A Metapopulation Perspective in Plant Population Biology

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ESSAY REVIEW

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Summary

1 A metapopulation approach considers the ecology and genetics of populations as a product of local dynamics and the regional processes of migration, extinction and colonization. While conventional metapopulation theory involves species with frequent population turnover, limited migration and random extinction, it is likely that metapopulation dynamics, broadly defined as the product of local population dynamics and dispersal, is a feature of all species.

2 Theoretical metapopulation models of single species make three critical insights. First, metapopulations will consist of a shifting mosaic of local populations linked through migration with only a fraction of the available habitat patches occupied at one time. Secondly, there is a threshold number of habitats available, below which the species cannot persist because extinction exceeds colonization. Thirdly, the antagonism between selective forces acting during recolonization and population growth can influence the evolution of phenotypic traits. Unfortunately, little empirical data is available to evaluate these ideas for plants or to address the broader issue of whether processes at a regional scale add anything to our understanding of population dynamics.

3 Plants may seem particularly appropriate for metapopulation analyses as a result of their immobility, strong spatial structure and restricted dispersal. However, a review of the literature revealed a paucity of studies that explicitly adopted a metapopulation approach, particularly in terms of testing theoretical models. We argue that this is because of the difficulty of measuring parameters such as extinction, colonization and migration that are central to most metapopulation models.

4 Plants possess a number of special features that present both challenges and opportunities for the development of new insights into the biology of metapopulations. Three particular characteristics, seed dormancy, restricted dispersal and local adaptation, need to be incorporated into existing theoretical models so they more accurately reflect the dynamics of plant metapopulations. Finally, more effort is needed to incorporate the explicit spatial structure of individuals within metapopulations and to investigate the effect that dispersion has on their growth and reproduction.

Keywords: colonization, demography, extinction, local adaptation, metapopulation, migration, plants, population genetics, seed dormancy

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Introduction

Species are rarely distributed continuously in space but rather are organized into local populations, interconnected to varying degrees through dispersal. As a result of this spatial structure, the demography and genetics of populations will be a product not only of local environmental conditions but also processes operating on a regional scale. While biologists have long recognized the discontinuities in species distributions (Andrewartha & Birch 1954; MacArthur & Wilson 1967), the formalization of this idea into ecological theory occurred only recently and generated the concept of the metapopulation, defined as an assemblage of populations existing in a balance between extinction and colonization (Levins 1969,

1970). The metapopulation perspective has provided a means of describing ecological processes at a spatial scale above the local population. This approach has provided new perspectives on (1) the proximate factors determining the geographical distributions of species (Carter & Prince 1988), (2) the ecological and evolutionary interactions between species and their stable coexistence (Burdon & Jarosz 1992; Antonovics 1994; Antonovics & Thrall 1994; Antonovics *et al.* 1994; Thomson 1994) and (3) population structure and the maintenance and organization of genetic variation (Wade & McCauley 1988; Whitlock & McCauley 1990). In addition, metapopulation concepts have a direct bearing on species persistence in fragmented habitats and hence to conservation biology (Nee & May 1992; Tilman *et al.* 1994; Karieva & Wennergren 1995; Schemske *et al.* 1995). Until this conceptual advance, most workers neglected regional influences and sought explanations for ecological phenomena primarily from studies of local populations.

Spatial patchiness is a noticeable feature of the distributions of most plants, particularly those occurring in ephemeral habitats. Such geographical structure is a prerequisite for the development of a metapopulation perspective, where the dynamics of any array of local populations may be governed by cycles of extinction and recolonization. Yet, the interconnectedness of local populations has been largely neglected in studies of plant population dynamics, and few empirical studies of plants have directly addressed the predictions of metapopulation theory. This gap in our understanding is reflected in the ecological and evolutionary literature. For example, in a volume devoted to metapopulation dynamics (Gilpin & Hanksi 1991), not a single paper dealt with the population biology of plants, and in two recent reviews on metapopulations (McCauley 1993; Hastings & Harrison 1994), plant studies were hardly discussed. Only a few studies that explicitly use a metapopulation approach have been published in the *Journal of Ecology* (e.g. Prince & Carter 1985; Perry & Gonzalez Andujar 1993; Cipollini *et al.* 1994).

The scant attention paid to metapopulation perspectives in plant ecology leads one to ask whether the reasons are historical or biological. Have plant ecologists failed to embrace metapopulation concepts because of the strong tradition of detailed demographic and physiological studies evident over the past two decades (Harper 1977; Grime 1979; Larcher 1980); or, has the development of a metapopulation approach been constrained by a mismatch between metapopulation concepts and the characteristic features of the population biology of plants?

Here we ask whether the application of a metapopulation perspective is likely to provide new insights into ecological and evolutionary processes in plants. We first examine the concept of a metapopulation and the central theoretical issues upon which research has been based. Second, we review the

existing empirical work on metapopulations in plants, and discuss the biological complexities of plants and the difficulty of imposing current concepts of metapopulations on many plant species. Finally, we explore the opportunities for research on metapopulation structure and dynamics in plants. Our review deals primarily with the metapopulation dynamics of single species, despite the growing literature on species interactions (Hastings & Harrison 1994; Thompson 1994).

What is a metapopulation?

Does the metapopulation concept apply to a limited set of species or do all species have metapopulations? Levins's original model has several restrictive assumptions and, as a result, has been applied primarily to a subset of species that exhibit a specific set of characteristics: subdivision into many similar-sized local populations, limited and random dispersal and frequent local extinction (Harrison 1991; Gilpin & Hanski 1991). This approach assumes that only those species whose regional distributions can be accounted for solely by extinction and colonization are true metapopulations. The study of metapopulation dynamics therefore demands that investigators study species in which these parameters can be measured. Metapopulation theory is perhaps most valuable for these species, since it is here that regional patterns of existence will not be predictable on the basis of local population dynamics alone. More recently, however, the metapopulation concept has been broadened to recognize that all species have local and regional dynamics, and therefore now includes species representing a wider range of life histories and population dynamics. Models have been refined to include the dynamics of local populations as reflected in demographic parameters such as mortality, fecundity, and growth rates as well as their spatial structure and probability of extinction (Hastings & Wolin 1989; Hastings 1991; Nee & May 1992; Tilman *et al.* 1994). Such refinements are resulting in an evolution of our concept of a metapopulation from a narrow definition applying to a restricted number of species to all organisms. These developments recognize that for the metapopulation concept to be useful to biologists, it should have generality. However, while such generality is a laudable goal, we believe the important question is: under what circumstances will a metapopulation approach provide novel insights into the biology of organisms under study?

An important issue for empirical studies concerns the criteria by which metapopulations are delineated in nature. In many ways, this problem is a larger-scale version of the age-old controversy over what constitutes a local population or deme (Crawford 1984). What constitutes a metapopulation is by no means straightforward and will involve the specific questions being addressed together with the practical

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issues associated with how best to sample the species in question. The boundaries of the metapopulation may vary from a single site (e.g. Addicott 1978) to an arbitrarily chosen area (e.g. 25 km × 25 km, Antonovics *et al.* 1994) to a geographical region (e.g. Dutch Rhine grasslands, Ouborg 1993; north-east Brazil, B. C. Husband & S. C. H. Barrett, unpublished data). Important issues to be considered in delineating the boundaries of the entire metapopulation and defining local populations within the metapopulation include the geographical structure of the species, the discreteness of the habitats occupied and the vagility of the species, in particular its dispersal characteristics. These factors will play a large role in determining the cohesion of populations within the metapopulation. For all but the most spatially explicit models, a metapopulation may be best applied to an area in which dispersal among habitats can be considered random. Using population genetic criteria, a metapopulation may then be the regional equivalent of a neighbourhood (Wright 1943), which is roughly defined as the area whose radius is twice the standard deviation of the dispersal distance (Crawford 1984). Alternatively, from a strictly demographic perspective, the metapopulation may be defined quite differently, for example, as the spatial scale within which the growth rate of all populations combined is at a stable equilibrium (D. W. Schemske, personal communication). Regardless of the criteria, the scale of the metapopulation is an important consideration because small metapopulations will have fewer local populations and therefore will be subject to stochastic variation in patch occupancy and metapopulation persistence (Hanski 1991).

Theoretical models and predictions for single species

Levins's (1969, 1970) metapopulation model, upon which most contemporary theory is based, depicts species in an array of habitat patches that are either occupied or unoccupied at any point in time. Empty patches are equally likely to receive colonists and all populations are equally likely to produce them. Changes in patch occupancy (*p*), or the status of the metapopulation, then, is described by:

$$dp/dt = mp(1-p) - ep \qquad (1)$$

where *m* is the colonization probability and *e* is the extinction probability. The fate of the metapopulation is a product of the balance between the colonization rate and extinction rate, which can be predicted without information on specific local dynamics. In reality, populations will differ in their size, habitat quality and spatial arrangement and hence will likely exhibit different extinction and colonization probabilities. Several metapopulation models have extended Levins's original work to explore the consequences of different life histories and geographical structures on per-

sistence of the metapopulation (Hanski 1982a; Lande 1987; Quinn & Hastings 1987; Hastings & Wolin 1989). Collectively, these models provide the following basic insights: (1) at equilibrium, the metapopulation should consist of a continually changing array of local populations; (2) because populations continually go extinct, a given species should occur in only a fraction of the available habitat patches; and (3) there will be a critical threshold number (or density) of patches required, below which extinction exceeds colonization and the metapopulation cannot persist. Hanski (1982a) has also shown that when extinction is a function of patch occupancy, the metapopulation at equilibrium tends to be driven towards either extinction or complete occupancy, suggesting that species that share a particular habitat should exhibit a bimodal distribution of patch occupancy.

Patch structure, as depicted in Levins's model, has important evolutionary implications, although these have only recently been expressed in the contemporary vocabulary of metapopulations. Population geneticists were perhaps the first to consider the ramifications of patch structure and colonization and extinction for populations. Wright's shifting balance theory (1943) proposes that populations that are subdivided will move to a higher adaptive peak through a random reshuffling of genes in small, isolated populations. This is followed by the disproportionate proliferation of the most fit populations through differential survival and colonization. Wright (1950) also developed the widely used 'island model' which depicts the distribution and magnitude of genetic variation in populations as a product of their size and random dispersal from surrounding populations. While extinction and recolonization were not depicted initially, the island model still represents a metapopulation to the extent that the composition of local populations is a product of regional as well as local processes. More recently, population genetic models have been used to determine whether extinction and recolonization would enhance or diminish genetic differentiation among populations (Slatkin 1977; Wade & McCauley 1988; Whitlock & McCauley 1990). These models show that the effects of population turnover on genetic variation depend on the probability of colonization (establishment in an unoccupied site) relative to migration (movement between existing populations) as well as the genetic composition of the colonists.

Wright and his contemporaries showed great foresight in developing population genetic models that incorporated both population structure and migration. However, these models have yet to be fully integrated with the body of metapopulation theory, reflecting the more widespread schism that exists between genetic and ecological approaches to population biology (Silvertown 1991). Two brief examples serve to illustrate this gulf. In most population genetic models there is no allowance for colonization and

extinction to vary independently yet this is a central feature of most metapopulation models. Migration between existing populations, on the other hand, is often not considered in metapopulation models, whereas this parameter has historically been of major significance to most evolutionary biologists (Wright 1943; Slatkin 1985).

Evolutionary biologists have also recognized that spatial heterogeneity, and hence a metapopulation structure, may have important implications for character evolution. Van Valen (1971) suggested that selection would act to maximize p, the occupancy of patches in a metapopulation. Therefore, characteristics that enhance dispersal and successful colonization should be under positive selection when extinction is frequent, since the persistence of the metapopulation is limited by the ability to colonize new habitat patches. Furthermore, selection in a population will differ during the 'lifespan' of a population, particularly for species experiencing changes arising through succession (Olivieri & Gouyon 1985), with traits promoting dispersal favoured during the founding of new populations and characters promoting persistence selected during the growth phases of the population (Olivieri *et al.* 1983; Peroni 1994). The evolutionary antagonism between selective forces acting during recolonization and population growth has been referred to as the 'metapopulation effect' and may also influence other life history characters (Olivieri & Gouyon 1996).

Empirical evidence

Metapopulation theory suggests that for some species regional processes can provide new insights into the dynamics of species that could not be garnered from studies of local populations alone. To what extent have these insights been demonstrated in natural populations? To date, most metapopulation studies have involved observations or correlative studies of various animal groups (reviewed in Gilpin & Hanski 1991; Hanski & Gilpin 1996). The results of these studies have provided empirical support for the assumptions that only a fraction of patches are occupied at any given time (Hanski 1982a), that small populations are most vulnerable to extinction (Williamson 1981; Schoener & Schoener 1983; Schoener & Spiller 1987) and that local abundance is often correlated with regional distribution (Addicott 1978). In general, few studies have examined how metapopulations are organized geographically and how ecological factors affect extinction and colonization. In addition, little consideration has been given to the relation between local and regional dynamics and insufficient studies are available to assess whether regional processes are likely to be important. Unfortunately, the use of plants for examining metapopulation processes and predictions has lagged even further behind.

A selected review of the literature revealed a scarcity of empirical investigations that have a direct bearing on metapopulation structure or dynamics in plants (Table 1). Most studies that have explicitly considered metapopulations have been either ecological or evolutionary in perspective, with few workers attempting to combine both approaches. The studies we have located represent a sample of plant species which is biased towards annual and short-lived perennials that inhabit ephemeral environments, perhaps because it is here that metapopulation dynamics are most obvious.

Few studies have examined, in detail, the distribution and demography of plants at a regional scale. In the studies available, plants were never uniformly distributed, but rather occurred in clumps (Erickson 1943; Antonovics *et al.* 1994; B. C. Husband & S. C. H. Barrett, unpublished data), even when the habitat appeared to be relatively homogeneous (Carter & Prince 1988). Other studies stressed the patchy distribution of species as a result of forest gaps (Horvitz & Schemske 1986; Alvarez-Buylla & García-Barrios 1991; Alvarez-Buylla 1994), animal disturbance (Platt & Weis 1985) or anthropogenic factors (Hanski 1982b). While patch structure is an obvious feature of many plants, these studies suggest that the spatial distribution of local habitats is unlikely to be uniform as conventional metapopulation models assume.

Of the studies identified in Table 1, many considered the importance of migration, colonization and extinction. However, these parameters were rarely measured directly; rather their importance was usually inferred from existing information on local demography using various modelling exercises. In most cases, the conclusion was that regional processes are substantial and may have an important impact on population dynamics and persistence. However, from this group of studies we cannot adequately ask whether regional processes are significant since few report the relation between demographic changes in local populations and the status of the metapopulation.

A metapopulation approach was recently used to determine whether patch dynamics could explain the persistence of the aquatic *Eichhornia paniculata* in the seasonally arid landscape of north-east Brazil (Husband & Barrett 1995; and unpublished). Annual censuses of 167 populations and surveys of available aquatic habitats across the species' geographical range revealed that, on average, 22% of sites present were occupied. Patch occupancy varied widely (range 0–47%) throughout the range and was positively correlated with the density of available habitats. This indicates the importance of having a large number of available habitats for the regional persistence of a species and is consistent with theoretical models in which metapopulation extinction will occur when colonization rates are too low because of lack of suit-

Table 1 Selected studies that explicitly consider plant metapopulations or population-level interactions at a regional scale. For each study, we report whether the demographic and/or genetic structure was documented for metapopulations, which metapopulation parameters (extinction, colonization, migration) were measured and whether the impact of these metapopulation processes was considered for the population at the local and/or regional spatial scale. Variables written in italics were examined through modelling exercises, and were not estimated in natural populations

Species	Metapopulation structure measured	Parameters examined	Spatial scale investigated	Reference
Ecological				
Cecropia obtusifolia	demographic, genetic	*colonization*, migration	local	Alvarez-Buylla & García-Barrios (1991)
				Alvarez-Buylla & Garay (1994)
Clematis fremontii	demographic	—	—	Erickson (1943)
Collinsia verna	—	*extinction*	local	Kalisz & McPeek (1993)
Cynoglossum officinale	demographic	extinction, colonization	local & regional	Van Der Meijden *et al.* (1992)
Lactuca serriola	demographic	—	regional	Prince *et al.* (1985)
Pedicularis furbishae	demographic	extinction, colonization	local & regional	Menges (1990)
Senecio jacobaea	demographic	extinction, colonization	local & regional	Van Der Meijden *et al.* (1992)
Silene alba	demographic	extinction, colonization	regional	Antonovics *et al.* (1994)
Stipa capensis	—	*migration*	local	Kadmon & Shmida (1990)
Evolutionary				
Acer rubrum	demographic	—	local	Peroni (1994)
Calathea ovandensis	demographic	*extinction, colonization*	local & regional	Horvitz & Schemske (1986)
Carduus spp.	genetic	*migration*	local	Olivieri *et al.* (1983)
Eichhornia paniculata	demographic, genetic	migration, extinction	local & regional	Husband & Barrett (1995) and unpublished
Lythrum salicaria	demographic, genetic	*migration*	local & regional	Eckert *et al.* (1996)
Plantago cordata	demographic, genetic	—	regional	Meagher *et al.* (1978)
Silene dioica	demographic, genetic	migration	regional	Giles & Goudet (1996)
Silene alba	demographic, genetic	colonization	regional	McCauley *et al.* (1995)
Thymus vulgaris	genetic	colonization	local	Couvet *et al.* (1986)

able habitats (Levins 1969). The annual extinction rate in populations of *E. paniculata* was 34% owing to drought, disturbance and severe flooding. In contrast to data from the animal literature (see above), extinction was independent of population size and age (Fig. 1). This result undoubtedly reflects the importance of environmental stochasticity that is experienced by many plants found in ephemeral habitats, where catastrophic changes in local environment can cause extinction, regardless of the demographic characteristics of local populations.

The consequences of extinction and colonization for genetic structure was recently examined by Giles & Goudet (1996) in island populations of *Silene dioica*. Islands of the Skeppsvik Archipelago in Sweden have been undergoing a constant rate of uplift since the last glaciation. As a result, islands of different altitude differ in time of emergence from the Baltic Sea and hence in the time available for colonization. Giles & Goudet used this information plus knowledge of the successional status of *S. dioica* to identify populations of different age and to compare the levels of genetic variation (isozymes) among populations. They showed that newly founded populations were more differentiated than those of intermediate age, indicating that the process of colonization tends to enhance genetic differences among populations. In addition, the lack of a relationship between geographical and genetic distances for young populations suggested that colonizers are coming from a wide

range of source populations rather than neighbouring ones. These results provide evidence for the importance of colonization in determining the genetic composition of populations in the metapopulation.

Evidence for phenotypic evolution resulting from the 'metapopulation effect', attributable to frequent extinction and recolonization, has been reported for several species. Workers at Montpellier (e.g. Domnee *et al.* 1983; Couvet *et al.* 1986) report that the frequency of females decreased with age in populations of gynodioecious *Thymus vulgaris*. They have suggested that this occurs because of intergenomic conflicts between nuclear and cytoplasmic genes governing the expression of gynodioecy and the fact that evolutionary forces in the founding stages of a population differ from those during establishment. Selection associated with high population turnover may also account for the maintenance of a seed heteromorphism in *Carduus*. Plants produce two kinds of seeds: those that are widely dispersed and nondormant and those that are poorly dispersed and dormant. Olivieri *et al.* (1990) proposed that this heteromorphism is maintained because of selection for frequent colonization. Specifically they hypothesize that genes favouring dispersal and colonization will be favoured at the time of colonization but selected against in the later stages of a population, when wide seed dispersal will be a costly waste of propagules. This may also help to explain why older populations produce more nondispersing seed.

A.

B.
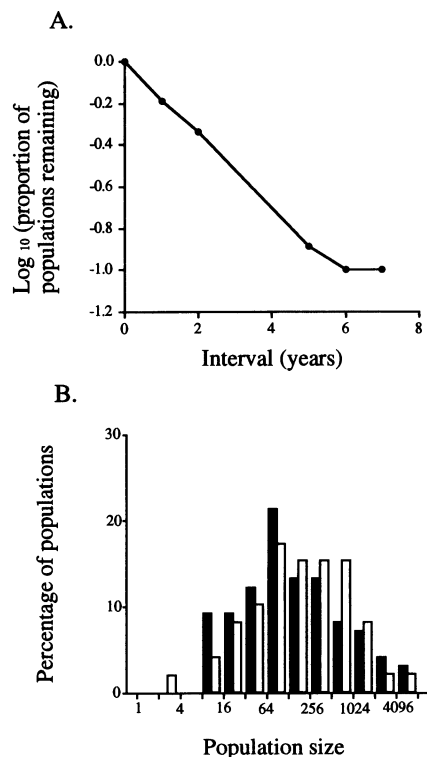
Fig. 1 Patterns of local population extinction in the annual aquatic *Eichhornia paniculata* from north-eastern Brazil. (A) Population persistence curve showing survivorship of populations over a one to seven year time interval. A total of 167 populations were censused for a minimum of two years with 30 populations observed for a seven year period. A straight line indicates that mortality rates are independent of population age. (B) The relation between extinction and population size. Of the 123 populations observed over a one year time interval, 39% went extinct. The mean initial size for populations that went extinct (■) was not statistically different from that in populations that persisted (□), based on a Mann–Whitney *U*-test ($U = 1925$; $P > 0.3$, $n = 123$). Geometric size classes were used to normalize the distributions (B. C. Husband and S. C. H. Barrett, unpublished).

A metapopulation approach has been used by J. Pannell of Oxford University (unpublished ms.) to model the effects of population structure on sex ratios in gynodioecious and androdioecious species. His models indicate that, for a metapopulation with a given mean colony life-span, there is a threshold level of gene flow between colonies below which females or males can no longer coexist with hermaphrodites. These results draw attention to the importance of considering migration and population structure for studies on the evolution of mating systems. In *Eichhornia paniculata*, evolution of self-fertilization is initiated by destabilization of its tristylous breeding system due to stochastic process operating in small populations (Barrett *et al*. 1989; Husband & Barrett 1992a). Measurements of gene flow indicate that migration among populations is not sufficient to maintain the polymorphism in certain parts of the range (Husband & Barrett 1995), given the small effective population sizes that occur in this species

(Husband & Barrett 1992b). In contrast, migration among populations appears to be sufficient to maintain trimorphism in native populations of *Lythrum salicaria* (Eckert *et al*. 1996); however, in the adventive range of this species, founder effects and geographical isolation likely account for the reduced number of trimorphic populations (Fig. 2).

Future research on plant metapopulations

An overwhelming finding of this review is the paucity of plant studies on population dynamics at the metapopulation level and, as a result, the ecological and evolutionary significance of metapopulation processes are not well understood. However, we believe that plants possess a number of special features that present both challenges and opportunities for providing new insights into the biology of metapopulations. We next consider three characteristics: seed dormancy, restricted dispersal and local adaptation.

As we have seen, a critical aspect of metapopulation theory is the extinction of local populations. While the assessment of extinction may be relatively straightforward in many animal populations, this task is complicated for many plant species because of strong seed dormancy. Should the criteria for extinction include all plants at a site, including dormant propagules, or is it permissible to consider extinction for the above ground parts alone? Should we consider re-emergence from the seed bank as simply colonization in time and treat it in a manner analogous

A.

B.
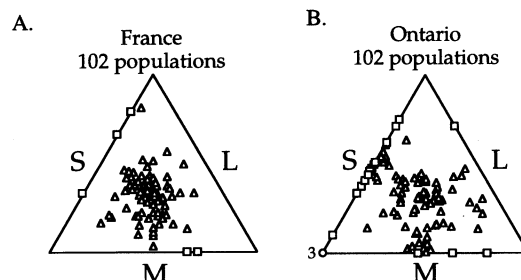
Fig. 2 Style morph frequencies of *Lythrum salicaria* from native populations in south-western France (A) and adventive populations in southern Ontario, Canada (B). Each side of the triangle represents one of the three style morphs (L, long-styled morph; M, mid-styled morph; S, short-styled morph), and each point represents the morph frequencies of one population. The distance of a point from a side is proportional to the frequency of a morph in that population. Points in the centre of the triangle have even morph frequencies. Trimorphic, dimorphic and monomorphic populations are represented by triangles, circles and squares, respectively. There is significantly higher evenness in morph frequencies and fewer nontrimorphic populations in native populations from France in comparison with the Ontario sample. The high degree of trimorphism in France appears to result from the high connectivity of populations within the agricultural landscape of this region and greater opportunities for migration among populations. Among the Ontario sample, three populations contained only long-styled plants (Eckert *et al*. 1996). Figure published with permission.

to colonization in space, which is clearly the most tractable solution, or is dormancy a qualitatively different phenomenon? While there have been no detailed studies that have considered dormancy in the context of plant metapopulations (but see Horvitz & Schemske 1986), Kalisz & McPeek (1993) have shown that seed dormancy in the annual *Collinsia verna* can decrease the probability of population extinction and increase the time to extinction as well as the population growth rate. These results suggest that seed dormancy may increase the proportion of patches occupied at one time and reduce the rates of colonization required to maintain a stable metapopulation. Both theoretical and empirical studies on the implications of seed banks for metapopulation dynamics are required.

While many plants have the capacity for long distance dispersal, it is well established that the majority of seeds are dispersed locally (Harper 1977; Silvertown & Lovett Doust 1993). Similar principles apply to the dispersal of pollen (Levin & Kerster 1974; Levin 1988). These features violate another of the basic assumptions of conventional metapopulation theory, in which dispersal and colonization occur randomly among habitats. A consequence of localized dispersal is that populations may have a clumped rather than a uniform distribution on the landscape, which may influence the dynamics and stability of the metapopulation. For example, populations that are clustered in space may increase metapopulation persistence by buffering local populations against factors likely to cause extinction. This has been referred to as the 'rescue effect' (Brown & Kodric-Brown 1977). This positive influence, however, may not always apply, particularly when neighbouring populations are subjected to similar environments. Using computer simulations, Harrison & Quinn (1989) found that such correlated environments can increase the vulnerability of the metapopulation to extinction.

One of the evolutionary consequences of localized dispersal is the development of fine-scale local adaptation in plant populations (Heslop-Harrison 1964; Bradshaw 1972). Most metapopulation models do not incorporate selection and assume random dispersal from local populations. This implies that migrants from different populations are likely to be equally well adapted to newly occupied habitats or that matings between plants from different populations are of similar fitness to those within populations. However, there is considerable evidence of local adaptation in plants (Antonovics 1976; Snaydon & Davies 1976; Aarssen & Turkington 1985), and recent studies (reviewed by Waser 1993) suggest that matings between different patches or populations can lead to reduced fitness via outbreeding depression. Clearly dispersal in plants does not always guarantee successful establishment and we are some way from understanding the ecological and genetic factors influencing successful colonization. Whether dispersal or local adaptation

limits species' distributions is not only a central issue for plant population biology but also for understanding metapopulations.

Our review has shown that a considerable gulf exists not only between demographic and genetic approaches to the study of plant metapopulations, but also between theory and empirical evidence. Much of the published literature on metapopulations involves theoretical work; however, most models are of little relevance to the practising ecologist because they lack biological realism and fail to incorporate ecologically relevant features of plant populations. The highly idealized depiction of metapopulations as an array of equally spaced or discrete populations on a computer generated grid needs to be replaced by more spatially explicit models that incorporate the distribution of all individuals on the landscape rather than just those occurring within well defined patches or populations. Isolated plants and areas of uneven distribution are likely to influence the magnitude of connectivity within metapopulations, yet most population biologists tend to avoid plants occurring in these situations. Empirical studies of the demography and fitness of individuals over the full range of spatial contexts in which plants occur are needed to determine how geographical structure influences metapopulation dynamics.

While we recognize that more spatially explicit models would be of value, it is important to acknowledge that, at the present time, even the most simple metapopulation models have yet to be fully evaluated for the best known model systems used by plant population biologists (e.g. *Anthoxanthum, Asclepias, Avena, Clarkia, Eichhornia, Impatiens, Limnanthes, Mimulus, Phlox, Plantago, Silene, Thymus, Trifolium*). This is almost certainly due to the difficulty of obtaining estimates for parameters such as patch occupancy, extinction and colonization, which can often operate on large spatial and temporal scales. In addition, parameters such as migration often involve rare events and in plants may be especially difficult to observe directly. However, it is worth at least acknowledging that our focus since the birth of population biology has been on the dynamics of local populations to the exclusion of any consideration of regional processes. A broadened research agenda that embraces a landscape-perspective on the demography and genetics of plant populations is required before the field of plant metapopulation biology can develop and mature.

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