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A global perspective on conserving butterflies and moths and their habitats

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Just living is not enough, said the butterfly, one must have sunshine, freedom and a little flower.
— Hans Christian Andersen

Introduction

Lepidoptera are one of the four major insect orders, and one of the best studied invertebrate groups, containing over 160,000 described species and an estimated equal number of undescribed species, arranged in 124 families (Kristensen et al. 2007). Lepidoptera occupy all except the very coldest terrestrial regions, but the Neotropics and Indoaustralian region have five times more species per unit area than the Palaearctic and Nearctic, and three times more than the Afrotropical region (Heppner 1991). They are scale-winged insects, traditionally divided into three major assemblages: micro-moths, butterflies and macro-moths (Kristensen et al. 2007).

The order represents a mega-diverse radiation of almost exclusively phytophagous insects, probably correlated with the great diversification of flowering plants since the Cretaceous (Menken et al. 2010). They provide many vital and economically important services within terrestrial ecosystems (e.g. nutrient recycling, soil formation, food resources and pollination). The scale of these contributions is illustrated by the estimate that blue tit (*Parus caeruleus*) chicks consume at least 35 billion caterpillars each year in the UK alone (Fox et al. 2006). Lepidoptera also have considerable human significance, both economic and scientific. A growing industry farms pupae for supply to butterfly houses across the world. One moth species has been domesticated in order to provide silk (i.e. *Bombyx mori*

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from the wild *B. mandarina*). For scientists, the group offers a model system valuable to studies of biodiversity conservation, ecology, ethology, genetics, (co)evolution and systematics (Samways 1995; Boggs et al. 2003).

Human appreciation of the beauty and vulnerability of (especially) butterflies has grown exponentially in recent decades, particularly in developed nations. For example, among the 40 national biodiversity mapping schemes extant in the UK, more than 2.5 million records were submitted for Lepidoptera thanks to the work of the Centre for Ecology and Hydrology, Rothamsted Research and Butterfly Conservation (BC) UK, with key input from amateur enthusiasts (butterflies 2.2 m; macro-moths 384 k) prior to 2000, roughly double the number received for all other invertebrates combined, or indeed for birds (1.2 m) (Thomas 2005). Despite a burgeoning interest in UK moths that has seen 12.4 million records amassed by over 5000 volunteer recorders in recent years (BC's Moths Count initiative) (see Chapter 8), butterflies are currently (and regrettably) probably the only taxon of terrestrial invertebrates across much of the world for which it is realistic to assess the scale and rates of change in species' ranges or populations (Lewis & Senior 2011). For the same reason, butterflies have been successfully used as charismatic flagships and umbrella species (see Box 14.1) in insect conservation programmes (New 1997; Thomas & Settele 2004; Fleishman et al. 2005; Guiney & Oberhauser 2009).

Long-term change in populations of Lepidoptera

Rates and causes

Before discussing practical conservation of Lepidoptera, it is necessary to consider their known rates and causes of change, and whether these are representative of other insect species (Thomas & Clarke 2004; Fleishman et al. 2005). In the UK, which has the longest history of rigorous recording, butterfly populations have changed dramatically since the 1850s. Some species have increased their range but most have declined, and 7% of British species are extinct. The mean decline in butterflies has been an order of magnitude greater than that of birds or vascular plants (or, where monitored, mammals), whether measured at the scale of single sites, regions or the entire nation (Thomas et al. 2004). Moreover, until the recent application of ecological principles to conservation described below, local extinction rates on nature reserves often exceeded those on commercially managed land, in sharp contrast to the stability achieved for vertebrates and plants (Thomas 1991).

The four methods of assessment available in the UK (Red Data Books (RDBs), species surveys, mapping and population monitoring schemes) are of shorter antiquity elsewhere but it is clear that UK declines are typical of other developed nations, and are exceeded by some (Maes & Van Dyck 2001). In The Netherlands, for example, 24% of 71 butterfly species became extinct during the 20th century while the number of breeding birds increased by 20% (Thomas 1995).

There is some debate as to whether butterflies are indicators of change in other insects: Hambler & Speight (2004) argued that butterflies have suffered higher extinction rates than other invertebrates according to UK RDBs; Thomas & Clarke (2004) attributed this discrepancy to an artefactual underestimate of decline inherent in comparing poor with well-sampled taxa, and showed that butterflies experienced similar extinction rates to other groups when sampling intensity is factored in. Moreover, observed extinction rates in dragonflies, bumblebees and macro-moths have unequivocally been slightly higher than those of UK butterflies (Thomas 2005; Conrad et al. 2006). Whilst clearly unrepresentative of certain species and functional types, because of their popularity, ease of study (e.g. conspicuous, day-active, often identifiable in the field) and patterns of species richness and endemism that mirror those of many other insects, butterflies are increasingly used as indicators of change in other taxa in Europe and to a lesser extent elsewhere.

Butterflies may be useful indicators of habitat change (Ricketts et al. 1999). We distinguish two types of indicator (Thomas et al. 2005): (i) the 'miners' canary' whose decline heralds future losses for less sensitive species; and (ii) taxa which mirror change or predict the presence (Fleishman et al. 2005) of poorly monitored organisms. Across Europe (Erhardt & Thomas 1991; Thomas 2005), butterflies in general are early warning systems for future change in vertebrate (apart from mega-fauna) and vascular plant populations. One family of butterflies, the Lycaenidae, provides ultra-sensitive indicators of coming change in other families, because many of them need two specialized larval resources (foodplants, ants) to co-occur (Thomas et al. 2005). We therefore advocate the application of standardized mapping and population monitoring schemes in nations where such schemes are absent, and the monitoring of other arthropod taxa.

Drivers of change

Of the main drivers of global biodiversity loss, the spread of exotic pest species and direct over-exploitation by humans have had negligible detectable impacts on populations of Lepidoptera (e.g. Collins & Morris 1985). So the banning of trade and collecting – the main measure applied in many nations today and for the first century of conservation practice in the UK – is inappropriate (unless coupled with habitat conservation), because it fails to account for the very different population dynamics and life-history traits of insects compared with vertebrates and many plants (Thomas 1995). This resilience arises because Lepidoptera populations typically have high intrinsic rates of increase wherever the quality of habitat is high, with individual females laying many eggs which subsequently experience high density-dependent mortalities (in unperturbed populations), especially in the later larval stages, allowing numbers to recover quickly if the previous generation of adults was depleted by collectors. Furthermore, collectors are seldom able to remove more than a small proportion of the effective breeding population of adult Lepidoptera per generation, because in most studied species the majority of eggs are laid within 2–5 days of each female's emergence, and for species with discrete generations, the short-lived individuals emerge over a period of 4–8 weeks.

Habitat loss, undoubtedly the prime culprit (Stewart et al. 2007), can broadly be divided into two processes (Thomas 1991): (i) the destruction of primary and species-rich secondary ecosystems by intensive modern agriculture, exotic-species forestry, mining, armed conflict and illicit crops (Dávalos et al. 2011) and, to a lesser extent, urbanization; (ii) the reduced size, increased isolation and degradation in quality of those fragments of potentially inhabitable biotopes that survive. The first process effectively eliminates all populations apart from pests of crops and exploiters of ruderal plants. The second is less clear-cut but equally harmful, especially in developed regions (see below).

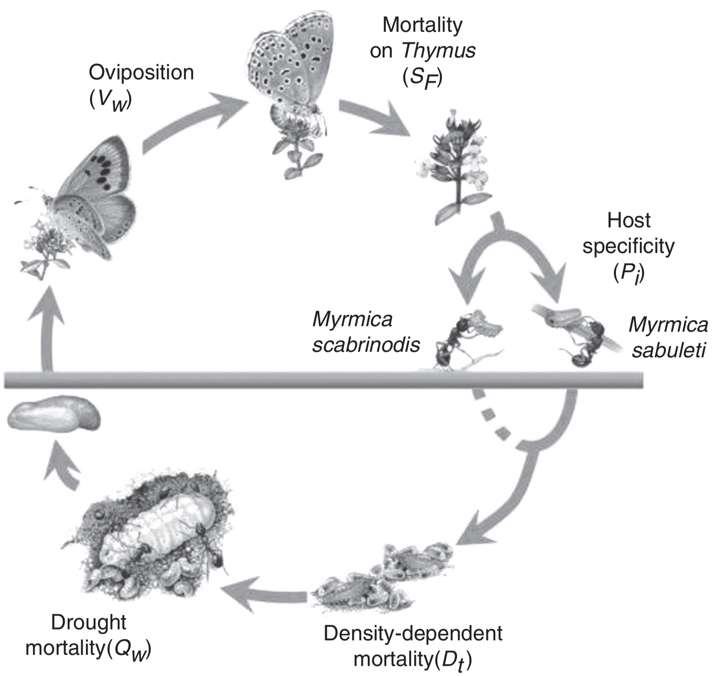
Another driver of population reductions is climate change. Its observed impacts on Lepidoptera are relatively minor so far but it is predicted to rival habitat change (with which it interacts) in future decades (van Swaay et al. 2010a). Already in the Holarctic, non-migratory species have shown southern or lowland contractions that exceed their northward or altitudinal shifts in ranges (e.g. Parmesan et al. 1999), whilst similar altitudinal shifts are detectable in moth communities in Borneo (Chen et al. 2009). The net impacts on Lepidoptera of future climate and land use changes are rightly a research priority.

Single-species conservation

Compared with tropical regions, species richness within temperate biomes is generally much lower, both in ecosystems as a whole and among the taxa they support. Lower diversity has undoubtedly made it easier to name and understand a large proportion of temperate

Box 14.1 From single-species to community and landscape conservation: *Maculinea arion* in the UK

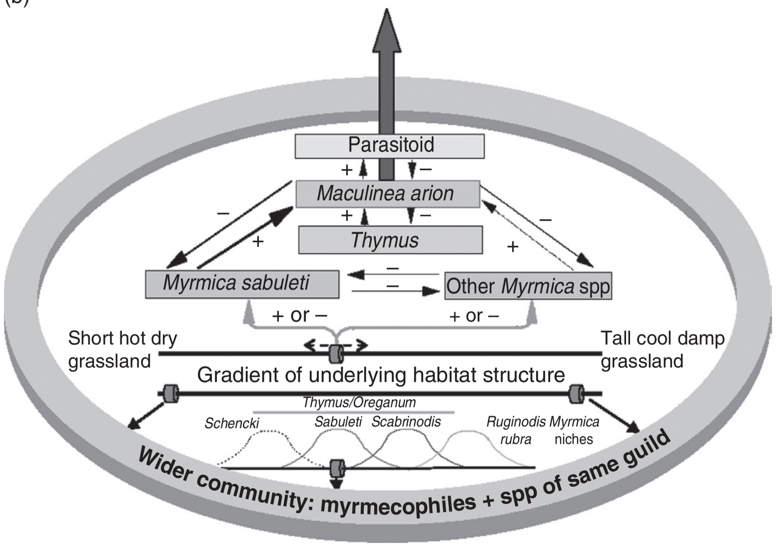
(a)



$$a_{t+1} = a_t S_F (P_{sab\,(t)} + cP_{sab\,(t)})\, D_t\, Q_w\, V_w$$
$$\text{where } D_t = a - b\, log(L_t/R_t)$$

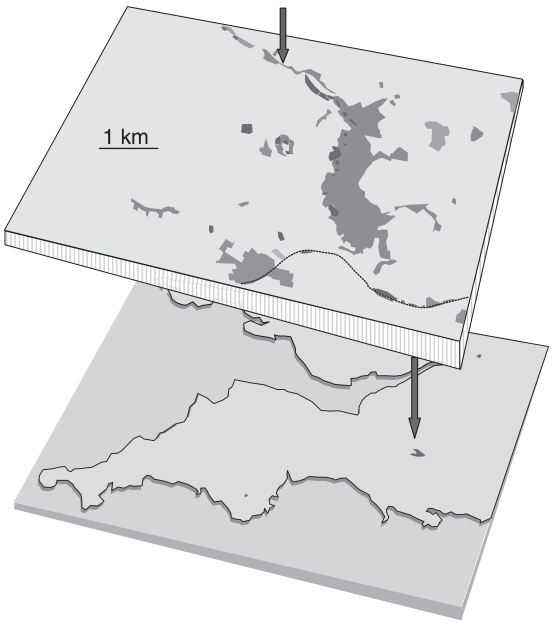
(a) *M. arion* is a globally threatened flagship butterfly with specialized larvae that briefly eat *Thymus* flowers before inhabiting *Myrmica* ant nests, where they prey on ant brood. A 6-year study identified and modelled the parameters driving its population dynamics (see Thomas et al. 2009 for symbols). The key discovery was its host specificity to one ant, *Myrmica sabuleti*, rather than to any *Myrmica* species.

(b)



(c)

(d)



(b) Different *Myrmica* ants occupy different niches within grassland; *M. sabuleti* dominates in warm short swards under UK climates. Land use changes resulted in the abandonment of most sites causing *M. sabuleti* to disappear or be displaced by unsuitable congeners, causing *M. arion's* extinction in the UK in 1979. Targeted conservation management shifted the sward structure (indicated by the position of sleeves along the habitat gradient in the diagram) back to the optimum for *M. sabuleti*, which quickly returned to dominate the turf. *M. arion* was then reintroduced from Sweden and increased rapidly, closely matching model predictions on 21 tested sites (Thomas et al. 2009, 2011). Not only did *M. arion's* immediate community of interacting rarities benefit, but the restoration of a disappearing type of habitat caused other Biodiversity Action Plan organisms belonging to the same guild to recover, including threatened plants, insects and birds.

(c) The collateral benefits from *M. arion* restorations justified conservationists in applying similar targeted management across the landscape, including the restoration of calcareous grassland and the creation of new habitat on railway constructions. *M. arion* has spread to 25 sites (dark patches), forming a meta-population of loosely connected colonies, as have other priority species. Mid-grey indicates woodland plantations form which most sites were restored.

(d) Today, similar programmes are being initiated in the other UK landscapes formerly inhabited by *M. arion*. In all regions, some sites are deliberately managed to create heterogeneous and suboptimal (but suitable) swards for *M. arion*, to buffer the new communities from extreme weather and to prepare for future climate change.

Part (a) adapted with permission from Thomas et al. (2009)

biodiversity, a process that began with the rise of 'natural history' in Europe during the 1700s. Hence, there is much more knowledge on distribution, ecology and life-history of Lepidoptera, and of many more species, in temperate regions than in the intrinsically more diverse tropical regions, where a significant percentage of taxa remains undescribed. Today, many temperate countries have valid Red List assessments of nearly all butterfly species, and in Europe there is even a continental Red List (van Swaay et al. 2010b) whereas tropical countries do not, or rather, only of subsamples (see below). However, only Norway and Finland have national Red Lists for moths, although other developed countries are considering them.

By contrast, tropical birds and mammals have received considerable attention, both because they are more popular and because their combined global species richness is only 5% of that estimated for Lepidoptera. The relatively small numbers of species-specific conservation actions in the tropics mainly focus on these popular taxa, whereas most species-specific conservation research is done within temperate regions. The lack of the ecological knowledge necessary for species-specific actions for tropical Lepidoptera, combined with financial constraints, may explain the contrast between conservation efforts for them (mainly as ecosystem protection) and in the west (mainly as species action plans) (New 2009; Bonebrake et al. 2010).

The current and welcome increase in species-specific research and action plans mainly focuses on regionally threatened habitat specialists, confined to rare biotopes within generally small nature reserves. The prospects for the insects targeted are improved by specific management measures applying evidence-based science. Although now well established, the introduction of ecological research to practical management marked a paradigm shift in Lepidoptera conservation (Hanski 1999). It resulted in the first successful recovery programmes of endangered species, following a >100-year period of failed (simpler) approaches such as the regulation of collecting and the establishment of biotopes as nature reserves without recourse to managing their internal structures or successional dynamics (Thomas 1991). In the UK, it is arguable that five butterfly species (*Satyrium pruni*, *Polyommatus bellargus*, *Hesperia comma*, *Melitaea athalia*, *Papilio machaon*) have been saved from national extinction by science-based management since the 1970s–90s, whilst three nationally extinct, globally threatened *Maculinea* species have been re-established on specifically managed sites in the UK or The Netherlands (Thomas et al. 2011; Wynhoff et al. 2011).

The single-species approach has therefore had several benefits. First and foremost, it has succeeded for several declining butterflies, whereas biotope protection *per se* historically failed to maintain them, for population extinction rates on nature reserves up to 1980 typically exceeded those on neighbouring land (Thomas 1991). Importantly, success breeds success in conservation, and the demonstrable recovery of (alas rather few) declining iconic species in Europe has greatly increased public and political interest in Lepidoptera, and has hugely increased the flow of funding, leading to wider gains. Among these are multi-million euro projects to protect pristine ecosystems and to restore and recreate degraded ones, which, although targeted for one species, inevitably support diverse communities of other threatened taxa (Bickmore & Thomas 2000; Thomas 2001; Settele & Kühn 2009).

Species-specific research and actions, e.g. the UK Biodiversity Action Plan, now increasingly include specialist moths among their priority species. The problem is that, given the increased pressures on the natural environment, it seems impossible to follow such an 'intensive care' approach for the majority of species in trouble (Merckx et al. 2010a). Worst off are generalists, many of which are also experiencing severe declines (Van Dyck et al. 2009), less popular taxa such as moths (Conrad et al. 2006), and species within the diverse communities of the tropics. The expensive, time-consuming and dedicated approach is obviously desirable to rescue highly threatened iconic species in desperate situations, such as the monarch roosts of central Mexico, and the Queen Alexandra's birdwing (the world's largest and perhaps most endangered butterfly) in Papua New Guinea (Thomas & Settele 2004). There is an argument that such care should be temporary and eventually relaxed as threat levels decrease. Perhaps the strongest arguments for its current continuation are: (i) beneficial umbrella impacts on other species, and (ii) the gaining of the knowledge required for designing efficient biotope-specific management.

We therefore believe there is currently still a need for both species-specific and biotope-specific approaches in temperate and (sub)tropical regions. The focus on biotopes should gradually be increased in temperate regions, including on land outside nature reserves managed for agriculture, silviculture and urban-industrial purposes such as road and railway constructions. At the same time, the species-specific conservation effort for highly endangered iconic tropical species should be considerably increased, especially those with severely restricted ranges. Indeed, a consequence of the lack of population studies in the tropics is the minimal knowledge of foodplants for larvae, and spatial structure and dispersal capabilities of most populations of tropical Lepidoptera (Bonebrake et al. 2010, but see Marini-Filho & Martins 2010).

From single sites to meta-populations: ecological conservation at landscape scales

The development of the modern ecological approach to Lepidoptera conservation included two paradigm shifts: first, the concept that surviving patches of habitat were declining in quality and had reduced (or no) capacity to support a valued species; and later, that irrespective of their quality, the surviving islands of habitat were too few, small and isolated for a meta-population of populations to persist in a landscape. In practice, the two concepts are inextricably entwined, both in their causes and in their consequences for population dynamics. The same socio-economic changes that lead to ecosystem destruction and fragmentation typically alter both successional dynamics and the development of plagioclimaxes within the surviving habitat islands (Thomas et al. 2001).

Apart from special cases, such as monarch butterfly overwintering sites, reduced habitat quality primarily affects fitness of Lepidoptera in the larval stage (Thomas 1991). In a degraded biotope, the larval foodplant typically remains abundant (in some cases increases) but grows in less suitable forms or with altered nutritional value in response to pollution, changed water levels or other attributes such as microclimate (Thomas et al. 2011). For most butterflies studied, the mean density of adults on isolated sites containing optimum larval habitat was around 100 times greater (spatially or temporally) than on those containing the lowest-quality source habitat that had supported a population for at least 10 consecutive generations. In contrast, fluctuations caused by weather and variation in adult resources (e.g. nectar, mating sites), were 10 to 100 times smaller. And only in one studied species (*Celastrina argiolus*) were interactions with an enemy (a specific parasitoid) sufficient to overrule the population variation due to habitat quality (Thomas et al. 2011).

In contrast, isolation of habitat patches affects mainly the adult stage, which is unexpectedly sedentary in most studied species of Lepidoptera, especially in habitat specialists. Increased isolation causes meta-populations to disappear from landscapes as populations die out, having failed either to track the generation of new habitat patches or resources across modern landscapes or to replenish those that go extinct (Hanski 1999). On the spectrum between classic 'blinking light' meta-populations or mainland-island ones, the positions of most populations of 'colonial' species of Lepidoptera have been a matter of some debate. The former structure probably approaches the norm for several Melitaenini and related fritillaries (Schtickzelle & Baguette 2009), but in other species may be a transient phase following habitat fragmentation, presaging the breakdown of the whole system (Harrison 1994).

At the applied level, there was an unwelcome dichotomy during the 1980s–90s in Europe between (i) spending scarce resources solely on improving the (degenerating) internal habitat quality of existing conservation sites for endangered guilds or species of Lepidoptera, rather than adding to the suite of reserves, and (ii) the exact opposite approach. Today an evidence-based consensus recognizes that it is equally important to address both processes. This resulted from a series of field studies from Thomas et al. (2001) onwards, which found that, whilst the density of individuals within a site reflects the quality of habitat within each occupied patch rather than its isolation or size, the chance of a patch being occupied in the first place was correlated strongly, independently and almost equally with both its isolation from neighbours and (again) the quality of the patch. Surprisingly, very few single-species studies (as opposed to whole communities of species) have shown patch size to be a significant predictor of occupancy once account is taken of habitat quality (Thomas et al. 2011). There are three explanations for the contribution of patch quality to meta-population stability in Lepidoptera: (i) for a given patch size, optimum habitat supports populations that are up to 100-fold larger, and hence more likely to persist, than those of low (but just suitable) source habitat; (ii) the former release more emigrants into the matrix to seek new sites, disproportionally so since individual butterflies hatching into high-density populations are more likely to leave their natal patch (Hovestadt *et al*. 2010); (iii) new sites containing high-quality habitat are more likely to be colonized successfully by an immigrant female, since the vulnerable period of low numbers is short (Thomas et al. 2011).

By applying the above principles, European conservationists concerned with Lepidoptera are (at last) matching the successes achieved for many plants and vertebrates (see Box 14.1). Still, there are key questions to be addressed by future research both at patch and landscape scales. To what extent are subsets of species regionally adapted to different biotic interactions or environmental conditions (e.g. local climate)? How responsive are local phenotypes to rapid environmental change, for example in selection for more dispersive forms or types physiologically adapted to a warmer climate or capable of switching foodplants or hosts? Although larval habitat quality and adult dispersal are the two overriding factors so far found to regulate populations and meta-populations in most studied Lepidoptera (Thomas et al. 2001), do other factors (e.g. adult resources) play a key role for populations elsewhere (Dennis 2010) or under tropical climates? How important is the matrix separating patches of breeding habitat in providing resources for adults or facilitating/obstructing their spread (Dennis 2010)?

Advancing towards multi-species conservation

As we argue elsewhere, with only half of the world's estimated Lepidoptera described and a minute proportion well studied, it is impossible to provide targeted conservation programmes for more than a small number of highly valued species, at least outside nations where diversity is exceedingly low (e.g. the UK). Moreover, very few nature reserves are managed primarily for Lepidoptera, although typically the plants, ants and (often more endangered) specific parasitoids with which each interacts benefit directly (e.g. Anton et al. 2007).

We have seen that declines in Lepidoptera are driven primarily by factors that affect all species, rather than by targeted overcollecting (see above). In addition, we have suggested that butterflies can be sensitive predictors of the impacts of environmental change on other organisms, as well as useful representatives of less conspicuous terrestrial insects (Thomas

2005). In theory, therefore, the restoration of optimum conditions for a rapidly declining butterfly will require restoring a type of habitat within existing biotopes, or a network of sites to landscapes, that should benefit the community characteristic of that configuration of habitat patches.

In practice, there are few examples of observed umbrella benefits resulting from single-species conservation of insects, which has caused its efficacy to be doubted (Stewart et al. 2007) despite abundant evidence in support from biotope manipulation for other taxa (e.g. Dunk et al. 2006). This is an inevitable consequence of a lack of resources to monitor collateral changes in most Lepidoptera conservation projects. In the USA, Launer & Murphy (1994) found that protection of all those serpentine soil-based grasslands in central California occupied by the federally protected butterfly *Euphydryas editha bayensis* would also conserve 98% of native spring-flowering plant species (although the percentage fell sharply if only the largest butterfly sites were targeted). In the UK (Thomas et al. 2011), the restoration of scrub habitats designed to increase *Satyrium pruni*, of chalk grassland for *Polyommatus coridon*, and of limestone and acid grasslands for *Maculinea arion* (see Box 14.1) produced rapid and diverse gains across a suite of declining insects, plants and (where studied) birds. In the case of *M. arion*, the beneficiaries included 33% of the declining butterfly species listed in the UK's Biodiversity Action Plan, as well as RDB-listed species of ants, beetles, flies, cockroaches, plants and birds. Most species increased because they were adapted to the warm early-successional grassland structures created for *M. arion* in the UK. Several also increased due to a direct or indirect relationship with ants. For example, alongside another *Viola* species, the UK-RDB *V. lactea* has myrmecochorous seeds that are particularly attractive to *Myrmica* ants, which after eating the eliasomes eject the seeds into sparsely vegetated soil around their nests. The consequences of up to a thousand-fold increase of *Maculinea arion*'s host-ant *Myrmica sabuleti* was a ca. 100-fold increase on three sites of *Viola* and a 10–15-fold increase (and new populations) of three fritillary butterflies whose larvae eat *Viola*, including *Argynnis adippe* and *Boloria euphrosyne*, two of the UK's most endangered insect species (Randle et al. 2005). In this respect the target butterfly, *M. arion*, acted as an indicator for a keystone species of ant, *M. sabuleti*, which dominates its habitat at its scale. Since most Lycaenidae (nearly a third of butterfly species) interact with ants as larvae or pupae, we suspect that they will prove to be an especially useful umbrella taxon for other groups.

Encouraging as these results may be, there is clearly a pressing need for future research and conservation practice to understand the ecological requirements of a spectrum of endangered Lepidoptera with enough precision to ensure the continuity of sufficient habitat for each component within a single heterogeneous ecosystem, for example as co-existing successional stages within woodland, heath and grassland. Equally clearly, this is more likely to succeed in multi-sited landscape-scale projects which, in our view rightly, have been the trend in recent years.

Two multi-species approaches

Landscape restoration

The successful landscape-scale conservation of multi-species assemblages basically boils down to either conserving/protecting 'pristine' landscapes or restoring human-altered landscapes. Although adequate protection of the world's remaining 'wilderness' areas is both more important and also more effective, such areas are dwindling worldwide. Human-altered landscapes keep extending ever larger, so conservation efforts within them are becoming relatively more significant. Overall, landscape-scale restoration approaches within such areas should minimize the fragmentation of specific habitat resources.

We believe it is useful to make a distinction between areas that (i) have a short history of human alteration, e.g. deforested in recent decades, (ii) have a long history, e.g. farmed for several centuries, and (iii) are 'pristine'. We argue that, above the general ecological conservation principles applying to all, successful conservation of the extant biodiversity in each needs a different approach.

The massive recent and ongoing deforestation/degradation of tropical forests (in several West African countries, forest cover loss exceeds 90%; Safian et al. 2011) has dramatic consequences for the highly diverse Lepidoptera fauna adapted to these climax ecosystems. Agri- and silvicultural mosaics where the percentage of converted original forest exceeds 30%, including selective logging of three or more large trees per hectare, show species compositional shifts with loss of many components of the butterfly community (Brown 1997). Hence, the only way to repair some of the damage is the combination of thorough protection of remaining patches of primary forests, successful regeneration of secondary forests, and targeted reforestation projects within agro-forestry systems and clear-cut areas (Schulze et al. 2004; Safian et al. 2011). Species recolonization rates depend primarily on life-history characteristics, patch size and biological structure, distance to source patches and permeability of the intervening matrix. Still, the often substantial dispersal/recolonization potential of tropical butterfly and moth communities allows them to regenerate several decades after clearance (Hilt & Fiedler 2005; Safian et al. 2011). Obviously, recent conversion by agriculture in areas originally not fully forested need protection and restoration of the original set of biotopes (e.g. Afromontane mosaic landscapes; Tropek & Konvicka 2010).

The situation is more complex in countries, such as most of Europe, with a long history of human alteration. Here, ultimate conservation goals are the subject of much, but not enough, debate. The natural climax forests and sparsely forested pastures kept open by mega-herbivores have been fully replaced, often millennia ago, by so-called semi-natural biotopes, which are essentially different versions of early- to mid-successional natural seral stages or plagio-climaxes, prevented from reverting towards forest. Only scattered fragments of ancient woodland remain, and these have suffered continuous disturbance as human needs for woodland products changed. For example, up to a century ago most European woodland was maintained as coppice or very open coppice-with-standards, to provide fuel and fencing materials, whereas today much woodland has a more uniformly closed shady canopy than is found in ancient forests with no history of disturbance. And since very old trees were no more valuable to humans than middle-aged ones, the rarest type of arboreal habitats in developed countries today are those associated with rotting wood on ancient trees: yet these saproxylic habitats support numerous endangered invertebrate specialists, especially Coleoptera and Diptera, and some moths (e.g. *Parascotia fuliginaria*). Although many species were undoubtedly lost over the centuries during this transition, others have managed to adapt successfully as specialists in these semi-natural biotopes (e.g. heaths, grasslands, hay meadows, marshes and coppiced woodland).

The intensification of agriculture and forestry and of urbanization since the 1950s, and more recently abandonment in response to socio-economic imperatives, has severely decreased these semi-natural biotopes in quantity and quality, and with them their specialist fauna and Lepidoptera. The Red List considers agricultural intensification and abandonment a major threat for almost 30% of European butterfly species (van Swaay et al. 2010b). As a result, most 'conservationists' seek to sustain or restore semi-natural biotopes, and do so by maintaining very specific disturbance regimes (often simply by copying traditional agricultural practices, since most large wild herbivores were excluded centuries ago) (New 2009). Nevertheless, popular management operations to influence vegetation structure, such as burning and grazing/mowing, need careful planning (mainly to ensure refugia) as they may destroy much of the existing invertebrate fauna if applied too intensively, too infrequently, on too large a scale or at unsuitable times of year (New 2009). Hence, although wrongly applied conservation management may have unintended negative consequences, management is seen as a good thing overall, whereas abandonment of human disturbance is often perceived as a threat.

The situation should not be black and white. Abandonment undoubtedly poses a threat to many specialist species that have become adapted to certain semi-natural biotopes, and is a threat to specialists that have nowhere else to go because natural succession dynamics are currently too disturbed and suitable natural patches are too small and/or isolated. On the other hand, abandonment will most certainly benefit some endangered specialist faunal groups too (e.g. closed-woodland Lepidoptera, saproxylic groups), and may also provide 'rewilding' opportunities in biotopes evolving towards mosaics including mature climax vegetation or natural successional stages such as coastal and river areas, wood gaps and high-altitude areas, although even here, open habitats may be much rarer than in prehuman landscapes, owing to the absence of most former natural herbivores, e.g. bison, aurochs, wild sheep and horses (and, more locally, beaver) in Europe (see Chapter 23).

We believe there should be room for both active management (i.e. restoration of semi-natural biotopes) and passive abandonment (i.e. rewilding), even at small spatial scales (Merckx et al. 2012a). They are complementary, and now is the time to designate areas to one or the other, on a European-wide scale. Such allocations should be done carefully, and for as many taxa as possible, taking into account many variables, such as historic and recent distributional data, international threat status and life-history traits, and they should have clear, quantifiable conservation goals. The information on butterflies (i.e. European Red List: van Swaay et al. 2010b; Prime Butterfly Areas in Europe: van Swaay & Warren 2003) will be a valuable input to such a multi-taxa exercise. The current and possible future distribution and intrinsic properties of nature reserves (e.g. Natura 2000 sites, UK Sites of Special Scientific Interest) and High Nature Value farmland, together with what will be politically and financially achievable through the soon to be revised Common Agricultural Policy, will all be instrumental in producing a road-map, with substantially increased funds and mechanisms for semi-natural biotope restoration, which will clearly delineate sites/areas best managed under each approach.

In addition, restoration of areas usually regarded as 'the matrix' in between (semi-)-natural patches, such as intensive farmland, brownfields and even urbanized areas, is of value too. These areas are currently often rather 'simple' and 'homogeneous' in terms of habitat resources, so restoration may make a relatively large difference to their conservation value (Tscharntke et al. 2005), as well as increasing the value of neighbouring (semi-)natural patches (Dennis 2010). Brownfield sites provide many opportunities for restoration of successional biotopes otherwise not strongly represented locally, and restoration plans should be tailored to focal species and/or generally improve biotopes by assuring a sufficient quantity, quality and spatiotemporal diversity of resources (New 2009; Dennis 2010). Restoration of intensive agricultural areas may be globally important given their huge and growing footprint. Here, the aim should be to reconcile intensive agricultural practices with wider societal benefits, including biodiversity. The question is how to decide which landscape elements to restore, how, and at what spatial scale in order to make farmland less hostile to a broad range of declining 'wider countryside' and rare, localized species (Merckx et al. 2010a).

Agri-environment schemes (AES) can reverse negative biodiversity trends by increasing resource heterogeneity and improving dispersal success (Shreeve & Dennis 2011). However, they must be made more efficient and cost-effective, so that they actually achieve their goals (Kleijn et al. 2006; Settele et al. 2009). One way to achieve this is by implementing specific measures for high-priority species within AES targeted at landscapes where such species occur, as this approach has been shown to benefit specialist butterfly species (Brereton et al. 2011). However, we argue that this species-specific approach must be complemented by a multi-species approach in order to more fully address the steep declines in farmland biodiversity. General AES that are focused on the restoration and implementation of vital landscape elements are key to this multi-species approach. Even simple AES management prescriptions applied to relatively small areas can benefit Lepidoptera populations. For example, the restoration and management of arable field margins has been shown to benefit a range of butterfly species, both on conventionally managed (Feber & Smith 1995; Feber et al. 1996) and organically managed (Feber et al. 2007) farmland. Hedgerow management can have a positive effect on declining species such as the brown hairstreak *Thecla betulae* butterfly (Merckx & Berwaerts 2010). In addition, we have recently discovered that the protection of existing hedgerow trees, and the provision of new ones, is likely to be a highly beneficial conservation tool for populations of moths, and probably many other flying insects too, as hedgerow trees provide a sheltered microclimate and other key habitat resources (Merckx et al. 2009a, 2010b, 2012b). Nevertheless, hedgerow tree and field margin AES options are likely to obtain best results for moth populations where farmers are targeted to join these schemes across the landscape, probably because this results in a landscape-scale joining up of habitat resources, which especially benefits the large proportion of moth species of intermediate mobility that use the agricultural biotope and move through it on a scale larger than the field scale (Merckx et al. 2009a,b, 2010b) (Figure 14.1).

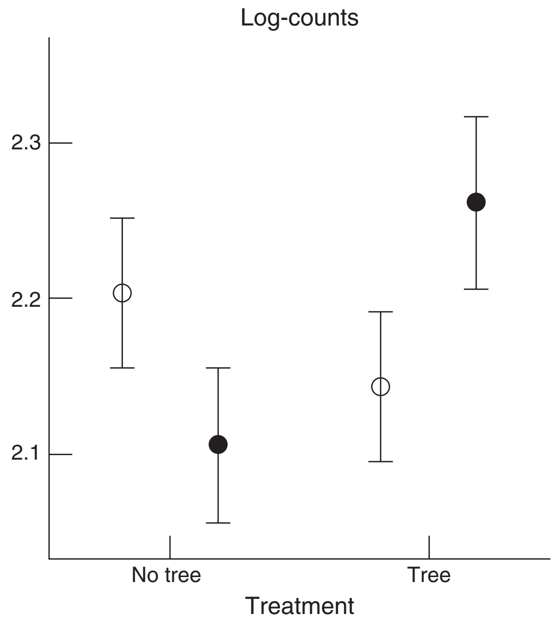


Figure 14.1 Fortnightly individual moth counts (log $N+1$) (with SE) contrasting the effects of presence/absence of a hedgerow tree on moth abundance within areas where farmers had (•) and had not been (○) targeted to apply for agri-environment schemes. Reprinted from Merckx *et al.* (2009a), with permission from Elsevier.

Landscape conservation

Sites with 'no' or little human disturbance, and with high biodiversity and/or threat levels, are candidates for landscape conservation, a very effective strategy for protecting endangered species and biotopes (Bruner et al. 2001). The number of national park declarations, mainly for biodiversity conservation purposes, has increased in recent years. Resources for these national parks are finite, and must be directed to the most important sites. GIS-based prioritization exercises with a multitude of data layers, including forest structure change and sound distributional and modelled occupancy data of threatened species, are a prerequisite.

The first threatened species assessments were published for mammals and birds in the mid-1960s. So far, out of the entire planet's biodiversity, only ca. 45,000 species have been assessed against IUCN criteria, mostly vascular plants and vertebrates, plus <1500 insects including ca. 300 Lepidoptera (Vié et al. 2008). The IUCN is now conducting assessments, using the Sampled Red List Index (SRLI) methodology, of the threat status of samples of 1500 species of the lesser known groups without complete Red Lists, such as many invertebrates. Recent initiatives include IUCN assessments of butterflies in Europe (van Swaay et al. 2010b) and the rest of the world (Afrotropics: Lewis & Senior 2011; Neotropics: Willmott et al. 2011).

Some site-based assessment methods have been developed with particular reference to butterflies. For example, Ackery & Vane-Wright (1984) proposed the concept of *critical fauna analysis*, whereby regions that contain certain local faunas are identified by their endemic species, and if these regions were protected, all species of a particular group would be too. Only a few analyses of 'critical faunas' have been conducted in tropical areas (e.g. Collins & Morris 1985; Hall 1999; Vane-Wright & de Jong 2003; Willmott 2003). Data are assessed to identify optimally efficient, single-site sequences of near-equal priority areas for a group using the complementarity principle (Vane-Wright et al. 1991; Williams 2001) and incorporating other criteria (Margules & Pressey 2000; Araújo et al. 2002). This method is also useful in assessing habitats on a broader geographic scale, where it is possible to detect areas of unusually high significance in understanding evolutionary processes (New 1997).

Van Swaay & Warren (2003) proposed a selection of Prime Butterfly Areas (PBAs) for threatened species in Europe. PBAs are defined as a preliminary selection of areas supporting species meeting three criteria.

- *Biogeography*: European range-restricted species
- *Conservation*: threatened species defined by IUCN criteria
- *Legislation*: species listed in Appendix II of the Bern Convention and/or the EU Habitats and Species Directive.

This initiative identified 431 PBAs (covering 1.8% of Europe). However, not enough is known of threatened species in tropical regions to apply this method there. Threat assessments for butterflies are available but are not yet comprehensive for the group as a whole. Wells et al. (1983) produced the first IUCN invertebrate RDB including some butterflies. The first national assessment for invertebrates was produced for England by Shirt (1987) and assessments of threatened butterflies for Europe by Heath (1981).

Only one family of butterflies, the Papilionidae (i.e. 'swallowtails'), has been assessed on a global scale (Collins & Morris 1985). This family has a pan-global distribution and includes both widespread and habitat-restricted species, making them well suited for conservation studies. They include some of the largest and most spectacular butterfly species, attracting the attention of amateurs and specialists alike, so their taxonomy and distribution are relatively well known. The assessments were made under earlier versions of IUCN criteria and were mostly qualitative; 170 papilionids were considered threatened or near-threatened in this study (Collins & Morris 1985). Later, New & Collins (1991) showed that nearly 14% of papilionid taxa are believed to be threatened or declining, plus 17% with no information to be assessed. The Lycaenidae is another major butterfly group that has been subject to some detailed conservation studies (e.g. New 1993; Thomas et al. 2005). This family is difficult to study due to its high diversity (almost 40% of all described butterfly species) and complex and poorly known taxonomy in many regions. The other major butterfly families (Pieridae, Nymphalidae, Hesperiidae and Riodinidae) have not had a global assessment.

Van Swaay & Warren (1999) provided the first comprehensive regional review of the status of butterflies for Europe (except Turkey and Cyprus). Out of 576 butterfly species assessed, 71 (12% of the total) were categorized as threatened, of which 19 were globally threatened species and 52 regionally threatened. In the tropical regions, hardly any such regional assessments have yet been done, though various assessments have been carried out at a national level, some of which use modified IUCN criteria or subjective assessments for butterflies and a few moth species (e.g. Colombia: Amat-García et al. 2007; Venezuela: Rodríguez & Rojas-Suárez 2008; Brazil: MMA 2008). However, those assessments do not cover the entire butterfly fauna of each country, and variation in the criteria used introduces discrepancies. For example, the high-elevation butterfly *Lymanopoda paramera* was separately assessed twice as it lives in the border region of Colombia and Venezuela. It was assessed as Vulnerable in Venezuela, but as Critically Endangered in Colombia, perhaps because different methodologies were used during the assessments, and/or the difference in extent of each national range. In addition, there are some *ad hoc* assessments of certain recently described species of Andean butterflies (e.g. Hall 1999; Willmott 2003; Huertas et al. 2009; Huertas 2011). However, less than 10% of the Neotropical butterfly fauna (ca. 45% of the world) has been assessed so far (Willmott et al. 2011).

Various site-based conservation assessment initiatives are based mainly on birds. The Important Bird Areas (IBAs) of Grimmett & Jones (1989) was later applied to plants as Important Plant Areas (IPAs) (PlantLife 2004), and then to all groups as Key Biodiversity Areas (KBA) (Langhammer et al. 2007). In order to be listed as a KBA, a site must support at least one globally threatened species, range-restricted species, biome-restricted species or congregation of species. Notably, in the context of invertebrates, the designation of KBAs does not require the identity of all threatened or range-restricted species, just that there is *a* threatened species at the locality. The KBA programme is less useful in tropical regions, where almost all habitats include some threatened species. As a result, a further important initiative is the Alliance for Zero Extinction (AZE) (Ricketts et al. 2005). AZE sites are defined much more restrictively (using three specific criteria) as the most important locality for an Endangered or Critically Endangered species. The Tropical Andean Butterfly Diversity Project (TABDP; www.andeanbutterflies.org) is currently developing a list of KBAs for the Neotropics based on the presence of threatened butterfly species studied in the IUCN SRLI (Box 14.2) (Willmott et al. 2011).

The lack of threat assessments for Lepidoptera and other invertebrates in the tropics has serious consequences. Research and conservation resources may not be adequately targeted or may rely upon passive conservation of other, better known, taxa. The lack of threat assessments may bias funding towards better known groups. Some grant research programmes require supported projects to concentrate on species rated as threatened. Consequently, one way of obtaining funding for Lepidoptera research has been to conduct surveys within multi-taxa studies involving other faunistic groups (e.g. Huertas & Donegan 2006). The NGO ProAves (www.proaves.org) has established various nature reserves and helped in the declaration of a national park in Colombia for threatened bird and butterfly species based on some of the latter studies.

Conclusion

Because of the now global dimension of rapid biodiversity decline, and its detrimental impact on humanity, we need to manage unsustainable land use and massive conversion and degradation of natural habitats. It is our duty to preserve and restore natural areas, not only because of their intrinsic value but also, from a utilitarian point of view, to avoid the functional breakdown of the ecosystems on which we depend. The worldwide ubiquity, abundance, sheer diversity, indicator capacity and both historic and current appeal to scientists and amateur naturalists make the Lepidoptera an excellent group to monitor conservation efforts worldwide, and they complement conservation narrowly focused on birds and mammals alone (not least because butterflies decline faster than birds and plants: Thomas et al. 2004). Here, while we have commented on how approaches to Lepidoptera conservation

Box 14.2 A case study: the Tropical Andean Butterfly Diversity Project (TABDP)

This project (www.andeanbutterflies.org) is a major initiative involving international collaboration among scientists, institutions and students working to establish a foundation for future research on the butterflies of the Andean region, a global biodiversity hotspot. The project was inspired by the BioMap Project (www.biomap.net) and started in 2005 as an international collaboration among institutions based in five Andean countries (Colombia, Peru, Bolivia, Venezuela and Ecuador), the UK and the USA. Threatened species and site assessments require baseline distributional data. This project sought to collect and collate these data, based largely on the resources and information available in museum collections.

The TABDP started from scratch in the capture of the data on the distribution of Neotropical butterfly species. A tailored database was designed to capture data on the locality, identification and other details of specimens in museums. Also, a manual for the use of databases (Willmott & Huertas 2006) and another for butterfly photography (Huertas & Willmott 2006), in both Spanish and English, were published. A database of ca. 200,000 records and photographs of the types of Andean species is now freely available online.

Building the capacity of host countries to conduct research on tropical Andean butterflies and train a new generation of researchers was a primary goal of this project. Around 300 students and professionals from various collections were trained in eight courses in five countries and a first Andean butterfly network, now with ca. 600 members, has been established. Threatened species assessments have been produced for 350 Neotropical butterfly species, in collaboration with the IUCN, using the SRLI methodology. Based on these assessments, the first KBAs based on butterflies have been proposed for South America (Willmott et al. 2011).

The TABDP data capture methods and threat assessment methods can be replicated for any insect group and applied in other conservation initiatives, for example using more species or at national or local levels. Projects and institutions should not spare any effort in improving data sources and providing accessibility. Research programmes and targeted surveys are key sources of data, which should be considered (and funded) as part of the conservation process. Locality information necessary to produce threat assessments can be gathered only with an army of naturalists or parataxonomists (Basset et al. 2004), trained in collating and analysing data effectively. However, as taxonomic expertise is crucial when doing the assessments, more people need to be trained and more resources be facilitated for core taxonomy.

differ between regions and land use types, we stress the importance of adopting a landscape scale allied to a resource-based view, both for single-species and for biotope/community conservation.

Rapid land use change, especially in recent decades, has caused serious declines in butterflies and moths worldwide, despite the recent designation of many new nature reserves (e.g. van Swaay et al. 2010b). It is hence clear that we need to go a lot further, with far greater long-term resources. Society should now start to invest massively on five fronts: (i) protecting and buffering natural areas (i.e. more, better managed and larger reserves), (ii) restoring and managing robust networks of semi-natural biotopes, (iii) rewilding areas where this is appropriate, (iv) improving typical 'matrix' areas, and (v) gathering data for poorly known areas and species concerning distribution, habitat requirements, population changes and taxonomy, which would also benefit such areas by increasing local awareness and by the production of field guides. Such an increased effort will not be in vain, as there is compelling evidence, for vertebrates at least, that conservation efforts can halt and even reverse biodiversity loss, provided there are sufficient resources and the collective will to protect critical habitat resources (Hoffmann et al. 2010). The efforts need to be monitored too. Lepidoptera are uniquely easy to survey for a better understanding of biodiversity change, and as recent experiences in Europe suggest that the challenge could be met, we call for projects to make rigorous population trend estimates in undermonitored regions (see also Pereira et al. 2010). Such projects would be especially welcome in the tropics, where few (if any) Lepidoptera monitoring schemes exist.

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