

## EMPIRICAL PERSPECTIVES

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Perhaps the greatest challenge in studying metacommunities is to link theoretical concepts to natural empirical systems. One problem is that many of the theoretical ideas recognized in this book have only recently been described (e.g., Chesson 1998; Hubbell 2001; Mouquet and Loreau 2002; Loreau et al. 2003; Leibold et al. 2004). Second, fully testing metacommunity ideas is demanding because it requires knowledge of both patterns and mechanisms involving multiple communities. Finally, testing the spatial dynamics of many interacting species could be challenging because it has been difficult to test theories involving the spatial dynamics of just two interacting species (e.g., Taylor 1990; Harrison and Taylor 1997). Nonetheless, there are ways of studying metacommunity ecology that are tractable and that go a long way toward testing the modern theories that dominate metacommunity ecology.

An obvious way to organize studies is to use the four conceptual metacommunity models Holyoak et al. have outlined in chapter 1. However, since addressing this framework was not the main aim of many chapters we instead organize our introduction around two of the greatest hurdles to applying theoretical definitions of metacommunities to empirical situations. These are that local communities do not always have discrete boundaries and that different species may respond to processes at different scales (Holyoak et al., chapter 1; Holt et al., chapter 20). Based on these problems, the examples presented in this volume might be placed into three categories.

## Collections of Discrete Permanent Habitat Patches

Habitat patches are relatively permanent and large a species could persist by remaining within patches without dispersal. However, if populations within patches were small or species interactions caused extinctions, then additional persistence mechanisms would be required. Species could also evolve to persist through dormant propagules (the temporal storage effect, e.g., Chesson 2000), or through dispersal and metapopulation dynamics (reviewed by Hoopes et al., chapter 2).

Studies of permanent patches that cannot support viable populations are typically by many clusters of small oceanic islands, with oceans providing barriers to dispersal to varying degrees depending on the taxa considered (Mehranvar and Jackson 2001). Similarly, ponds and lakes often have biotas that are strongly

bounded by terrestrial habitat, but the degree to which the intervening terrestrial habitat is a barrier varies between taxa. These systems also often contain considerable variation in physical or biotic conditions from patch to patch. Chapter 8 by Cottenie and De Meester describes an interconnected system of ponds, some with and some lacking fish predators. They show that local abiotic and biotic conditions are critical to the species composition and densities of assemblages of zooplankton. The system falls somewhere between the species-sorting and mass effects perspectives, depending on the data that are considered. The rock pool and zooplankton system presented by Kolas and Romanuk (chapter 9) is another system in which patches are constant in their positions but vary considerably in their characteristics and may also dry out during the year. The authors suggest that physical conditions seem to be critical to organizing the communities and creating a hierarchy of scales, and argue that both species sorting and neutral dynamics could explain different aspects of dynamics.

Two chapters present empirical results from systems where patches are permanent but appear to be more uniform. In chapter 6, Gonzalez discusses experimental evidence from a system consisting of carpets of epiphytic moss that contains a species-rich assemblage of microarthropods. These moss carpets represent readily manipulable microlandscapes. A series of experiments conducted in northern England demonstrated that altering landscape connectivity, and hence community isolation, influenced various community properties, such as local and regional diversity and secondary productivity. This example shows effects of dispersal on local and regional species diversity and the author suggests that the mass effects perspective is particularly relevant to dynamics in this system. An unmanipulated field system provides a second example of this kind. Van Noubuy and Hanski (chapter 4), describe a system consisting of hundreds of patches containing a food web consisting of up to three plants, two butterfly species, five primary parasitoids and two hyperparasitoids. The study provides a convincing demonstration of the role of spatial dynamics and other factors in altering local species diversity, and does so in a food web context. It provides one of the best empirical examples of the patch dynamics perspective and presents interesting links with food web ideas (e.g., Holt and Hoopes, chapter 3).

### Temporary Patches Distinct from a Background Habitat Matrix

Species in landscapes where patches vary in position both spatially and temporally may be strongly dependent on traits related to spatial dynamics such as dispersal and dormancy (Harrison and Taylor 1997). If patches are in constant positions across generations we are more likely to see selection for dormancy strategies than dispersal (McPeck and Kalisz 1998). However, if patches vary in location from generation to generation species will not necessarily be able to persist through becoming dormant. Pitcher plants form temporary patches of aquatic habitat, requiring dispersal of at least some of the inhabitants, which

range from bacteria to insects (Miller and Kneitel, chapter 5). Miller and Kneitel show that their system shows elements of dispersal-limitation (indicating patch dynamics) and species sorting. They review both local and regional dynamics using a variety of experimental and observational evidence. The inhabitants of water-filled tree holes (Kitching 2000) and fungal-fruitlet bodies (Worthen 1989) are other potential examples of this kind of community.

### Permanent Habitats with Indistinct Boundaries

The final category is the most elusive, consisting of systems in which habitats are more permanent and boundaries are less distinct. In such systems it is not always clear that spatial dynamics are necessary for persistence; however a variety of pieces of empirical work suggest that they are important. Davies et al. (chapter 7), describe an experimentally manipulated landscape containing *Eucalyptus* forest that was fragmented by planting woodland consisting of a nonnative species of pine. They show that assemblages of ground dwelling beetles are characterized by different population dynamics within fragments than in more spatially continuous habitat. Mass effects, where species move from the pine habitat matrix to the *Eucalyptus* fragments offer one potential explanation for their findings. It is a fascinating study system that shows excellent opportunities for further analysis. In other study systems species have been shown to readily disperse across habitat boundaries (e.g., weeds invading roadside areas in serpentine chaparral habitats; Harrison 1999). In systems with fuzzy boundaries between habitats, the degree to which spatial dynamics are relevant is likely to vary depending on the degree of habitat specialization. Habitat specialization influences the organisms' perception of habitat size and isolation (Harrison 1997). The Davies et al. study provides some evidence that metacommunity dynamics based on discrete local communities can help us to understand these situations, in part by encouraging authors to think about different patterns within their datasets.

We encourage readers to question the nature of evidence for metacommunity dynamics and how inference might be further improved. The coda section at the end of the book summarizes some of the emerging patterns that the editors perceive. It is apparent from the chapters in part 2 of this book that an empirical-theoretical synthesis is well under way, and that continuing this work offers a rich world of possibilities to a broad range of kinds of ecologists.

### Literature Cited

- Owson, P. 1998. Making sense of spatial models in ecology. Pages 151–166 *in* J. Bascompte, and R. V. Solé, eds. *Modeling spatiotemporal dynamics in ecology*. Springer Verlag, New York, NY.
- . 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

- Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in California serpentine chaparral. *Ecology* 78:1898.
- \_\_\_\_\_. 1999. Local and regional diversity in a patchy landscape: Native, alien, and endemic herbaceous serpentine. *Ecology* 80:70–80.
- Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics: a critical review. Pages 27–42. In I. Hanski, and M. E. Gilpin, eds. *Metapopulation dynamics: Ecology, genetics and evolution*. Academic Press, San Diego, CA.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.
- Kitching, R. L. 2000. *Food webs and container habitats: The natural history and ecology of phytoplankton*. Cambridge University Press, New York, NY.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. E. Hochberg, R. D. Holt, J. J. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez, A.. 2004. The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Loreau, M., N. Mouquet, and R. D. Holt. 2003. Meta-ecosystems: A theoretical framework for a spatial ecosystem ecology. *Ecology Letters* 6:673–679.
- McPeck, M. A., and S. Kalisz. 1998. On the joint evolution of dispersal and dormancy in metapopulations. *Advances in Limnology* 52:33–51.
- Meenanvar, L., and D. A. Jackson. 2001. History and taxonomy: Their roles in the core-satellite hypothesis. *Oecologia* 127:131–142.
- Mouquet, N., J. L. Moore, and M. Loreau. 2002. Plant species richness and community productivity: Why the mechanism that promotes coexistence matters. *Ecology Letters* 5:56–65.
- Taylor, A. D. 1990. Metapopulations, dispersal, and predator-prey dynamics: An overview. *Ecology* 71:429–433.
- Worthen, W. B. 1989. Effects of resource density on mycophagous fly dispersal and community structure. *Oikos* 54:145–153.

## CHAPTER 4

# Metacommunities of Butterflies, Their Host Plants, and Their Parasitoids

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The great bulk of population biological research on butterflies is focused on single species, but in reality butterfly populations are dynamically coupled with other populations representing species at higher, lower, and equal trophic levels. Often these interactions take place in fragmented landscapes because the focal butterfly may use only one or a few larval host plant species, which may be habitat specialists with fragmented distributions. Butterfly eggs, caterpillars, and pupae are attacked by a range of more or less specialized parasitoids (Dempster 1983; Shaw and Fitton 1989; Van Nieuhuys and Hanski 2004), which themselves host hyperparasitoids (parasitoids of the primary parasitoids). The behavior and population dynamics of the parasitoids are often influenced by the host plants of their host butterfly (Price et al. 1980; Vet and Dicke 1992; Hochberg and Ives 2000), so there are direct links between species on the first trophic level (plants) and species at the third trophic level (parasitoids). The patchy distribution of the host plants combined with the specificity of the butterflies and their natural enemies leads to metacommunity dynamics in the plant-butterfly-parasitoid assemblage, which often includes on the order of ten species. These species are typically interacting with yet other species, which may be less specific and whose populations are often less strongly spatially structured than the populations of the butterflies; their host plants and the specialist parasitoids. For instance, the host plants may support polyphagous herbivores in addition to the specialist butterflies, and all the insect species may be attacked by diseases, generalist arthropods, and vertebrate predators. Thus we view closely interacting species around the focal butterfly as embedded in a more comprehensive community made up of species that may have different spatial distributions than the focal plant-butterfly-parasitoid metacommunity. This may be a common situation in nature in general.

We present an overview of metacommunities associated with butterflies, with a particular focus on a well-studied species of checkerspot butterfly, the Glanville fritillary (Hanski 1999; Ehrlich and Hanski 2004). We illustrate several ecological processes taking place in metacommunities with examples drawn from the metacommunity of the Glanville fritillary and its host plants and parasitoids, including plant-butterfly interactions, the trade-off between competitive ability and dispersal rate/ability in competing species, tritrophic interactions involving the host