Editorial

A special issue on insect habitats

This issue arises from concerns that we have about how habitats for insects are defined, especially in the application of landscape scale studies to their conservation. If habitats are only partially or are inappropriately defined then the predictive power and interpretation, – the scaling of components – of landscape studies becomes questionable. Furthermore, attempts to define habitats using the wrong measures will not lead to successful conservation of single species, let alone multi-species assemblages. These concerns have been outlined in recent papers (Dennis et al. 2003, in press; Shreeve et al. 2004). Primarily they focus on four issues: (i) the common practice of treating vegetation units as surrogates for habitats in landscape scale studies, (ii) the assumption that all resources required by an organism are contained in a hostplant patch for phytophagous insects, (iii) the preoccupation with quantity (size) of resources and their spatial arrangement at the expense of the quality of those resources and (iv) the neglect of the intervening ground, the so-called matrix, in the function of population units at the landscape scale. Although most of these issues emerged from a butterfly perspective, they are equally relevant to other organisms and require careful examination in the shift from concern over single species to species assemblages involving different trophic levels.

The papers in this issue, ranging over five insect orders (Coleoptera, Lepidoptera, Hymenoptera, Orthoptera and Diptera), usefully illustrate some of the problems in applying 'habitat' as a concept. Habitat is not just a convenient term or label but requires fundamental understanding to underpin the conservation of insects in a rapidly changing environment. Elements of the four issues mentioned above arise in the contributions:

Vegetation units, habitats and biotopes

There is clearly a mismatch between vegetation units and insect habitats, and a habitat can be made up of very different vegetation types (e.g., the butterflies *Plebejus argus* L., Dennis 2004; *Callophrys rubi* L., Vanreusel and Van Dyck unpublished data); even so, two of the contributions usefully show how vegetation units can be applied to understanding spatial dynamics of organisms. Goulson et al. illustrate this nicely in relation to generalist and specialist bumblebees in Britain and New Zealand; they show how rare species are not always biotope specialists and that generalists can become specialists from loss of certain biotopes (e.g., *Bombus subterraneus* and *B. distinguendus*). Other biotopes provide refuges (e.g., coastal fringe) from being relatively unaffected by human pressures. Clearly, the issue here from the perspective of how insects interact with the environment is one of scale; critical to the specialism in bees is the availability of resources within biotopes. Rarity is also demonstrated to be not just an edge of range issue, but can affect range centres (Shreeve et al. 1996) as some bumblebees are rare wherever they occur; there is likely to be biotope bias in this process of centre of range rarity that is associated with their value as a human resource and their vulnerability to interference. Such rarity, when not easily explained, as in the case of many bumblebees, evokes the concept of habitat based on resources (Dennis and Shreeve 1996); the implication is that a resource(s) is missing, something that only autecological research on the affected species can disclose. Although increasing the size of biotope classes, by categorising vegetation units to a higher level, may increase the probability that the biotope includes all the relevant resources for a species this is not guaranteed. The second paper is a far-reaching continental-scale analysis by van Swaay et al. on trends in butterfly populations in relation to broad biotope occupancy (i.e., grasslands, woodlands, wetlands) and the threats to those biotopes. It is a sobering account of wholesale losses and the impact on biodiversity. This multi-species or species assemblage view is, in our opinion, essential for the preservation of diversity in Europe and we return to this issue

below. However, although the biotope perspective is useful in determining large-scale changes it has to be borne in mind that small organisms, like insects, respond, at the species level, to far finer grained changes of resource abundance and distribution. Thus, at the biotope level there is no expectation that all components of a biotope will show similar responses to changes within that biotope. From an evolutionary perspective this is not surprising; our current biotopes and broad communities represent unique assemblages that have not occurred within previous interglacials (Tallis 1991; Dennis et al 1995; West 1977; Huntley 1988).

Resources and host patches

The conjunction of all resources for a phytophagous organism with a vital host resource for early stages is clearly an important one for landscape scale studies (e.g., metapopulations) based on hostplant patches (e.g., Hanski and Thomas 1994; Brommer and Fred 1999; Gutierrez et al. 2001; Anthes et al. 2003). It may also have relevance for non-phytophagous insects' dependence on hosts. This issue arises in three contributions. Maes et al. nicely illustrate resource use in a grasshopper (*Oedipoda caerulescens*) and a butterfly (*Hipparchia semele*) and the difference in dependence on resources not necessarily coinciding with food supplies, viz., shelter and therefore scrub development among dunes in Belgium. What is neat about this work is that it demonstrates different resource requirements not just by the different sexes but different phenotypes of the same sex in different weather conditions; different colour morphs of *O. caerulescens* occupy different areas in relation to their need for thermoregulation and anti-predator resources that vary with weather conditions. In a second contribution, Fayt et al. disclose the difference in dependence of two saproxylic insect groups (longhorn beetles and hoverflies) on adult resources (nectar supplies), and therefore on different light conditions, but which share dependence on dead wood for early stages. Shaw in his perceptive contribution on parasitic wasps documents resource requirements for this higher level trophic group and how these differ for ecological divisions such as idiobionts (parasitoids preventing their hosts to grow any further) and koinobionts (parasitoids allowing their hosts to continue growth).

Habitat quality vs. patch size and spacing

The importance of resource quality in habitat patches is becoming increasingly recognised (Dennis and Eales 1997, 1999; Thomas et al. 2001); this extends to conditions outside so-called habitat patches in the matrix (Dennis 2004). Resource quality, as a direct issue, emerges in contributions by Fowles and Smith on *Euphydryas aurinia*, Shaw on parasitic wasps and Fayt et al. on saproxylic hoverflies and longhorn beetles. Fowles and Smith analyse the metapopulation structure of *E. aurinia* in Wales (UK) and in doing so identify five supporting grassland categories (different management regimes) occupied by the larval hostplant; these categories maintain very different densities of the target species. Shaw's contribution vitally raises our awareness of resource range in relation to the ecological divisions for parasitic wasps; quality is manifestly affected by host species and it is also affected by human impact such as agrochemical toxin inputs. As Fayt et al. demonstrate, resource (habitat) quality for Belgian saproxylic longhorns and hoverflies is an issue at local and landscape scale; overmature tree retention, simulating light conditions in ancient woodland, wind-throw at local scale, and reduction of conifer load at landscape level, are all significant factors in explaining saproxylic insect diversity. A recent study on parasitoids associated with saproxylic beetle hosts in boreal spruce-dominated forests in Sweden has indeed indicated that only a management strategy promoting the widest diversity of dead wood types would preserve the entire ichneumonoid assemblage, and that the sensitivity of parasitoids to vegetation management is greater than that of their hosts (Hilszczański et al. 2005). Just how the matrix matters to species' ecology has been considered recently by Dennis et al. (in press.). For many species, the matrix, with the right management, can be converted into vital habitat. This has profound implications for con- servation strategies; recognition of the potential of the matrix and its modification may make con- servation more successful at the landscape scale than a narrow focus on isolated reserves. Fowles and Smith indicate just what this means for a

minimum viable metapopulation for Welsh *E. aurinia*.

Multi-species vs. single species approaches

If the task of conservation were limited to a few species, a species by species approach based on detailed autecological research would be entirely appropriate. Even then, it is a mammoth task identifying and conserving resources for a single species. Unfortunately, the task is nothing like so simple. A vast number of species of many orders are involved and the resources for survey and management are desperately limited. The potential losses are well illustrated by van Swaay et al.'s contribution on diversity losses among European butterflies for broad classes of biotopes. This fundamental problem is well illustrated by two of the contributions from government organisations, the Countryside Council for Wales (CCW) and English Nature (EN). Fowles and Smith (CCW), in a no-nonsense approach to the practical problems of surveying and decision making with few resources, demonstrate the difficulties in conserving the butterfly *Euphydryas aurinia* in Wales. Because of the large area to be surveyed it has been necessary to apply 'quick-and-dirty' surveying classes to 'field' units rather than survey resources directly. The findings nevertheless are vitally important, if distressing; the butterfly is faced with systematic changes to grassland biotopes that are eroding the quality of resource units in whole metapopulations, many of which now carry extinction debt. For many insect species we simply do not have information on their resources. Recently there has been an effort to collect biological data on them, as for British butterflies, so as to predict their response to environmental changes (Shreeve et al. 2001; Dennis et al. 2004). Here, Webb and Lott (EN) describe an ambitious, but absolutely essential, programme to develop a habitat-based invertebrate assemblage classification system (ISIS). The objective is to produce an invertebrate assemblage system for English terrestrial and freshwater systems for assessing the quality and conditions of sites for conservation. This approach, based on expertise from a large number of specialists, recognises the sheer scale of multi-species conservation, and the need to fuse botanists and entomologists into working part-

nerships. It hits at the practical dimension, as does Fowles and Smith's concern with *E. aurinia*, in ensuring that work can be easily put into practice, but on the daunting scale of all invertebrates. These two pieces of practical conservation hold a sobering message for academic research: we need to be able to translate elegant models and concepts into practical solutions. If our research fails to do that, then it is not much use for conserving biodiversity.

At this multi-species scale we need to consider the implications of species' habitats. We know that habitats comprise a range of resources, that they do not neatly coincide with single vegetation units, and that resources vary in quality within and between vegetation units (Dennis et al. in press). The challenge is to provide simple measures of resource availability for multi-species contexts. The ISIS system offers the opportunity of developing indicator species that measure the availability of resources at sites and of providing quick assessments of changes. In doing this, it has the remit of addressing variability in resources for species occupying specific environmental conditions. It soon becomes clear that for this work no single insect group (order) is sufficient as an indicator group. True enough, perhaps, butterflies are excellent indicators of broad scale changes to the environment, such as climate change and wholesale losses in extent and quality of broad vegetation classes (Thomas 2005). But, at a finer scale of individual vegetation units (e.g., National Vegetation Classification units of the UK, Rodwell 1991 *et seq*.) they are not sufficiently speciose or ecologically diverse to do the job (Maes and Van Dyck 2005). This is well illustrated by the contribution of Fayt et al. on saproxylic longhorn beetles and hoverflies. As for indications as to what is actually happening to sites and whole landscapes, there are two levels infrequently addressed but of great importance. A crucial aspect to change is what is happening to different trophic levels. Shaw's contribution is of particular importance here, because this 'layer above', of parasites, is given insufficient attention. One of the first signs of a failing landscape will almost certainly be at the higher levels of dependency and Shaw's call for research on the ecology of parasites should ensure that they too are firmly embedded in the ISIS system for site appraisal. Another aspect of change is a strategic interpretation of what is likely to

happen in different environments. Studies of C-S-R strategies in British butterflies (Hodgson 1993; Dennis et al. 2004) indicate that species founded on different strategies differ in vulnera- bility to environmental changes. This finding is echoed here at a higher trophic level for carnivo- rous beetles in an intriguing contribution by Eyre: there are strong elements of disturbance and pro- ductivity in carnivorous beetle assemblages as well as in phytophagous insects. However, there are other aspects to this that are beyond the scope of this special edition. The way that community functionality and species dynamics change in relation to environmental changes and resource losses and changes will be partly determined by the relative importance of interactions between species of different trophic levels. Systems dominated by 'top–down' interactions are likely to respond differently to those dominated by 'bottom–up' interactions (e.g., Polis and Strong 1996; Gurev-itch et al. 2000). Whilst higher trophic levels may give the first indications of failing landscapes, the consequences for the lower trophic levels will differ dependent on which mechanism dominates. Knowledge of these aspects in reality, as opposed to theory, is limited.

From the contributions in this special edition and their contextual background it is clearly evident that there is a long way to go in under-standing the importance of resources to defining habitats and thus understanding how species respond to environmental changes. The message emanating from these studies is that such faunal heterogeneity requires resource heterogeneity and multi-species approaches to maintaining species diversity. Perhaps the greatest challenge is in translating the developing recognition of the scale of insect resources into practical conservation, where the focus remains primarily on vegetation based habitat units or biotope approaches.

We suggest that there are three issues that need a co-operative approach from invertebrate con-servationists. The first is to develop our under-standing of whether there are common factors that drive insect strategies, and thus their co-occurrences. The second is an urgent need to develop openly accessible databases of insect resource requirements, facilitating understanding of the potential from the microhabitat to the landscape scale. The third is to develop a com-prehensive, reliable and complementary set of indicator taxa coming from different trophic levels and ecological groups (plants, vertebrate and invertebrate species; Kotze and Samways 1999). Without these we will not understand how species respond to anthropogenic influences and we will not be able to halt the acceleration in biodiversity loss by 2010, a commitment made by 190 countries at the 2002 Johannesburg World Summit on Sus-tainable Development.

References

Anthes N., Fartmann T., Hermann G. and Kaule G. 2003. Combining larval habitat quality and metapopulation struc-ture – the key for successful management of pre-alpine *Euphydryas aurinia* colonies. J. Insect Conserv. 7: 175–185.

Brommer J.E. and Fred M. 1999. Movement of the Apollo butterfly *Parnassius apollo* related to host plant and nectar plant patches. Ecol. Entomol. 24: 125–131.

Dennis R.L.H. 2004. Butterfly habitats, broad-scale biotope affiliations, and structural exploitation of vegetation at finer scales: the matrix revisited. Ecol. Entomol. 29: 744–752.

Dennis R.L.H. and Eales H.T. 1997. Patch occupancy in *Coenonympha tullia* (Lepidoptera: Satyridae): Habitat quality matters as much as patch size and isolation. J. Insect Con-serv. 1: 167–176.

Dennis R.L.H. and Eales H.T. 1999. Probability of patch site occupancy in *Coenonympha tullia* (Mü ller) (Lepidoptera: Satryinae) determined from geographical and ecological data. Biol. Conserv. 87: 295–301.

Dennis R.L.H., Hodgson J.G., Grenyer R., Shreeve T.G. and Roy D.B. 2004. Host plants and butterfly biology. Do host-plant strategies drive butterfly status? Ecol. Entomol. 29: 12–26.

Dennis R.L.H. and Shreeve T.G. 1996. Butterflies on British and Irish Offshore Islands: Ecology and Biogeography. Gem Publishing, Wallingford, Oxon.

Dennis R.L.H., Shreeve T.G. and Van Dyck H. 2003. Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos 102: 417–426.

Dennis R.L.H., Shreeve T.G. and Van Dyck H. 2005. Habitats and resources: the need for a resource-based definition to conserve butterflies. Biodiver. Conserv. in press.

Dennis R.L.H., Shreeve T.G. and Williams W.R. 1995. Taxo-nomic differentiation in species richness gradients among European butterflies (Papilionoidea, Hesperioidea): contri-bution of macroevolutionary dynamics. Ecography 18: 27–40.

Gurevitch J., Morrison J.A. and Hedges L.V. 2000. The inter-action between competition and predation: a meta-analysis of field experiments. Am. Nat. 155: 435–453.

Gutierrez D., Leon Cortes J.L., Menendez R., Wilson R.J., Cowley M.J R. and Thomas C.D. 2001. Metapopulations of four lepidopteran herbivores on a single host plant, *Lotus corniculatus*. Ecology 82: 1371–1386.

Hanski I. and Thomas C.D. 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to but-terflies. Biol. Conserv. 68: 167–180.

Hilszczañ ski J., Gibb H., Hjä´ lte´ n J., Atlegrim O., Johansson T., Pettersson R.B., Ball J.P. and Danell K. 2005. Parasitoids (Hymenoptera, Ichneumonoidea) of saproxylic beetles are affected by forest successional stage and dead wood charac- teristics in boreal spruce forest. Biol. Conserv. 26: 456–464.

Hodgson J.G. 1993. Commonness and rarity in British butter-flies. J. Appl. Ecol. 30: 407–427.

Huntley B. 1988. Europe. In: B. Huntley and T. Webb (eds), Vegetation History. Kluwer Academic Publishers, Dordr-echt, pp. 341–383.

Kotze D.J. and Samways M.J. 1999. Support for the multi-taxa approach in biodiversity assessment as shown by the epigaeic invertebrates in a Afromontane forest archipelago. J. Insect Conserv. 3: 125–143.

Maes D. and Van Dyck H. 2005. Habitat quality and biodi-versity indicator performances of a threatened butterfly versus a multispecies group for wet heathlands in Belgium. Biol. Conserv. 123: 177–187.

Polis G.A. and Strong D.R. 1996. Food web complexity and community dynamics. Am. Nat. 147: 813–846.

Rodwell J.S. 1991. *et seq*. British plant communities, Vol. 1–5. Cambridge University Press, Cambridge.

Shreeve T.G., Dennis R.L.H. and Pullin A.S. 1996. Marginal-ity: scale determined processes and the conservation of the British butterfly fauna. Biodiver. Conserv. 5: 1131–1141.

Shreeve T.G., Dennis R.L.H., Roy D.B. and Moss D. 2001. An ecological classification of British butterflies: ecological attri-butes and biotope occupancy. J. Insect Conserv. 5: 145–161.

Shreeve T.G., Dennis R.L.H. and Van Dyck H. 2004. Resources, habitats and metapopulations – whither reality? Oikos 106: 404–408.

Tallis J.H. 1991. Plant Community History. Chapman and Hall, London.

Thomas J.A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Phil. Trans. R. Soc. Lond. B 360: 339–357.

Thomas J.A., Bourn N.A.D., Clarke R.T., Stewart K.E., Simcox D.J., Pearman G.S., Curtis R. and Goodger B. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proc. R. Soc. Lond. B 268: 1791–1796.

West R.G. 1977. Pleistocene Geology and Biology. Longmans, London.

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