

Probing the primacy of the patch: what makes a metapopulation?

J. R. PANNELL* and D. J. OBBARD

Department of Plant Sciences, University of Oxford, Oxford OX1 3RB, UK

The use of the term ‘metapopulation’ has broadened substantially since its inception to include, for example, subdivided populations that are not necessarily prone to local extinction, and populations with a locally patchy distribution that are not clearly subdivided into discrete demes. This broadened scope has coincided with an exponential increase in the number of articles applying the term (Hanski & Simberloff 1997; Pannell & Charlesworth 2000), but it has arguably come at a cost of precision. In their useful review of the literature on large-scale spatial dynamics in plants, Freckleton & Watkinson (2002) have blown the whistle on this trend. They argue that metapopulations ought only to describe an array of populations (i) that are prone to local extinction, and (ii) that also inhabit discrete and recognizable habitat patches. The first of these criteria is uncontroversial, although the rate of local population extinction that is biologically significant will depend on the nature of the questions being addressed. We believe that the second criterion, however, fails to recognize the utility of the metapopulation approach in studies that are not focused specifically on patch occupancy rates. In this sense, our view thus differs from that of Freckleton & Watkinson (2002), as well as from views expressed recently by Bullock *et al.* (2002), who also emphasize the importance of fixed habitat patches in defining a metapopulation.

It is of course true that many applications of the metapopulation concept in ecology and conservation need to address patch occupancy rates explicitly, and thus require the *a priori* identification of habitat patches. In a reply to Ehrlén & Eriksson’s (2003) critique of their review, Freckleton & Watkinson (2003) emphasize this point. If we are interested in ensuring the regional conservation of a metapopulation, then efforts must be directed towards the conservation of habitat, whether currently occupied or not. But the dynamics of population turnover in a metapopulation affect not only the regional persistence or survival of a species, but also its population genetics (reviewed in Pannell & Charlesworth 2000) and evolution (reviewed in Ronce & Olivieri 2003) – whether or not we can identify its habitat. Bullock *et al.* (2002) state that ‘a basic premise of metapopulation theory and models [is] that extinctions make habitat patches available for colon-

ization’ (p. 291). We agree with the implication that an empirical definition of a metapopulation ought to be consistent with its use in the theoretical literature. However, not all theoretical metapopulation models assume the existence of fixed habitat patches.

It seems that our differing views stem, at least in part, from a failure to integrate genetic or evolutionary aspects of metapopulation biology with ecological or demographic ones. For example, Freckleton & Watkinson (2002) adopted an entirely demographic perspective in their review and did not consider population genetic structure, because ‘metapopulation theory is not concerned with the movement of genes *per se*’ (p. 421). However, the metapopulation perspective has been used fruitfully in both ecology and population genetics, and indeed the concept was first considered by Wright (1940) in the context of population genetics long before Levins (1969, 1970) explicitly introduced the term. Ives & Whitlock (2002) have recently noted that ‘population genetic metapopulations’ may not necessarily equate with ‘ecological metapopulations’, because extinction–colonization dynamics need not affect both the demography and the genetic structure of a species to the same extent. However, because the same underlying processes make the metapopulation concept valuable in population genetics and ecology, consistency in applying the term is desirable.

Subdivided populations vs. habitat patches

The main point we wish to make is that, whilst it is clearly true that species that occupy discrete habitat patches will occur in discrete groups, the discrete nature of the groups themselves will affect important aspects of a species’ biology, irrespective of the underlying causes. Indeed, Levins (1970) stressed the importance of a patchy habitat principally in its creation of an insular distribution of organisms. Reduced insistence on the identification of discrete habitat patches recognizes that what really matters in a metapopulation is that the extinction of groups is balanced by founding of new groups within the range of the metapopulation, i.e. not necessarily within a set of fixed and recognizable patches, which may by nature be temporary and difficult to observe. From an ecological point of view, an inability to identify unoccupied habitat may make the metapopulation approach difficult to apply, because the proportion of occupied patches will often be an

important state variable. From a population-genetics perspective, by contrast, the most useful information for the application of metapopulation theory will be the colony age distribution (Wade & McCauley 1988). In situations where colony age correlates with the successional stage of the patch (e.g. Giles & Goudet 1997a), patch characterization may be useful, but this will not always be possible or necessary.

Ultimately, group discreteness depends on limited mixing between groups through dispersal (migration). The point at which dispersal erodes group identity enough to make the metapopulation concept unhelpful is to some extent arbitrary, but essentially it will depend upon the biological question being addressed. For example, neutral gene frequencies will begin to differ appreciably between demes in a subdivided population without local extinction, when m , the proportion of individuals in extant demes that were migrants in the previous generation, exceeds $1/N$, the reciprocal of the local population size. Thus, groups can be viewed as being relatively discrete when $Nm < 1$ (Wright 1951). In a metapopulation with extinction, patterns of neutral diversity are only affected appreciably by population turnover when e , the population extinction rate, exceeds m (Slatkin 1977; Pannell & Charlesworth 1999, 2000). Subdivided populations in which local processes are dominant, described by Freckleton & Watkinson (2002) as 'regional ensembles', will meet the criterion $e < m < 1/N$. In subdivided populations with migration dominant over both extinction ($m > e$) and the local effects of drift ($m > 1/N$), the effects of genetic bottlenecks that follow colonization events are quickly eroded, so that the average effects of extinction can be ignored. Similarly, the effects of selection, e.g. in fuelling local adaptation or manifest in inbreeding depression, depend on the genetic identity within and differentiation between populations, which in turn depend on relative rates of extinction, migration and drift (Whitlock & McCauley 1990; Whitlock 2002). As a final example, the relative degree of group identity, quantified in terms of the relatedness of interacting individuals, directly determines the efficacy of kin selection (Hamilton 1964).

Note that none of these theoretical scenarios is spatially explicit, and none assumes fixed habitat patches. Nor have several empirical tests of metapopulation genetic theory needed to heed the existence of discrete habitat patches (e.g. Antonovics *et al.* 1994; Richards *et al.* 1999; McCauley *et al.* 2000; Richards 2000), although they may occur (see Gaggiotti *et al.* 2002 for a population-genetic study where the explicit recognition of habitat patches was useful). An interesting example is that of *Silene dioica* on islands in the Baltic Sea (Giles & Goudet 1997b), which Bullock *et al.* (2002) cite as a rare instance of a true plant metapopulation – even though this system violates their stated premise that 'extinctions make habitat available for recolonization'. The habitat of *S. dioica* on these Baltic islands is indeed patchy in the extreme, but it is the

patchiness of the groups that has been the focus of analysis, and the same sort of analysis could equally have been employed if the species had occurred as a 'shifting cloud' of populations in a continuous habitat (*sensu* Freckleton & Watkinson 2002) or a system of populations involved in 'habitat tracking' (*sensu* Harrison & Taylor 1997). Comparisons of metapopulations with and without a patchy habitat are badly needed from both a demographic and a population genetic perspective, but in the absence of empirical data it is not clear that they must be different.

The question of scale

Freckleton & Watkinson (2002) and Bullock *et al.* (2002) rightly emphasized the need to distinguish between local and regional scales: a metapopulation approach might be appropriate for analysis of processes occurring at a regional scale, but not for processes operating below the local scale. Ehrlén & Eriksson (2003) have replied that any subdivided population might be regarded as a metapopulation if the appropriate spatial and temporal scale of analysis is adopted. We agree with Freckleton & Watkinson (2003) that this perspective seems unhelpful. What matters is whether the biological attribute under study is affected by population turnover at a regional scale. It therefore seems clear that the local dynamics in Freckleton & Watkinson's (2002) 'spatially extended population', where the spatial dimensions of groups of organisms are extended and moved by the diffusive effects of local dispersal, do not constitute an important component of the (regional) dynamics of a metapopulation.

Nevertheless, the potentially extendable and mobile groups of such spatially extended populations may usefully be regarded as the sub-populations or demes of a metapopulation if they are sufficiently isolated from other such patches and their origin is the result of a colonization event through non-local dispersal. This may be abiotically (e.g. by wind or water) or biotically assisted, and may thus differ qualitatively from local dispersal. Even where colonization and gene flow amongst extant populations are due to the same process of dispersal, however, Ibrahim *et al.* (1996) have shown that discretely subdivided populations can result in a continuous habitat as a result of the stochasticity of dispersal and colony establishment when the dispersal curve has a long tail. The important point is not the possible significance of the mode or absolute distance of dispersal, but whether dispersal leads to a colonization event, i.e. to the establishment of a new discrete group. In population-genetic and evolutionary models, it is typically the repeated bottlenecks associated with colonization that give rise to the metapopulation effects (Olivieri *et al.* 1997) that are not seen in (spatially extended) local populations, such as particular patterns of genetic (reviewed in Pannell & Charlesworth 2000), mating-system (reviewed in Barrett & Pannell 1999) and life-history variation (reviewed in

Ronce & Olivieri 2003). Migration amongst established groups tends to erode these effects, which cannot be produced by local dispersal.

Population turnover that gives rise to metapopulation effects may of course occur in species with discrete habitat patches (e.g. Ebert *et al.* 2002), but discrete and identifiable habitat patches are not essential. It is difficult, for example, to make sense of variation in sex ratios and sex allocation in several gynodioecious (e.g. van Damme 1986; Manicacci *et al.* 1997; Taylor *et al.* 1999; see Frank 1989) and androdioecious plant species (reviewed in Pannell 2002) without invoking population turnover in a metapopulation – even though these species may occupy continuous habitat as a ‘shifting cloud’. The temporal scale over which population turnover occurs may make the metapopulation dynamics difficult to study directly, but their effects may be apparent just the same. Indeed, under certain circumstances metapopulation processes may be inferred indirectly on the basis of these effects (Pannell 2001; and unpublished manuscript).

Freckleton & Watkinson (2002) argued that plants such as *Vulpia ciliata* and *Silene alba* should not be regarded as metapopulations, because it is difficult to determine what constitutes a suitable habitat patch for these arable weeds (see their paper, pp. 430–431, for the relevant references). However, both of these species may occur as spatially discrete groups of individuals. In the case of *V. ciliata*, they note that ‘the only regional-scale phenomenon that cannot be predicted [on the basis of local-scale processes] is the origin of new populations’ (p. 430). The low rate at which this occurs may be uninteresting from an ecological or demographic point of view, and in this sense investigators would be right in rejecting a metapopulation approach to analysis or management. However, from a genetic perspective these rare metapopulation events may be important in defining the structure of a species (Pannell & Charlesworth 1999). Similarly, although *S. alba* appears to occupy a continuous habitat in roadside vegetation, the spatially discrete nature of groups of individuals has been shown to have important genetic consequences concerning the genetic rescue of inbred populations by immigrants (e.g. Richards 2000), in much the same way that it occurs in species with discrete habitat (e.g. Ebert *et al.* 2002).

Conclusions

Both Freckleton & Watkinson (2002) and Bullock *et al.* (2002) recommended a more precise terminology for describing the structure and regional dynamics of subdivided plant populations. Their taxonomies are useful in that they focus much needed attention on the important differences that occur between structures that have otherwise been referred to broadly as metapopulations. These differences are not just semantic, and it therefore seems useful to recognize them with an appropriate nomenclature. Nevertheless, we believe

that consistency in the use of the term metapopulation is needed. This would be served by affording priority to the discrete and ephemeral nature of groups of individuals in defining a metapopulation, rather than to the presence of discrete habitat patches that may or may not underlie a given population structure. The identification of habitat patches will doubtless make metapopulation analysis easier from certain points of view, and patches may be of direct relevance to the ecology and conservation of species. However, the discrete nature of the groups of organisms involved is more fundamental. This is underscored by the successful adoption of the metapopulation terminology and approach in evolutionary and population-genetic analysis of species that do not occupy readily identifiable habitat patches.

Acknowledgements

We thank R. P. Freckleton for helpful discussion, and J. Silvertown and three anonymous referees for constructive comments on the manuscript. We gratefully acknowledge a Long Studentship (The Queen’s College, Oxford) awarded to D.J.O. and funding to J.R.P. through NERC grant NER/B/S/2002/00225.

References

- Antonovics, J., Thrall, P.H., Jarosz, A. & Stratton, D. (1994) Ecological genetics of metapopulations: the *Silene 1–Ustilago* plant–pathogen system. *Ecological Genetics* (ed. L. Real), pp. 146–170. Princeton University Press, Princeton, NJ.
- Barrett, S.C.H. & Pannell, J.R. (1999) Metapopulation dynamics and mating-system evolution in plants. *Molecular Systematics and Plant Evolution* (eds P. Hollingsworth, R. Bateman & R. Gornall), pp. 74–100. Chapman & Hall, London.
- Bullock, J.M., Moy, I.L., Pywell, R., Coulson, S.J., Nolan, A.M. & Caswell, H. (2002) Plant dispersal and colonisation processes at local and landscape scales. *Dispersal Ecology* (eds J.M. Bullock, R.E. Kenward & R. Hails), pp. 279–302. Blackwell Science, Oxford.
- van Damme, J.M.M. (1986) Gynodioecy in *Plantago lanceolata* L. IV. Frequencies and spatial distribution of nuclear and cytoplasmic genes. *Heredity*, **56**, 355–364.
- Ebert, D., Haag, C., Kirkpatrick, M., Riek, M., Hottinger, J.W. & Pajunen, V.I. (2002) A selective advantage to immigrant genes in a *Daphnia* metapopulation. *Science*, **295**, 485–488.
- Ehrlén, J. & Eriksson, O. (2003) Large-scale spatial dynamics of plants: a response to Freckleton & Watkinson. *Journal of Ecology*, **91**, 316–320.
- Frank, S.A. (1989) The evolutionary dynamics of cytoplasmic male sterility. *American Naturalist*, **133**, 345–376.
- Freckleton, R.P. & Watkinson, A.R. (2002) Large-scale spatial dynamics of plants: metapopulations, regional ensembles and patchy populations. *Journal of Ecology*, **90**, 419–434.
- Freckleton, R.P. & Watkinson, A.R. (2003) Are all plant populations metapopulations? *Journal of Ecology*, **91**, 321–324.
- Gaggiotti, O.E., Jones, F., Lee, W.M., Amos, W., Harwood, J. & Nichols, R.A. (2002) Patterns of colonization in a metapopulation of grey seals. *Nature*, **416**, 424–427.

- Giles, B.E. & Goudet, J. (1997a) A case study of genetic structure in a plant metapopulation. *Metapopulation Biology: Ecology, Genetics, and Evolution* (eds I. Hanski & M.E. Gilpin), pp. 429–454. Academic Press, San Diego.
- Giles, B.E. & Goudet, J. (1997b) Genetic differentiation in *Silene dioica* metapopulations: estimation of spatiotemporal effects in a successional plant species. *American Naturalist*, **149**, 507–526.
- Hamilton, W.D. (1964) The genetical evolution of social behaviour, I and II. *Journal of Theoretical Biology*, **7**, 1–52.
- Hanski, I. & Simberloff, D. (1997) The metapopulation approach, its history, conceptual domain, and application to conservation. *Metapopulation Biology: Ecology, Genetics, Evolution* (eds I. Hanski & M.E. Gilpin), pp. 5–26. Academic Press, San Diego.
- Harrison, S. & Taylor, A.D. (1997) Empirical evidence for metapopulation dynamics. *Metapopulation Biology: Ecology, Genetics, Evolution* (eds I. Hanski & M.E. Gilpin), pp. 27–42. Academic Press, San Diego.
- Ibrahim, K.M., Nichols, R.A. & Hewitt, G.M. (1996) Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. *Heredity*, **77**, 282–291.
- Ives, A.R. & Whitlock, M.C. (2002) Inbreeding and metapopulations. *Science*, **295**, 454–455.
- Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237–240.
- Levins, R. (1970) Extinction. *Some Mathematical Questions in Biology* (ed. M. Gerstenhaber), pp. 77–107. American Mathematical Society, Providence.
- Manicacci, D., Atlan, A. & Couvet, D. (1997) Spatial structure of nuclear factors involved in sex determination in the gynodioecious *Thymus vulgaris* L. *Journal of Evolutionary Biology*, **10**, 889–907.
- McCauley, D.E., Olson, M.S., Emery, S.N. & Taylor, D.R. (2000) Population structure influences sex ratio evolution in a gynodioecious plant. *American Naturalist*, **155**, 814–819.
- Olivieri, I., Gouyon, P.H. & Gilpin, M.E. (1997) Evolution of migration rate and other traits: The metapopulation effect. *Metapopulation Biology: Ecology, Genetics, and Evolution* (ed. I. Hanski), pp. 293–323. Academic Press, San Diego.
- Pannell, J.R. (2001) A hypothesis for the evolution of androdioecy: the joint influence of reproductive assurance and local mate competition in a metapopulation. *Evolutionary Ecology*, **14**, 195–211.
- Pannell, J.R. (2002) The evolution and maintenance of androdioecy. *Annual Review of Ecology and Systematics*, **33**, 397–425.
- Pannell, J.R. & Charlesworth, B. (1999) Neutral genetic diversity in a metapopulation with recurrent local extinction and recolonization. *Evolution*, **53**, 664–676.
- Pannell, J.R. & Charlesworth, B. (2000) Effects of metapopulation processes on measures of genetic diversity. *Philosophical Transactions of the Royal Society of London Series B-Biology Sciences*, **355**, 1851–1864.
- Richards, C.M. (2000) Inbreeding depression and genetic rescue in a plant metapopulation. *American Naturalist*, **155**, 383–394.
- Richards, C.M., Church, S. & McCauley, D.E. (1999) The influence of population size and isolation on gene flow by pollen in *Silene alba*. *Evolution*, **53**, 63–73.
- Ronce, O. & Olivieri, I. (2003) Life history evolution in metapopulations *Metapopulation Biology* (eds I. Hanski & O.E. Gaggiotti), in press. Academic Press, San Diego.
- Slatkin, M. (1977) Gene flow and genetic drift in a species subject to frequent local extinction. *Theoretical Population Biology*, **12**, 253–262.
- Taylor, D.R., Trimble, S. & McCauley, D.E. (1999) Ecological genetics of gynodioecy in *Silene vulgaris*: relative fitness of females and hermaphrodites during the colonization process. *Evolution*, **53**, 745–751.
- Wade, M.J. & McCauley, D.E. (1988) Extinction and recolonization: their effects on the genetic differentiation of local populations. *Evolution*, **42**, 995–1005.
- Whitlock, M.C. (2002) Selection, load, and inbreeding depression in a large metapopulation. *Genetics*, **160**, 1191–1202.
- Whitlock, M.C. & McCauley, D.E. (1990) Some population genetic consequences of colony formation and extinction: genetic correlations within founding groups. *Evolution*, **44**, 1717–1724.
- Wright, S. (1940) Breeding structure of populations in relation to speciation. *American Naturalist*, **74**, 232–248.
- Wright, S. (1951) The genetical structure of populations. *Annals of Eugenics*, **15**, 323–354.

Received 13 August 2002

revision accepted 22 March 2003