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Preface: Insects and plants in space

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During the past two decades, ecologists have increasingly recognised the importance of the spatial context in their studies of individuals, populations and communities (Levin 1992, Tilman & Kareiva 1997, Holt 2002). A rapidly expanding literature demonstrates how the spatial distribution of habitats can affect all aspects of ecology, from population genetics and single-species dynamics to community composition and evolutionary change (Hanski & Gaggiotti 2004). Spatial ecology is certainly "one of the most visible developments in ecology and population biology in recent years" (Hanski 1999: p. 261). In fact, it seems like very little in ecology makes sense except in the context of space.

Interactions between insects and their host plants have long been one of the most actively studied fields of ecology. But the question of how the interplay between plants and their herbivores is affected by the spatial setting is a rather recent one, with entries scattered in the literature. This volume provides our attempt at a unifying overview. It is, by no means, a thorough review of the subject field. What we want to achieve is something different: to stimulate research by compiling a set of papers illuminating the manifold impacts of space on insects on plants.

This volume was born out of a workshop held at the Tvärminne Zoological Station between 5 and 9 November 2004. The event was called *Spatial ecology of insect–plant interactions*. However, while editing this volume, we realized that we had arrived at quite an entomocentric perspective, and decided to rename it accordingly. Our focus is no doubt on the insect side of things. But the plants, and spatial variation in their quality, do form the necessary backdrop for the spatial ecology of herbivorous insects. Hence, paraphrasing Erkki Haukioja (2003), we have consciously tried to put the plant back into insect–plant interactions — a perspective that insect ecologists sometimes tend to forget.

The contents of this volume are structured around patterns and processes at three hierarchical levels: spatial variation in host plant quality, the dynamics and evolution of insect populations, and structure and processes in insect communities.

The opening section examines host plants as resource patches for insects. How different are plants from each other? Is host plant quality a key factor in generating spatial patterns in the abundance and distribution of insects? Denno *et al*. (2005) start by putting the question into perspective. Drawing on a large body of evidence from leaf-hoppers, they show that the relative importance of top-down and bottom-up forces may vary substantially in space, with the effects of host-plant quality dominating in some parts of the landscape and that of predators in others. Haukioja (2005) then draws attention to the variety of ways in which host plants may create spatiotemporal patterns in insect abundances. Perhaps most importantly, he emphasizes that host plants may not only limit insect abundances through direct bottom-up effects, but also through effects at higher tropic levels with reverberations travelling bottom-up, then down again. Mopper (2005) examines host plant quality from an evolutionary perspective. If host plant individuals differ enough from each other, local insect populations may actually become adapted to the specific characteristics of their host. While earlier work has revolved around insect attributes that may favour such local adaptation, Mopper focuses on the plant part. Perhaps, she argues, individual variation in plant phenology is the key dimension that insects adapt to. This emphasis on variation in host plant quality runs in interesting contrast with the contribution by Gripenberg and Roslin (2005). They show that for a host-specific moth, individual host trees form patches of similar quality, and that the local presence or absence of the moth is more affected by the exact location of the tree than by its quality. In the final paper in this section, Singer and Wee (2005) use checkerspot butterflies to examine spatial patterns of insect–host plant associations. Just as the opening study by Denno *et al*. (2005), they show how the relative strength of different processes varies in space — in this case with the spatial scale examined. As scale increases, the role of insect behaviour in generating spatial pattern decreases, and that of population dynamics increases.

The second section of this volume centres on the structure and dynamics of herbivorous insect populations. Weisser and Härri (2005) show just how dynamic insect populations on plants may be, with frequent extinction and colonisation events occurring at every level examined: from individual ramets of the host plant to islands occupied by thousands of ramets. The long-term persistence of such a system can only be attributed to colonization events balancing extinctions in a metapopulation context. Hanski and Meyke (2005) then review processes and patterns in one of the so far best-studied metapopulations: the Glanville fritillary butterfly inhabiting dry meadows with its two host plant species. The authors illustrate the importance of spatial structure by contrasting time series from larger areas with processes occurring within individual meadows. While many classical analyses concern aggregate populations from large areas, such spatial averaging will unavoidably mask many causal processes acting at finer spatial scales. Roland (2005) uses fine-scale resolution for another purpose. By examining short time series from multiple sites, he analyzes how the configuration of the surrounding landscape affects central population parameters in the forest tent caterpillar. Importantly, he finds that forest cover (and hence forest fragmentation) affects the parameters of density dependence in the moth, probably through effects on the movements of its parasites. The closing study in this section also emphasizes interactions among herbivorous species and their parasites. Harrison *et al*. (2005) model spatio-temporal patterns in the outbreaks of two insect species sharing the same host plant. By including interactions among the plant, the herbivores and their natural enemies, they are able to predict — and to empirically confirm — several patterns in the abundance of herbivorous insects.

The third section in this volume ventures deeper into the fascinating field of multispecies interactions, examining spatial structure and processes in insect communities on plants. Tscharntke *et al*. (2005) first review fluxes of insects between different parts of agricultural landscapes. They document how strongly the abundance and distribution of species in a given habitat may be affected by processes in the surrounding landscape, with profound implications for local community structure and functioning. This study is complemented by a review by van Nouhuys (2005), who examines variation in the ways insect species respond to landscape context in general, and to habitat fragmentation in particular. She argues that although the sensitivity of a species might generally increase with rising trophic level, this relationship is significantly blurred by several species-specific factors such as resource breadth and dispersiveness. Morris *et al*. (2005) then focus on a particular type of interspecific interaction — apparent competition, as mediated by natural enemies shared among multiple herbivorous species within a community. In this work, the inclusion of a spatial component has only recently begun, but Morris *et al*. suggest a way forward. Finally, Novotny and Weiblen (2005) take the step from a population-centred approach to patterns at the level of species richness. Focusing on species turnover among sites, they argue that few spatial patterns will be caused by the dispersal limitation of herbivorous insects, but rather by specificity to local conditions. Given the scarcity of direct observations on insect dispersal, this study ends our volume with an implicit plea for further studies of the dispersal of herbivorous insects.

When read from cover to cover, we trust that this volume will provide one clear-cut take-home message: that spatial location affects all aspects of insect–plant interactions, from the daily fate of a single larva to the long-term evolution of the local insect community. At the same time, it suggests several avenues for future research. While we hope that every reader finds several specific ideas to tickle his or her imagination, we would like to comment on three needs that we, ourselves, find particularly urgent to address. The first one relates to dispersal. If we do not know the capacity of a species to traverse the landscape, we cannot understand its response to the spatial context (Levins 1968). While almost every study in this volume makes explicit reference to dispersal, very few include rigorous estimates of the scale over which it occurs. Much work is needed before we can say anything general about the dispersal capacity of different insect taxa. This will be hard to accomplish, but our toolbox is rapidly being replenished (Turchin 1998, Bullock *et al*. 2002, Ovaskainen 2004). The second need concerns the inclusion of multispecies interactions. Again, almost every paper in this volume illustrates how several species influence each other simultaneously — not only the plant and the insect that feeds on it, but several insect species and several trophic levels both above and below them. Attempts to model and understand how space enters these complex interactions has only just begun (e.g. Tscharntke & Hawkins 2002), but the potential reward is clearly illustrated by the papers of e.g. Harrison *et al*. (2005) and Morris *et al*. (2005). In this context, the potential for host-plant mediated effects to traverse several trophic levels emerges as an intriguing perspective (van Nouhuys & Hanski 2002, Haukioja 2005). Finally, two chapters illustrate the need for us to get down to lower latitudes. The study by Novotny and Weiblen (2005) shows the urgent need for direct studies on insect dispersal in tropical environments; the chapter by Morris *et al*. (2005) provides a refreshing illustration of how experimental studies can be conducted in a tropical rain forest environment. After all, this is where most insect–plant interactions occur (Erwin 1982, Ødegaard *et al*. 2000, Novotny *et al*. 2002).

In conclusion, while this volume just potentially provides a glimpse of the state of the art in an emerging field, it certainly shows that there is much left for us to do. Good science generates new questions, and we hope that this volume raises several. With this task completed, we should end by acknowledging the invaluable contribution of a large number of authors and institutions. The volume itself was sponsored by the Metapopulation Research Group and the Spatial Ecology Programme at the Department of Biological and Environmental Sciences. Both organizations receive their core funding from the Academy of Finland, to which we extend our warmest thanks. We would also like to thank the Tvärminne Zoological Station for providing such a nice venue for the workshop. A large number of authors and reviewers worked hard to produce this volume — we are deeply indebted to all of them. Finally, we would like to acknowledge the invaluable contribution of Krzysztof Raciborski, our meticulous technical editor, who took great pride in producing the neat and visually attractive print product that you now hold in your hands.

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