heterogeneity and connectivity in the metacommunity. The assumptions of our source–sink metacommunity model are such that both effects of dispersal are important; we now discuss each in turn.

10.4.5.1 Diversity as insurance

Biodiversity can buffer ecosystem productivity against strong environmental variation as long as species with an appropriate environmental trait is present and able to grow under the prevailing environmental state (recently called 'response diversity' Elmqvist *et al.* 2003). Environmental niches of this type have been studied before in a single patch case and are thought to be a common mechanism by which diversity may buffer function over long time-scales (Chesson *et al.* 2002, Lehman and Tilman 2000, Gonzalez and De Feo 2007). When associated with dispersal and asynchronous environmental variation across communities, environmental niches can provide a robust mechanism for long-term species coexistence (e.g. a spatial storage effect, Chesson 2000).

The increase in the mean productivity with species richness in our metacommunity model stemmed from the compensatory dynamics between species through time. Longer-term studies of diversity and productivity in grasslands have revealed the importance of compensatory dynamics for the function and stability of grasslands (McNaughton 1985, Dodd *et al.* 1994, Bai *et al.* 2004). In our model the functional species trait (rate of nutrient uptake) was linked to the environment state. Because we assumed that species were evenly separated along the temporal environmental gradient, fluctuations in the environment altered the relative competitive ability of each species, which drove the strong compensatory dynamics we observed. Any environmental factor (biotic or abiotic) that imposes a shared source of mortality and disrupts phase synchrony in interspecific responses to the environment will reduce the insurance effects we show here (Ives *et al.* 1999). Although increasing interspecific synchrony will decrease the insurance effects evident in our model, it will conversely increase the species diversity necessary to generate the same level of insurance. Thus in spatially heterogeneous landscapes more species will be required to achieve the same level of buffering as environmental fluctuations become more phase-synchronized among communities.

Compensatory fluctuations in total community biomass also occurred in space across the metacommunity. Total metacommunity biomass was thus buffered by the out-of-phase variation in patch-to-patch community biomass. The propagation of this spatial insurance effect to the metacommunity level arose because of our assumption that the environment varied out-of-phase across local communities. Increasing the spatial autocorrelation in the environmental conditions will diminish phase difference amongst patches. At this scale phase synchrony will increase the number of patches required to achieve the same level of spatial insurance; two patches that fluctuate out-of-phase are sufficient to strongly buffer productivity, whereas a greater number of patches are required to generate the same effect as communities become increasingly in phase across the metacommunity. In general spatial autocorrelation decays with distance (Koenig 1999). The rate at which spatial autocorrelation decays with distance will determine the number of patches and the inter-patch distance required to maximize phase asynchrony, and ultimately, the scale at which spatial insurance effects are most pronounced. Spatially explicit versions of our model will be needed to address these important issues.

10.4.5.2 Dispersal and spatial averaging

Decreasing the rate of dispersal in the metacommunity has a significant direct effect on the mean and variability of ecosystem productivity and biomass. This direct effect of dispersal occurs independently of diversity and has been shown for single species metapopulation models (Holt 1993, Ives *et al.* 2004, Holt *et al.* 2005, Matthews and Gonzalez 2007). From these previous results the expected relationship between dispersal rate and mean biomass is unimodal with a peak at low to intermediate rates of dispersal. We have shown (Fig. 10.4) that this is indeed the case for most species in the metacommunity, the exception being the species that dominate the metacommunity at low and high rates of dispersal that show a U-shaped relationship between dispersal rate and mean biomass. Figure 10.4 also reveals differences between species in the level of dispersal that caused a peak in mean abundance; different species tend to contribute to the spatial averaging component of the spatial insurance effects as dispersal is increased. Overall, spatial averaging plays a relatively more important role in spatial insurance effects as diversity declines at higher rates of dispersal (Loreau *et al.* 2003).

Although theoretically spatial averaging is well understood there is relatively little empirical evidence. Good evidence for spatial averaging has been found in single-species microcosms (e.g. Ives *et al.* 2004, Gonzalez and Matthews 2007) and in a single multispecies microcosm experiment (Fig. 3 in Matthiessen and Hillebrand 2006). Clearly, much more empirical work is required to establish the importance of spatial averaging for the functioning and stability of fragmented landscapes.

10.4.5.3 *Empirical tests of the theory*

Recent years have seen several experiments address the effects of dispersal on the relationship between biodiversity and ecosystem functioning (Gonzalez and Chaneton 2002, France and Duffy 2006b, Matthiessen and Hillebrand 2006). The results of these experiments are broadly consistent with the spatial insurance hypothesis although none represents a precise test of the model we used.

Matthiessen and Hillebrand (2006) constructed laboratory metacommunities of benthic microalgae. They enhanced the rate of dispersal from the experimental 'regional pool' (aquaria) into the local communities (open-top, upright plastic tubes in the aquaria) by increasing the frequency at which the algae were scraped from the bottom of the aquaria and resuspended into the water column. As predicted by the spatial insurance hypothesis they found unimodal relationships between dispersal rate and local species richness and biovolume (a measure of primary production). When they used species richness as the predictor, variable biomass production showed the saturating, concave-down function typical of many biodiversity-ecosystem functioning experiments and similar to that shown in Fig. 10.3e. No attempt was made to study the community dynamics in this relatively short-term microcosm experiment.

Gonzalez and Chaneton (2002) used corridors to sustain dispersal from a large continuous block of habitat to satellites of isolated fragments of moss inhabited by a diverse community of microarthropods. In this experiment secondary production of this decomposer community was the ecosystem function of interest. Local extinction occurred in the isolated moss fragments after several months of delay, but not in those maintained by dispersal (corridor-sustained rescue effects). Fragments unconnected by corridors maintained two-thirds less secondary biomass than those connected by corridors. Thus dispersal seemed to buffer the ecosystem's capacity for organic matter processing in these experimentally fragmented habitats. However, dispersal rate was not controlled in a manner that could test the range of effects encompassed by the spatial insurance hypothesis.

France and Duffy (2006b) created experimental seagrass metacommunities in mesocosms and examined the effect of adding dispersal corridors on ecosystem functioning and stability. The dispersal corridors allowed mobile grazers to move from community to community, and thereby affect rates of grazing and primary production. Dispersal tended to decrease diversity (alpha and beta) and increased the temporal variability of local grazer abundance. Also dispersal tended to reduce spatial variability in grazer abundance, and enhanced grazer impacts on edible algae. Overall, results were considered inconsistent with the spatial insurance hypothesis, although because the main outcomes of the model are non-linear the theory also predicts destabilizing effects on functioning and stability; unfortunately, dispersal rates were not estimated during the experiment and so it is difficult to assess how they were affected by the presence of corridors. Importantly, there is a clear a mismatch between the assumptions of the theory that is based on dynamics of competition, and the multitrophic experimental system France and Duffy (2006b) used to test it. Further theory examining the diversity and functioning of food webs in metacommunities (e.g. Holt and Loreau 2002) is required to understand the results from this and other ecosystems with trophic complexity.

Although these experiments have tested various aspects of the spatial insurance hypothesis, none provides a complete test. The model assumes strong spatio-temporal heterogeneity that has highly dynamic affects on the outcome of competition. Under these assumptions dispersal has a strongly non-linear effect on diversity and ecosystem functioning. Future tests of the spatial insurance hypothesis will therefore require good experimental control of a number of factors – metacommunity size, dispersal rate, spatio-temporal heterogeneity – and the direct measurement of local and regional diversity and ecosystem functioning over extended periods of time.

10.5 Conclusions

This chapter has emphasized the spatial dimension of the relationship between biodiversity and ecosystem functioning. All the results we have raised have broad implications for the conservation and management of fragmented landscapes. First, we considered the link between local and regional processes using simple rules to scale diversity and function with area. Our results suggest that species loss due to habitat destruction may have delayed impacts on local function (a *functioning debt*). These results complement the idea that area loss will have the greatest functional effects as higher trophic levels suffer higher rates of extinction (Dobson *et al.* 2006). Spatial processes, just like multitrophic interactions, have the potential to generate complex non-linear effects on biodiversity and ecosystem functioning. Second, we indicated that spatial variance in species richness (perhaps caused by habitat fragmentation) should be taken into account when scaling the mean relationship between biodiversity and ecosystem functioning from local to regional scales.

We used a source–sink metacommunity model to examine various aspects of how spatial and temporal variability in the environment can be buffered by diversity. The metacommunity framework is a valuable way to link local and regional scales. The model predicts positive relationships between diversity, productivity, and stability. These results suggest that changes in landscape connectivity and fertility (resource flow) following anthropogenic fragmentation may alter both species diversity and ecosystem processes at local and regional scales. Because of the non-linear effects of dispersal, both increasing and decreasing landscape connectivity can either increase or decrease diversity and the temporal and spatial variability of (meta)ecosystem processes (Loreau *et al.* 2003b). The impact of reduced dispersal will depend upon the initial level of landscape connectivity and the dispersal ability of the organisms considered. Experiments addressing how scales of resource heterogeneity and dispersal interact to affect ecosystem diversity and stability are needed.

Recent work has established an important link between ecological and economic aspects of the insurance value of biodiversity (e.g. Armsworth and Roughgarden 2003, Baumgärtner 2007, and Chapter 18). Biodiversity has insurance value in economic terms because management decisions that alter biodiversity can affect the mean and variance of returns associated with an ecosystem good in a variable environment. Thus a risk adverse resource manager should optimize levels of biodiversity by, for example, adjusting the area and connectivity of a nature reserve (Armsworth and Roughgarden 2003), or sustaining pollinator services by maintaining pollinator-preferred habitat. This insurance value of biodiversity exists in addition to the direct and indirect (use and non-use) benefits normally associated with biodiversity. The theory outlined in this chapter stresses that knowledge of spatial processes across ecosystems will be essential if we are to understand the effects of fragmentation on the ecological and economic impacts of biodiversity loss.

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