ESSAY REVIEW

Large-scale spatial dynamics of plants: metapopulations, regional ensembles and patchy populations

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Summary

1 We present a critical review of the application of metapopulation theory to the regional dynamics of plants. We consider whether there is evidence that regional populations of plants show a metapopulation structure. We then review the alternatives to the metapopulation regional population structure for plants.

2 Although metapopulation theory primarily deals with regional dynamics, it is, however, also commonly applied to patch dynamics within local populations ('metapatch' systems). These apparently analogous systems are very different: systems of patchy local populations do not exhibit the dissociation of processes operating at different spatial scales that is characteristic of metapopulations.

3 The parameters of classical metapopulation studies, such as colonization, re-colonization and extinction, may be hard to measure for many plant populations, in particular for populations with long-lived seedbanks.

4 The assumption of metapopulation theory that suitable habitat occurs as discrete patches within a matrix of unsuitable habitat is not always true, as regional populations of some species may exist on largely uninterrupted swathes of suitable habitat. Alternatively, suitable patches may be hard or impossible to define *a priori*.

5 Using detailed case studies from the literature we outline a possible classification of the spatial dynamics of plants at both regional and local scales.

6 At the regional scale we define: *metapopulations*, in the classic sense, where regional persistence is governed by the processes of patch colonization, extinction and recolonization; *regional ensembles*, systems of essentially unconnected local populations persisting in an ill-defined mosaic of suitable and unsuitable habitat; and *spatially extended populations*, essentially a single extended population occupying large tracts of suitable habitat, but whose regional dynamics are essentially a simple extension of local dynamics.

7 Although a range of forms of local spatial dynamics exist, these are qualitatively different from the forms of population structure at the regional level.

Key-words: extinction, migration, patch dynamics, population dynamics, spatial dynamics

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Introduction

Questions concerning the distributions and dynamics of organisms at a large scale in a spatial context have always been at the centre of evolutionary and ecological research (Wright 1931; Fisher 1937; Skellam 1951,

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1952; MacArthur & Wilson 1967; Levins 1969, 1970). In ecology, the theories of island biogeography and metapopulation dynamics have been particularly influential in this respect as they have offered a quantitative basis from which to analyse regional scale ecological dynamics (Hanski & Simberloff 1997). The recent rise of metapopulation theory has been particularly important in understanding large-scale population dynamics (Hanski 1999). Metapopulation theory has highlighted that the scaling from local to regional dynamics may not be straightforward, and that the regional scale

availability of habitat, migration and extinction all play a role in determining whether a system of local populations of a species can persist.

Metapopulation theory has been extremely influential in the study of animal populations (Hanski 1999). However, it is not clear what role metapopulation theory has to play in plant ecology. A recent review, for example, concluded that 'plants may seem particularly appropriate for metapopulation analyses as a result of their *immobility, strong spatial structure and restricted dispersal*' (Husband & Barrett 1996, our italics). Harrison & Taylor (1997), by contrast, concluded that where '… *small-scale habitat heterogeneity, localized interactions and limited migration* …' are the rule (our italics), theories of population dynamics lie 'outside the conceptual domain of metapopulation dynamics' because such systems violate the basic assumptions of metapopulation models. This would seem to be true of many plant populations and there is therefore some considerable discrepancy concerning the level and scale at which metapopulation theory may be considered applicable to plant populations.

The original notion of the metapopulation (Levins 1969, 1970) has been extended in order to encompass a wider class of population structures, including non-equilibrium and mainland-island forms (Hastings & Harrison 1994; Harrison & Taylor 1997; Hanski 1999). These forms retain the essential features of the original metapopulation theory. These key elements are the processes of interpopulation migration and local population extinction, as well as the regional distribution of suitable habitat as discrete patches within a larger matrix of unsuitable habitat. In contrast, in plant ecology, some authors have defined metapopulation dynamics as generally as 'the product of local population dynamics and dispersal' (Husband & Barrett 1996) while others have claimed that 'metapopulations (systems of interconnected populations) are more likely to be the rule, not the exception' for plant populations (Antonovics *et al*. 1994). At the same time others have questioned whether metapopulations are likely to be very common in plants (Bullock *et al*. 2002). Whether or not this is the case, there exists little evidence on which to sustain this view (Husband & Barrett 1996).

The issue of whether populations show a metapopulation structure is not merely an issue of semantics. For instance, the persistence and dynamics of metapopulations are critically dependent on the amount and regional configuration of suitable habitat (e.g. Hanski 1997). In contrast, the dynamics of a population existing on an undisturbed continuous area of suitable habitat would simply be an extrapolation of local processes. Thus, determining the form of regional dynamics is not simply a matter of typology, and this links directly to demographic parameters and ecologically important aspects of population organization (Thomas & Kunin 1999).

Previous attempts to classify the regional dynamics of plants have been incomplete. Grubb (1988) proposed a classification with two main components, namely the recruitment process and the pattern of disturbance experienced by the population. However, his system did not consider migration, or the regional availability of suitable habitat. Eriksson (1996), by contrast, developed a scheme set within the framework of metapopulation theory, and proposed a novel structure that applied specifically to plants: a *remnant population* is defined as 'systems of local populations in which some are maintained despite having a local population growth (λ) below 1' (Eriksson 1996, p. 249). This, for example, includes many populations that are maintained as a bank of dormant seed in the face of conditions that are unsuitable for plant growth. Although this system is a starting point, it seems likely that it is not extensive enough to include the full range of regional population structures that we might expect to observe.

The aim of this paper is to review critically how the metapopulation paradigm influences our view of the regional dynamics of plant populations, and to examine the role of metapopulation theory in plant ecology. Our review complements that of Bullock *et al*. (2002), who reach similar conclusions concerning the prevalence of metapopulations in plants. At one level we point out that the metapopulation concept has been misapplied to local dynamics. At another scale, however, we argue that several forms of regional plant population structure exist, and that the metapopulation is only one form of large-scale plant population distribution.

The metapopulation concept

The incorporation of the metapopulation concept into ecology has been important because of the links that the theory proposes between local and regional dynamics. We therefore begin by briefly summarizing these in order to set the scene for our subsequent discussion.

We begin with some definitions of terms. The *region* in which a species lives represents a large area that encompasses a set of *local populations*. The region may therefore delimit the entire range of a species, or some fraction of its total range. The local population is a smaller assemblage of the species that is spatially segregated from other such groups. The term *local* refers to processes (e.g. births, deaths, dispersal) operating below this scale. Frequently, the local population is regarded as occupying a *patch* of habitat. Such patches may be different from the surrounding habitat in suitability for the species.

The metapopulation theory proposes that the regional population persists as the result of a balance between the processes of local population extinction and between patch migration. For the regional population of a species to persist as a metapopulation, four conditions therefore need to hold. These are (Hanski 1997): (i) suitable habitat occurs in discrete patches that may be occupied by local reproducing populations; (ii) even the largest local populations have a measurable

risk of extinction (unless the largest population is the source of a source-sink system); (iii) habitat patches must not be too isolated to prevent recolonization following local extinctions; and (iv) local populations do not have completely synchronous dynamics (or the dynamics of the global population will not be much longer than that of the local populations).

Given these conditions, the main prediction of metapopulation theory is that a threshold number or density of suitable patches is required for large-scale metapopulation persistence. This means that we cannot predict the dynamics of the metapopulation as a simple function of the local dynamics within patches, because the larger scale processes of migration and colonization, as well as the regional distribution of patches, determine metapopulation dynamics. Local-scale dynamics are important only inasmuch as they affect these processes. The converse of this is also necessarily true for most types of metapopulation: within a metapopulation, local dynamics cannot be understood without reference to large-scale processes.

A review of the evidence on regional population structuring

We conducted a review of the regional dynamics of plants in order to determine whether metapopulation processes are generally important and what range of alternative structures occur. We based our review on Table 1 of Husband & Barrett (1996), extending their data set by increasing the amount of information extracted from each study and by including more studies (Table 1). Specifically, we evaluated each study according to nine criteria. We first determined whether the term 'metapopulation' was used in the original paper and whether the study concluded that the population exhibited a metapopulation structure. Note that studies are included in which the term metapopulation is not used. These, however, are studies that have subsequently been cited in a metapopulation context (Erickson 1943; Watkinson 1985; de Jong & Klinkhamer 1988; Kadmon & Shmida 1990; Kalisz & McPeek 1993). Following Husband & Barrett (1996), we recorded the metapopulation structure examined (in terms of whether dispersal of propagules or gametes was measured), the parameters that were explored (in terms of movements and population dynamics) and the spatial scale at which the study was performed. Note that we are only concerned with the regional dynamics of populations, whereas Husband & Barrett (1996) also considered the application of metapopulation terminology to population genetics. The regional structure of populations will impact on the genetic structure of populations. However, metapopulation theory is not concerned with the movement of genes *per se*; hence, we do not consider this issue further. We also recorded whether data were presented showing evidence for colonization, population extinction and population recolonization (as opposed to making assumptions

about or modelling these processes), as well as whether the study was able to define explicitly what constituted a suitable habitat patch.

In agreement with Husband & Barrett (1996) we found only a few examples (*n* = 44) of the application of the metapopulation concept to plant regional dynamics. Taken as a whole, however, these studies generated several distinct themes, which we develop in the following sections.

A PATCHY POPULATION IS NOT A METAPOPULATION

A number of the studies in Table 1 have applied the terminology derived from the metapopulation literature to describe essentially local dynamics; these are studies for which the metapopulation term has been used and this structure inferred, but for which the scale of data collected and analysis is essentially local. Perry & Gonzalez-Andujar (1993) and Valverde & Silvertown (1997), for example, acknowledge that the metapopulation framework was designed to predict dynamics at different scales from those considered in their models. In these systems, populations persist as a series of patches containing individual plants that are then closely and frequently linked by dispersal. In this spirit, Perry & Gonzalez-Andujar (1993) coined the term 'metapopulation neighbourhood model' to describe their approach applied to an array of patches of an annual plant. Similarly, Thomas & Kunin (1999) suggest that when populations do not exist in discrete patches, metapopulation models may be applied by arbitrarily delimiting patches, for example as an array of quadrats. Each of these might then be considered as a patch, and rates of immigration, emigration and extinction measured at this level.

There are two fundamental issues concerning the unqualified application of the metapopulation terminology to such systems. First, there is the link between regional and local dynamics: in metapopulations local dynamics do not simply scale-up to predict regional dynamics, whilst local dynamics are influenced by the regional population. Local population models predict local dynamics, by definition, as a function of local, even individual-based, parameters and functions. Hence, in predicting dynamics they lack the processes operating across large spatial scales.

The second conceptual problem with applying the notion of the metapopulation to local-scale dynamics is that whereas the metapopulation concept relies on local populations occupying discrete patches of suitable habitat, this is not the case for many plant populations. In models such as the coupled-map lattice formulation used to model the local dynamics of a number of species (e.g. Gonzalez-Andujar & Perry 1993; Watkinson *et al.* 2000a), where patches are arbitrarily delimited as small square or hexagonal quadrats for convenience of modelling or measurement, the parallels are unclear and perhaps misleading if drawn.

Table 1 A survey of the literature relevant to plant metapopulation dynamics. The survey was extended from Table 1 of Husband & Barrett (1996). The table indicates the main study species, whether the term metapopulation was used in the original study and whether it was inferred that the species population assemblage in question comprised a metapopulation. The structure measured and parameters examined, together with the spatial scale(s) at which the study was performed, are indicated. Information is provided on whether data are presented on colonization, extinction and re-colonization, and whether it is possible to define a suitable patch. The population type categories follow Table 2

Species	Metapopulation Term	Metapopulation Inferred	Structure measured	Parameters examined	Spatial scale	Colonization	Extinction	Re-colonization	Potential patches defined	Population type	Reference
Eichhornia paniculata	Yes	Yes	Demographic Genetic	Migration, extinction	Local & regional	Yes	Yes	Yes	Transient pools found along roadsides	1 & 2	Husband & Barrett (1995, 1998)
Hypericum-cumulicola	Yes	Yes	Demographic	Colonization	Local & regional	Transplants into unoccupied sites	No	No	Yes	1 & 2	Quintana Ascencio et al. (1998)
Pedicularis furbishiae	Yes	Yes	Demographic	Extinction Colonization	Local & regional	Yes	Yes	Not clear, but possibly	In general terms, but specific patches were not identified	1 & 2	Menges (1990)
Silene latifolia	Yes	Yes	Demographic Genetic	Genetic isolation	Regional	No	No	No	No	1 & 2	Delmotte et al. (1999)
Valeriana salina	Yes	Yes	Demographic	Patch occupancy	Regional	Yes	No	No	Yes, only one out of 31 patches never occupied	1 & 2	Ericson et al. (1999)
Various	Yes	Yes	Demographic	Extinction, Colonization	Regional	Population	Population	Yes	Not explicitly defined	1 & 2	Ouborg (1993)
Amphicarpaea bracteata	Yes	Yes	Demographic	Migration, Colonization	Local & regional	No	No	No	No	2	Parker (1999)
Clematis fremontii	No	No	Demographic	Density, distribution, patch occupancy	Local & regional	No	No	No	Yes, but with exceptions	2	Erickson (1943)
Helianthus exilis	Yes	Yes	Demographic	Colonization, Migration of pollen	Local & regional	Transplants into unoccupied	No	No	Yes, and distribution closely mirrors available habitat	2	Wolf et al. (1999)
Howellia aquatilis	Yes	Yes	Demographic	Extinction	Local & regional	No	Yes	Local, but include seedbank	Yes, multiple regression used to determine habitat	2	Lesica (1992)
Linum marginale	Yes	Yes	Demographic Genetic	Pathogen resistance	Regional	No	No	No	Yes, in qualitative terms	2	Burdon et al. (1999)
Lythrum salicaria	Yes	Yes	Demographic Genetic	Migration	Local & regional	No	No	No	No	2	Eckert et al. (1996)
Silene diocia	Yes	Yes	Demographic Genetic	Migration	Regional	Yes	No	Not necessary for persistence as new patches formed	Yes, and new patches continually arising	2	Giles & Goudet (1997) Ingvarsson & Giles (1999)
Silene latifolia	Yes	Yes	Genetic	Colonization (pollen; anecdotal)	Regional	Anecdotal	No	No	No	2	Kaltz et al. (1999)

Table 1 *Continued*

Species	Metapopulation Term	Metapopulation Inferred	Structure measured	Parameters examined	Spatial scale	Colonization	Extinction	Re-colonization	Potential patches defined	Population type	Reference
Silene vulgaris	Yes	Yes	Demographic Genetic	Colonization (pollen)	Local	Local	No	No	No	2	Taylor *et al.* (1999)
Sparganium erectum	Yes	Yes	Demographic	Mode of reproduction, population age	Local & regional	No	No	No	No	2	Piquot *et al.* (1998)
Various	Yes	Yes	community indices	annual flux of species	Local & regional	No	Yes	No	Yes	2	Porembski & Barthlott (1997)
Vulpia ciliata	Yes	rejected	Demographic	Extinction, Colonization	Local & regional	Local & population	Local & population	not observed	concluded that it is not possible to	2	Watkinson *et al.* (2000a)
Asarum canadense	Yes	Yes	Demographic	dispersal, Colonization	Local & regional	Local dispersal only	No	No	No	2 & 3	Cain *et al.* (1998)
Lactua serriola	Yes	Yes	Demographic	Colonization	Regional	Yes, but not explicitly	Yes, but not explicitly	Yes, not explicitly	No, arbitrary 100 m lengths of motorway verge used	2 & 3	Prince *et al.* (1985), Prince & Carter (1985)
Zostera marina	Yes	Yes	Demographic	Dispersal, colonization	Local	Local dispersal only	No	No	No	2 & 3	Orth *et al.* (1994)
Phrygilanthus sonorae	Yes	Yes	Demographic	Colonization	Local	Dispersal	No	No	Yes, patches defined as individual hosts	3	Overton (1994)
Senecio acobaea	Yes	Yes	Demographic	Extinction, Colonization	Local & regional	Local, but include seedbank	Local	Local, but include seedbank	No	3	van der Meijden *et al.* (1992)
Silene alba	Yes	Yes	Demographic genetic	Colonization	Regional	Yes	No	No	Not able to; used arbitrary sections of road	3	McCauley *et al.* (1995)
Silene alba			Demographic	Extinction, colonization	Regional	Local	Local	not distinguished from local colonization	not able to; used arbitrary sections of road	3	Antonovics *et al.* (1994)
Cakile dentula	No	No	Demographic	Migration	Local	Local	No	large-scale dispersal from areas of high to low density		3 & 4	Watkinson (1985) van der Meijden *et al.* (1992)
Cynoglossum officinale	Yes	Yes	Demographic	Extinction, colonization	Local & regional	Local	Local	populations recolonized from seed pool	No	3 & 4	van der Meijden *et al.* (1992)
Various	No	No	Demographic	Extinction, colonization	Local & regional	Population	Population	Populations recolonized from seed pool	No	3 & 4	de Jong & Klinkhamer (1988)

Table 1 *Continued*

Species	Metapopulation		Structure measured	Parameters examined	Spatial scale	Colonization	Extinction	Re-colonization	Potential patches defined	Population type	Reference
	Term	Inferred									
Cecropia obtusifolia	No	No	Demographic Genetic	Colonization, migratoin	Local & regional	Local dispersal only	No	No	Yes, but Locally at scale of small gaps in forest	4 & 5	Alvarez-Buylla & Martinez Ramos (1990), Alvarez Buylla & Garcia Barrios (1991), Alvarez Buylla & Garay (1994)
Lindera benzoin	Yes	Yes	Demographic	Extinction, colonization	Local	No	No	No	Yes, gaps in canopoy	4 & 5	Cipollini (1994)
Primula vulgaris	Yes	Yes	Demographic	Colonization, extinction	Local	No (local dispersal only)	Yes, gap creation	No	Yes, gaps in canopy	4 & 5	Valverde & Silvertown (1997)
Carduus spp.	No	No	Genetic	Migration	Local	Local dispersal only	No	No	No, but existence inferred	5	Olivieri et al. (1983)
Stipa capensis	No	No	Demographic	Migration	Local	No	No	No	No	5	Kadmon & Shmida (1990)
Aster kantoensis	Yes	Yes	Demographic	Local population flux	Local	No	No	No	Attempted via sowing experiment	6	Takenaka et al. (1996)
Avena sterilis	Yes	Yes	Demographic	dispersal, Extinction	Local	Local dispersal only	Local	No	Yes, but as 1-m wide hexagons for modelling purposes	6	Gonzalez Andujar & Perry (1995), Perry & Gonzalez Andujar (1993)
Collinsia verna	No	No	Demographic	Extinction	Local	No	Local	No	No	6	Kalisz & McPeek (1993)
Various	Yes	Yes	Demographic	Colonization (recruitment)	Local	No (local recruitment only)	No	No	No	6	Eriksson (1997)
Primula sieboldii	Yes	Yes	Demographic	Migration	Local & regional	Local dispersal only	Seed set as a surrogate	No	No	–	Washitani et al. (1996)
Silene alba	Yes	Yes	Genetic	Colonization (pollen)	Local	Yes	No	No	No	–	Richards et al. (1999)

In the case of, for example, *Primula vulgaris* or *Cecropia obtusifolia* persisting in transient gaps in the forest canopy (e.g. Alvarez-Buylla 1994; Valverde & Silvertown 1997), or mistletoes (*Phrygilanthus sonorae*) on individual trees (Overton 1994), the analogy between local dynamics and a metapopulation is easier to see because a distinct scale of local patchiness may be defined. Nevertheless, even in these cases the scale of the spatial dynamics is local rather than regional in nature.

DEMONSTRATING THE EXISTENCE OF PLANT METAPOPULATIONS

In emphasizing the dissociation of local and spatial dynamics, evidence for metapopulation dynamics requires that we have measures of population dynamics across large spatial scales and in particular the following: (i) colonization; (ii) extinction and recolonization; and (iii) the frequency of suitable patches. These are the empirical measures required to assess the four conditions outlined by Hanski (1997) (above). When these parameters are known it is possible to classify dynamics based on a continuous axis of 'compensation' that measures the relative importance of regional and local processes (Thomas & Kunin 1999). Moreover, in terms of demonstrating that populations show metapopulation dynamics, evidence that recolonization of patches occurs is particularly important.

As is clear from Table 1, a range of studies have looked at the dynamics of plant populations based on data from both regional and local scales. By contrast, only five studies have attempted to measure colonization, extinction, recolonization and patch density, despite 28 claims for metapopulation status. Importantly, most studies have inferred a metapopulation structure based on a detailed study of local dynamics and then a more cursory examination of the regional distribution of the species.

Direct estimates of migration are extremely hard to obtain for many plant species, and indirect evidence is necessary to infer how plants colonize vacant sites. Harrison *et al.* (2000) found, in five species of annual and short-lived plants, that colonization was a function of distance from the nearest existing population. Thus short-range dispersal is implicated as the main factor in the establishment of new populations. In general, as most plants lack specialized dispersal mechanisms, this kind of pattern may be expected to be extremely common.

In principle the processes of population extinction and colonization are readily measured: extinction occurs when there are no individuals left occupying a patch; colonization occurs when an unoccupied patch becomes occupied. The survey of the literature on colonization and recolonization makes clear, however, that two important complications arise in applying these notions to plant populations: first, how do we measure patch extinction for a species with a highly persistent

seedbank, and secondly, how do we define a suitable patch?

When a pool of persistent dormant seed exists it is not clear whether a newly observed population has been formed following colonization of previously unoccupied habitat or whether the population is derived from dormant seed in a patch that was occupied at some time in the past (Bullock *et al.* 2002; van der Meijden *et al.* 1992) regard regeneration from the seed bank as constituting recolonization in the sense used in metapopulation models. The problem with equating 'dispersal in space' with 'dispersal in time' is that whereas the dynamics of the metapopulation as a whole is dependent only on the current state of the system when dispersal occurs in space, the state of the system in the long-distant past has to be accounted for when dispersal in time through the seed bank is included. This, at least, requires the introduction of a further state variable to the modelling (i.e. patches are not simply suitable and 'occupied' or 'unoccupied', but also may be categorized as 'unsuitable and occupied'). The implications of this for metapopulation models are, however, largely unexplored.

In metapopulations habitat is distributed as discrete patches within a mosaic of unsuitable habitat. A certain fraction of these patches are unoccupied (Hastings & Harrison 1994; Quintana-Ascencio *et al.* 1998); if, on the other hand, most suitable patches are occupied, all we need to do to understand regional dynamics is to measure the distribution of suitable patches in order to predict regional abundance. In some plant populations it is possible to identify potential patches (Table 1): in *Eichhornia paniculata*, for example, a suitable patch is a transient pool by a roadside (Husband & Barrett 1995, 1998). Moreover, Husband & Barrett (1995, 1998) and Ericson *et al.* (1999) were able to explore how the number of local populations related to the number of suitable patches for *E. paniculata* and *Valeriana salina*, respectively.

In these two examples it was possible to define *a priori* what constituted a suitable patch. By contrast, Watkinson *et al.* (2000a) were unable to define explicitly what constituted a suitable patch for the annual *Vulpia ciliata*. Populations of this species were found in a variety of types of location with new populations arising unpredictably in a range of sites. Whilst, of course, there exists a finite range of sites within which local populations can persist if introduced, the requirements of this species are not so specialized that these can be clearly identified, and it is not clear in any case whether these would constitute discrete patches.

In summary, measuring the regional components of population dynamics within the framework of the four conditions required to demonstrate metapopulation dynamics reveals a number of key processes that determine population dynamics and persistence. Thus the exercise of devising a scheme for classifying regional dynamics is not simply an exercise in semantics: rather, this represents an important step in determining how populations persist at the regional scale.

Towards a classification of plant spatial dynamics

What is evident from Table 1 is that in some cases the notion of metapopulation structure works well, but that in others it does not. Specifically, in many plant populations, regional processes do not dominate dynamics as the metapopulation theory proposes. Instead, local processes play an important role in determining dynamics across a range of scales. In this section we therefore use this distinction between the role of local and regional processes to outline a tentative classification of the regional and local spatial dynamics of plants. In doing so we highlight that metapopulations represent only one extreme of the range of possible types of dynamics.

Our review of studies on the regional and spatial dynamics of plants (Table 1) suggested six categories for classifying spatial dynamics (Table 2). In Table 1 we have categorized the studies reviewed according to this classification. In Table 2 we have outlined brief definitions of the categories we identified. We propose three broad categories of regional dynamics (1–3) and three of local dynamics (4–6). It is, however, important to note that in Table 1 we have categorized the study (i.e. the combination of data and analysis presented) rather than the dynamics of the species. In particular, categories 4–6 are categories of local dynamics, and need have no bearing on the form of regional dynamics.

In order to elaborate upon Table 2, in this section we review in detail an example of each of these regional population structures. In doing so we aim to highlight the parallels and differences between observed population structures and metapopulation dynamics. The system we outline is not exhaustive and further categories of regional dynamics certainly exist.

REGIONAL DYNAMICS

We have defined three broad categories of regional dynamics: metapopulations, regional ensembles and spatially extended populations. The rationale for this split is the link between local and regional processes, and hence whether population persistence is largely a function of processes operating at the local or regional scale (Fig. 1). In a previous review, Thomas & Kunin (1999) classified regional dynamics within a modelling framework by considering two demographic axes: (i) a 'compensation axis' representing the extent to which internal ($B - D$, birth minus death) and external processes ($I - E$, immigration minus emigration) dominate the dynamics of a population; and (ii) a 'mobility' axis (($I + E$) − ($B + D$)) describing the involvement of a local population in regional ($I + E$) rather than local ($B + D$) processes. Most plants have restricted dispersal and we would expect to see that most species occupy only a very restricted range along the mobility axis. In addition, we consider that the regional availability of suitable habitat is a key factor in plant populations. We therefore link internal (B, D) and regional-scale

processes (I, E) to the availability of suitable habitat, measured as the difference between suitable and unsuitable habitat, $S − U$. This latter axis is particularly important as it defines whether populations tend to occur in discrete patches: when $S \gg U$, suitable habitat is effectively continuous, whereas if $U \gg S$, suitable habitat is rare.

The first category is the metapopulation. In metapopulation dynamics, regional processes dominate (Fig. 1a), whether populations persist as classic metapopulations or mainland-island systems with predominantly source-sink populations. In both cases the amount of suitable habitat is low (i.e. $U > S$). Local processes are important only in that they determine the probability of local population extinction or the number of individuals dispersing to other patches. On average, local populations exist at an equilibrium ($B = D$), but patch extinction occurs and leads to the periodic eradication of local populations. Relatively high rates of both immigration and emigration (on average $I = E$, measured across all populations, in both classic and source-sink systems) lead to recolonization and compensate for extinction. Thus in the metapopulation it is not possible to understand local processes without reference to the regional population. Local patch occupancy is a function of migration between patches and the process of recolonization as well as the amount of suitable habitat.

We have termed a second category 'regional ensembles' (Fig. 1b). Such populations are dominated by local processes and the constituent populations of the regional population may be basically unconnected. In some respects this is like the non-equilibrium metapopulation. We wish, however, to draw two important distinctions that may apply to many plant populations. First, it may not be possible to define what a potential patch is for many populations (see below), although in general suitable habitat is rare ($U \gg S$). However, in a non-equilibrium metapopulation, suitable habitat exists as discrete patches that are readily defined. Secondly, non-equilibrium metapopulations are ultimately destined for extinction, with the time to extinction of the metapopulation being the same as the time to extinction of the largest population (Hanski 1999). However, this need not be the case for regional ensembles (e.g. Watkinson *et al.* 2000a). Here we recognize three forms of regional ensemble. For remnant and shifting cloud populations, habitat exists either in discrete patches or continuously and both local population extinction and colonization tend to be infrequent. Note that the remnant form of regional ensemble includes populations that persist as banks of dormant seed (Eriksson 1996), so that many populations measured at the vegetative stage may appear to be in decline ($D > B$). As discussed above, it is difficult to accommodate the seed bank within current metapopulation models. The shifting cloud form of regional ensemble includes those cases where a series of local populations periodically arise or become extinct, but

Table 2 Classification of the regional dynamics of plant populations based on the distinction between local and regional dynamics. See main text for further details. 1 to 3 represent forms of regional population (A), while 4 to 6 are forms of local population (B). Note that 4 to 6 are more properly regarded as a classification of studies rather than populations and in principle the local population may adopt any of the regional structures

(A) Regional populations

Population type	Definition	Habitat	Local population extinction	Migration/ colonization	Recolonization	Example
(1) Metapopulations (regional processes dominate)	Series of local populations, existing on discrete patches linked by dispersal resulting in colonization of vacant sites; sites are vacated by extinction events.					
(a) Classic	All patches equally as likely to be colonized/become extinct.	Discrete patches	Frequent	Common	Common	*Eichhornia paniculata (Brazilian populations)*[1]
(b) Source-sink/ mainland-island	Most patches incapable of supporting a persistent local population. Populations in these patches are maintained by immigration from one or a small number of source populations.	Discrete patches	Frequent	Very common	Very common	*Eichhornia paniculata (Jamaican populations)*[2]
(2) Regional ensembles (regional and local processes both important)	A series of local populations which are basically unconnected. Suitable patches may be hard to define *a priori*. Local populations may be highly persistent.					
(a) Remnant population	Most populations do not grow or persist in the vegetative state from one year to the next, but are maintained through a bank of dormant seed.	Discrete patches or	Rare	Infrequent	Nil	Desert annuals[3]
(b) Shifting cloud	Regional populations persist as a series of populations that give the appearance of occurring on discrete patches, yet may not have specific habitat requirements. Recolonization of extinct patches is rare or does not occur.	Discrete	Variable	Variable	Nil	*Vulpia ciliata*[4]
(c) Island populations (= nonequilibrium metapopulation)	Extreme case in which colonization and migration re nil. Typically only a few local populations that are likely to become extinct.	Discrete	Rare	Nil	Nil	*Liparis loeselii*[5]
(3) Spatially extended population (local processes dominate)	A basically continuous population existing on a large area of suitable habitat. Migration is nonexistent with population spread occurring as a consequence of local dispersal. Dynamics are the product of local processes.					
(a) Patchy population	A population existing in a continuous area of habitat that has become fragmented into a small number of clumps that are effectively unconnected and give the appearance of patches.	Continuous	Nil (high levels of within-population mortality/ extinction)	Low	Nil	*Lactuca serriola*[6]
(b) Extended local population	Population is distributed almost continuously across a large area. Dynamics and dispersal are entirely local, however.	Continuous	Nil (low levels of within-population mortality/ extinction)	Nil	Nil	*Silene alba*[7]

Table 2 *Continued*

(B) Local populations

Population Type	Definition	Habitat	Local patch	Dispersal	Distribution	Example
(4) Spatially structured local populations	A local population within which spatial structure is important in determining dynamics and abundance.					
Metapatches/gap dynamic populations	Within an area of habitat at only a small proportion of discrete patches are suitable for occupation and hence plants are not distributed cotinuously, but occur only in patches.	Discrete Patches	Variable	Moderate to high	Patchy	*Cecropia obtusifolia*[8,9]
(5) Spatially unstructured local population	A population in which dynamics are essentially continuous in space. Spatial structure may develop owing to the effects of localized dispersal and interactions with the effects of disturbance.	Continuous	Variable	Short distance	Continuous or patchy	
(a) Patchy local population	High levels of mortality and past history give the appearance of patchiness.	Continuous	High	Short distance	Patchy	Arable weeds[10]
(b) Continuous local population	Dynamics are essentially invariant within a well defined area of suitable habitat.	Continuous	Low	Short distance	Continuous	Annual pastures[11]
(6) Local population	Population studied at a very scale (e.g. on a few m^2). Such studies are entirely concerned with local processes and make observations that do not concern regional dynamics.	Continuous	NA	NA	NA	

References: [1]Barrett & Husband (1997); [2]Husband & Barrett (1991); [3]Venable *et al.* (1993); [4]Watkinson *et al.* (2000a); [5]Wheeler *et al.* (1998); [6]Prince & Carter (1985); [7]McCauley *et al.* (1995); [8]Alvarez-Buylla (1994); [9]Silva Matos *et al.* (1999); [10]Wilson & Brain (1991); [11]Watkinson *et al.* (2000b).

where migration is variable and recolonization is nil (i.e. both I and E are very close to zero). The sizes and persistence of such populations are entirely a function of local processes. The extreme form of regional ensemble is represented by island populations, where the regional population is represented by one or very few isolated populations. This latter form is most similar to the non-equilibrium metapopulation, although we do not classify this form of regional structure as a form of metapopulation as the key metapopulation processes of immigration, emigration and recolonization play no role in the persistence of such populations.

The final category of regional population is the 'spatially extended population', where the regional ensemble is simply a spatially extended form of the local population (Fig. 1c). The metapopulation notion does not apply to such populations because habitat is continuous rather than patchy (i.e. S >> U, with U being close to zero). In patchy populations, patchiness may arise as a consequence of disturbance and local dispersal. However, this is not a consequence of habitat limitation as in classic metapopulation models, but is rather a consequence of spatially restricted dispersal and population growth. In the extreme, patchiness may be low and populations may exist as an extended continuous swathe; the whole population is essentially linked and can be considered as an extended local population. The difference between these two forms of population structure essentially lies with the extent of within-population mortality/extinction (Table 2).

To make explicit this classification we review in detail three case studies for which it is possible to address all four of the metapopulation criteria outlined above. In doing so we highlight how our classification dissociates the regional and local components of population dynamics.

Metapopulations: Eichhornia paniculata *(category I)*

Eichhornia paniculata is an emergent aquatic annual that occurs in transient pools formed along roadsides in the caatinga of north-east Brazil. The habitat in which it occurs is very dry for most of the year, but annually a narrow window of opportunity exists for germination, growth and reproduction during the rainy season. Populations establish in pools of water that are created at this time, which are discrete and represent suitable patches. Recruitment in pools is through either immigration of seeds, or from seed produced in the previous year, there being no permanent seedbank in this species. The ecology and genetics of *E. paniculata*
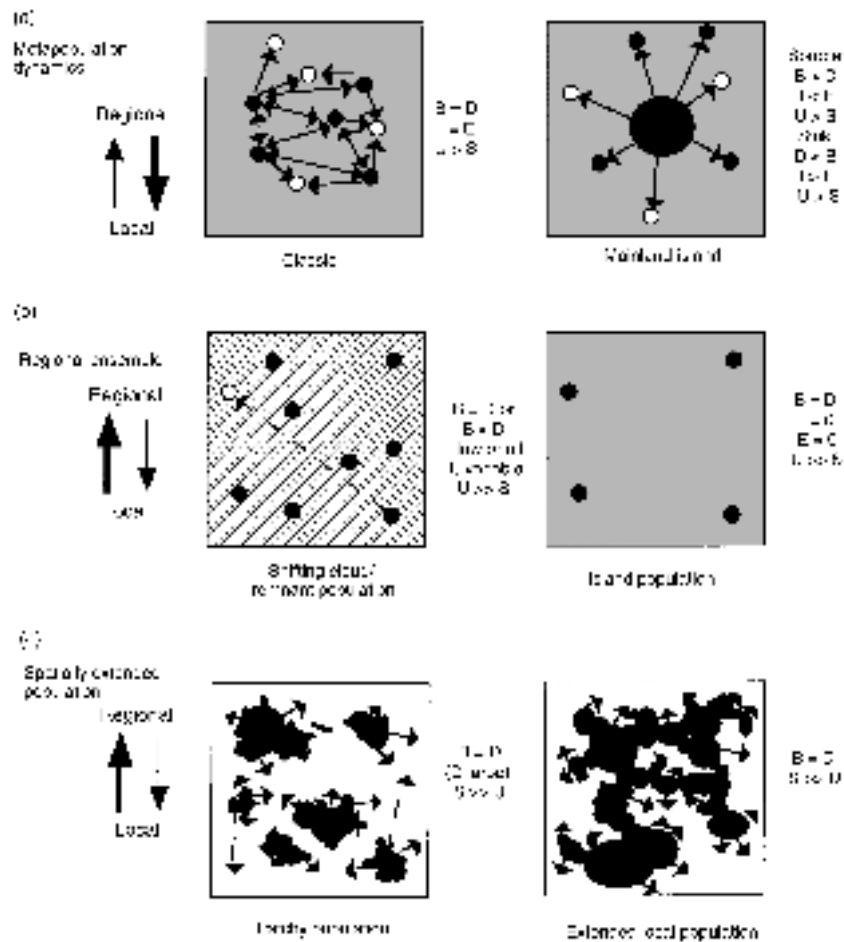
Fig. 1 Schematic outline of plant regional dynamics (see Table 2 for details) and how these are defined by simple demographic parameters, B (births), D (deaths), I (immigration) and E (emigration), as well as the amount of suitable (S) and unsuitable (U) habitat (see main text for more detailed explanation). (a) Well known metapopulation forms in which regional processes are dominant. In such populations potential patches (circles) exist within a matrix of unfavourable habitat (grey). Occupied patches (filled circles) commonly produce migrants (arrows) that colonize unoccupied patches (open circles). In the classic form all patches are more or less the same and contribute equally to producing migrants. In the mainland-island form a focal mainland population serves to maintain a series of smaller island populations. (b) Regional ensembles in which local processes are dominant. Long-range migration is rare or nil and local populations are basically unconnected. In shifting cloud populations the habitat matrix is basically unfavourable but suitable patches are hard to identify *a priori*: this is represented by the striped area, which represents unoccupied habitat that cannot be classified as either suitable or unsuitable for occupation with any certainty. Populations may opportunistically exploit a range of potential habitat and migration is rare and unpredictable (dashed arrow), with the consequence that the regional population does not occupy a fixed array of well-connected subpopulations, but instead exists as an amorphous cloud of unconnected patches. The remnant population is a form of shifting cloud population where populations may persist as a bank of dormant seed. An extreme condition is the island population (equivalent to the non-equilibrium metapopulation) in which all metapopulation processes have broken down (i.e. there is basically no immigration, emigration or recolonization), in which no suitable habitat exists other than in already occupied patches, and in which extinction of the regional population is almost inevitable. (c) Spatially extended populations in which local processes are dominant (i.e. I and E are not included as these represent regional processes). In such populations (drawn on the same scale as (a) and (b)), local process entirely determine regional dynamics. The whole habitat is potentially suitable (hence the square is unfilled) but long-distance migration is very rare and populations spread through local dispersal. The regional dynamics may be simply predicted by extrapolation of the local dynamics to a large scale. In patchy populations, subdivision into apparent patches has occurred, e.g. through disturbance. In extended local populations, the whole population is essentially linked.

in this region have been studied in detail (Husband & Barrett 1992a,b, 1993, 1998; Barrett & Husband 1997). In particular, these studies have been able to quantify the key features of the regional dynamics of this species through large-scale surveys and monitoring of population dynamics in 1982 and 1987–89.

No data on large-scale migration of seed were available, although it is thought that movement of seeds by vertebrates (birds and cattle) as well as through flash

floods in the rainy season may be responsible for the large-scale movement of seeds between pools. Using the information derived from this analysis, Husband & Barrett (1998) were able explicitly to evaluate the regional dynamics with respect to the four conditions outlined by Hanski (1997) and discussed above. Specifically: (i) Suitable habitat occurs in discrete patches; pools are discrete and isolated from other potential patches. (ii) Even the largest local populations

have a substantial risk of extinction: the probability of population extinction was unrelated to population size, hence all populations were equally likely to become extinct. (iii) Habitat patches must not be too isolated to prevent recolonization; migration has not been directly quantified. Genetic analysis of the populations indicated that levels of migration between populations are low, however, and no information on recolonization was presented. (iv) Local populations do not have completely synchronous dynamics: population extinctions occurred in each monitoring period, whilst at the same time other populations survived and new ones arose.

Even though condition (iii) cannot be evaluated fully based on current information, the evidence for this species points persuasively towards a metapopulation structure for the species in this region. Interestingly, another study on the regional dynamics of the same species in Jamaica (Husband & Barrett 1991) pointed to the regional population in this area having a mainland-island organization, with genetic evidence for multiple and recurrent introductions from mainland Brazil. This difference in population structure between the two systems elegantly demonstrates the importance of the metapopulation organization and the dissociation of local and regional dynamics. Whilst the local dynamics of the populations are basically the same in both cases, large-scale processes, in particular the regional configuration of suitable habitat and the scale of migration, serve to determine both the local and regional-scale dynamics. This illustrates clearly the importance of determining the form of the regional dynamics for understanding how plant populations persist.

Regional ensemble: Vulpia ciliata (category II)

Vulpia ciliata (ssp. *ambigua*) is a winter annual grass that has been studied at a range of spatial scales (Carey 1991; Carey & Watkinson 1993; Carey *et al.* 1995; Watkinson *et al.* 2000a). In particular, the system of populations in eastern England has been monitored from the point of view of exploring the links between large- and fine-scale determinants of abundance. The regional population of this species consists of approximately 40 small (generally < 10 m^2) populations that appeared to be an ideal candidate for a metapopulation analysis.

There are four reasons why the system of populations that constitute the regional population of *V. ciliata* cannot be fitted easily within the more conventional metapopulation framework. (i) It is difficult to define what constitutes a suitable patch. Carey *et al.* (1995) were able to create a 'climate envelope' for *V. ciliata* as well as to correlate the occurrence of *V. ciliata* with a relatively narrow range of soil types. This enabled identification of a number of areas that may be considered suitable for the species. There is no suggestion, however, that suitable areas occur as discrete patches, and even when they do, the species rarely occupies the

entire area. Populations frequently occur discretely in a patchy manner: this, however, may be a consequence of highly restricted dispersal limiting population spread, rather than habitat limitation (Watkinson *et al.* 2000a). (ii) Existing populations or patches are not linked through dispersal. There are no migration or dispersal mechanisms by which existing populations are linked. New populations arise through rare migration events (Watkinson *et al.* 2000a). However, migration between existing patches seems unlikely. The dynamics of populations are separate, in terms of the lack of flux of individuals between populations, and correlated in that populations experience similar weather conditions, and hence within-season patterns of dynamics are similar across the region. (iii) The fates of the populations at the regional scale are very well predicted by local scale processes. Both the levels of persistence (the half-life of populations is in the order of 30 years, and many populations are older) and the spatial extent of existing populations (generally in the order of tens of square metres) may be accurately predicted directly from models derived from local-scale processes (Watkinson *et al.* 2000a). The only regional-scale phenomenon that cannot be predicted in this way is the origin of new populations. (iv) Large-scale migration is probably extremely rare and population extinction rates are low. There are no specialized mechanisms for the long-distance transport of seeds, so persistence is not a consequence of the buffering effect of immigration. The extreme persistence of populations results from buffering effects of strong density-dependence, which compensates for the occurrence of smaller scale disturbances that remove small blocks (approx. 10×10 cm) of individuals.

The overall impression that was formed of the dynamics of this species was of a system of basically independent local populations for which suitable habitat is hard to define. Although superficially the regional population appears to have the characteristics of a metapopulation, the detailed analysis of regional dynamics in relation to local processes makes it clear that the regional population structure is quite distinct from a metapopulation. To express this notion therefore we refer to the system as a 'regional ensemble'. That is, a system of unconnected local populations that do not occur within discrete habitat patches, and for which regional dynamics and persistence are predicted (at least on a short to intermediate time-scale) by locally derived processes.

Spatially extended population: Silene alba (category III)

Silene alba is a dioecious perennial herb, common throughout the north of the United States of America (USA). The population dynamics of this species, as well as its genetics and interactions with a pathogenic smut fungus (*Ustilago violacea*) have been described in detail by Antonovics *et al.* (1994) and through a series

of detailed studies (Alexander 1989; Antonovics & Alexander 1992; McCauley *et al.* 1995; Thrall & Antonovics 1995; McCauley 1997). These studies were based on surveys conducted within a 25×25 km area in south-western Virginia, USA. The surveys looked at *c.* 7000 roadside segments of *c.* 40 m length within this area, constituting nearly 150 km in total. 'Populations' were defined as the individuals within individual segments; to a large extent this designation was subjective and a matter of convenience (Antonovics *et al.* 1994).

In terms of the four conditions required for a classic metapopulation structure: (i) The habitat requirements of this species are not specialized and it is not therefore possible to distinguish either discrete suitable patches or to be able to classify individual roadside segments as being suitable or unsuitable. (ii) Both colonization and extinction of patches were observed at moderate rates: colonization rates of 0.19–0.69 per existing patch per annum, and extinction probability of 0.09–0.30 per existing patch per annum. However, colonization was spatially dependent (50% of newly colonized patches are within 50 m of an already colonized segment), indicating that local dispersal was the prime mechanism for seed movement, rather than long-distance migration. (iii) Recolonization was not distinguished from colonization, although it presumably occurred. (iv) It is not possible to determine whether local patches have generally synchronous dynamics, although presumably they would respond similarly to factors such as weather, but differ in the kinds of disturbance experienced.

There are a number of important respects in which the dynamics of this regional population do not fit well with the definition of a metapopulation, some of which are discussed by Antonovics *et al.* (1994). The regional dynamics of this species may be best described by an array of patches where within-patch dynamics are determined by local density-dependence (e.g. competition between plants for resources or between seeds for microsites), and between-patch dynamics are determined by local dispersal, mainly in the form of seeds dispersing from their natal patches to those immediately adjacent. In this sense the regional dynamics result simply from a very large scaling-up of the local dynamics. To this end we would describe the population as a 'spatially extended system'.

The persistence of populations of this species is therefore not dependent on the regional configuration of habitat, but instead depends on factors that determine local dynamics, particularly within patch density-dependence and local dispersal, together with patterns of local disturbance (Antonovics *et al.* 1994).

LOCAL DYNAMICS

The main focus of our review is the regional scale. The studies in Table 1, however, suggest some important distinctions between studies of spatial dynamics at the local level (categories 4 to 6 in Table 2). Of the three categories of study, two relate to genuine differences

between the demographic characteristics of species and are worth briefly exploring further. Category 6 is a local analysis of population dynamics, and the prime focus of a study of this sort is not to determine the nature of spatial dynamics.

Spatially structured local populations: metapatches and gap dynamics (category IV)

The local dynamics of a range of species are fundamentally determined by spatial processes. These include the dependence on gaps for successful recruitment or the occurrence of parasites on discrete hosts. In these cases, population dynamics are not governed by very short distance interactions between individuals competing for resources. Rather, the demography of these species is defined in terms of a characteristic level of patchiness. As discrete patches can be defined for these species, and these may be occupied or unoccupied, they may appear analogous to metapopulation models. The dynamics of these species are not of the metapopulation form, however, as gaps simply define where recruitment occurs, and not where whole populations may occur. Moreover, a gap is a transient patch and colonization in particular may only be possible over a very short time period.

As an example of a spatially structured local population, we discuss a pioneer tree, *Cecropia obtusifolia*, the dynamics of which have been studied by Alvarez-Buylla & GarcÌa-Barrios (1991), Alvarez-Buylla (1994) and Alvarez-Buylla & Garay 1994). The key feature of the spatial dynamics of this species is the requirement of gaps within the canopy for recruitment. The forest matrix within which the species occurs contains a range of types of patches, but the species can recruit only into gaps of sufficient size (> 100 m^2). The consequence of this is that the population is structured spatially according to the frequency of the different patch types. In particular dynamics are patchy at the scale (100 m^2) of suitable gap sizes and need to be modelled at this scale rather than assuming spatial homogeneity (Alvarez-Buylla 1994). We consider this not to be a metapopulation because this system is a single spatially structured local population rather than a series of local populations linked by dispersal.

Spatially structured local population (category V)

These are populations occurring within areas of homogeneous habitat, but where populations have become extremely patchy. The best examples of these include arable weed populations where, as a consequence of spatial variations in invasion rates or in the removal of plants through herbicide applications, populations have become extremely patchy within basically continuous arable fields (e.g. Marshall 1988). This is also a property of a range of theoretical models (e.g. Durrett & Levin 1994; Pacala & Levin 1997) and arises when population densities become low and where dispersal

and interactions within populations are localized. This form of population structure generates apparent subdivisions of populations that may be misinterpreted as being extrinsically determined, for example resulting from variations in soil fertility leading to a restricted range of suitable patches. In such examples, the habitat is not patchy, but rather suitable habitat is continuously distributed and apparent patchiness results from the intrinsic spatial dynamics of the species. Hence the fundamental scale for study is inappropriate for a metapopulation analysis. Here we differentiate patchy and continuous local populations on the basis of the magnitude of local population extinction that results in either very patchy or relatively continuous populations.

Local population (category VI)

Local populations involve studies that yield no information on the regional or spatial organization of populations. For example, quadrat-based monitoring at a small scale yields information on local dynamics but no information on regional processes. For example, the dynamics of populations of *Vulpia ciliata* described above were studied within 2 m × 1 m quadrats. On their own the data from these quadrats yielded information on very local spatial dynamics (Watkinson *et al*. 2000a) but could not enable prediction of the nature of dynamics at larger scales. To achieve this, additional information on migration between several such populations would be required.

Conclusions

It is wrong to regard the issue of whether or not the regional population of a species is a metapopulation as simply a matter of semantics: if this were the case then metapopulation theory would have contributed nothing to our understanding of ecological systems. Instead, the development of metapopulation ecology has re-focused the long-standing interest of ecologists in large-scale ecological processes (Dytham 2000). A practical example of this, for example, is the approach to species conservation suggested by metapopulation theory (e.g. Tilman *et al*. 1994; Hanski 1999). If the regional population of a species of conservation concern constitutes a metapopulation, then conservation efforts need to be directed towards the regional availability of suitable habitat; if metapopulation processes are weak then species conservation should be directed at a population level. Accurate and explicit characterization of the importance of metapopulation processes is therefore of key importance. We have attempted to highlight this, in the context of dissociating local vs. regional processes for plant populations.

There are a number of problems for future analyses of plant regional dynamics. Most notably there are issues regarding the measurement and modelling of plant regional dynamics. The problems with measurement are well known, especially that of estimating

rates of migration. Genetic analysis would seem to be a promising way of addressing this problem. On the theoretical side, problems for future research include developing models for regional dynamics that include seed banks as well as patch models that include the extremely localized dispersal common to most plants. Moreover, the studies on *V. ciliata* and *S. alba* highlight the importance of measuring local dynamics at the same time as studying the regional populations. This reinforces the argument of Thomas & Kunin (1999) that a full description of local and regional processes, as well as their interaction, is required to interpret regional dynamics. To this end we have highlighted the importance of the availability and nature of suitable habitat, which is likely to be very important in plants given the restricted range of most species along the mobility axis of Thomas & Kunin (1999).

We have not attempted a complete typology of plant spatial dynamics. Instead we agree with Thomas & Kunin (1999) that this is not possible except in very general terms. Here we have used an outline classification of spatial dynamics seen in plant populations to illustrate a range of spatial dynamics and the processes that are responsible for them. In comparison with the well-known metapopulation classification, it is clear that in the absence of the classification we have proposed, most plant regional populations would be described as non-equilibrium metapopulations. However, within such a grouping a wide range of forms of regional organization exist and such a broad classification would not be useful. It is interesting and exciting that such a range exists within the comparatively small number of populations that have been studied in enough detail to distinguish local and regional processes. The metapopulation concept has focused attention on these issues and, in this respect, is therefore one of the most important recent developments in ecology.

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