

# Insect Conservation: A Synthetic Management Approach

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Annu. Rev. Entomol. 2007. 52:465–87

First published online as a Review in  
Advance on September 1, 2006

The *Annual Review of Entomology* is online at  
ento.annualreviews.org

This article's doi:  
10.1146/annurev.ento.52.110405.091317

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0066-4170/07/0107-0465\$20.00

## Key Words

insect conservation, management strategies, synthetic management, threats

## Abstract

Threats to insect diversity range from habitat loss and invasive alien organisms to environmental contamination and biological control. Many of the threats are synergistic, with the joint impact of habitat loss and global climate change being highly adversely synergistic. Recent research on insect conservation has elucidated some basic principles for conservation management. There are six basic principles that are interrelated and together provide guidelines for synthetic conservation management of insects. They are maintain reserves (principle 1), maintain as much quality landscape heterogeneity as possible (principle 2), reduce contrast between remnant patches and neighboring disturbed patches (principle 3), outside reserves, introduce land sparing (principle 4), simulate natural conditions and disturbance (principle 5), and connect similar patches of quality habitat (principle 6). These six principles constitute a coarse-filter, landscape approach. Permeating all six is the principle of maintaining healthy population levels, which require the combined support of the metapopulation trio of large patch (habitat) size, good patch quality, and reduced patch isolation. In addition to these six coarse-filter principles is an overlay of the fine-filter, species approach, in which particular species are given focused attention and management.

## **HISTORICAL BACKGROUND: WHY WE NEED TO CONSERVE INSECTS**

Insects are enormously successful organisms, both in terms of numbers of species and abundance (164). Their diversity at the family level has been increasing over the last 400 million years, with about 600 families living today (106). At the species level there has not been such a steady increase, with many species lost at the end of the Cretaceous. Most of extinct species were specialists (105).

During the past few hundreds of thousands of years, with the advance and retreat of glaciers, there have been few insect species extinctions (34, 145). Insect populations in the Northern Hemisphere have responded to these chills and thaws by moving southward during the glacials. They have also moved up and down mountains, which has generated new species (78). These movements were unimpeded by the human-fragmented landscape.

During the Pleistocene and early Holocene, mammalian herbivores probably played a significant role in opening up the landscape (2), as they do today on the African savanna (155, 166). This vertebrate impact has been highly significant for many insect species because it leads to a myriad of microhabitat types. Beginning ~6000 years ago, this began to change as humans suddenly, in geological and evolutionary time, altered the landscape. Trees were felled and indigenous game were replaced by domestic livestock. Britain alone lost 20 of its log-inhabiting beetle species (68).

Since then there has been an acceleration of anthropogenic impact on insect populations, with an estimated 11,200 species having gone extinct since the year 1600 (120). Some estimates are that half a million insects may go extinct in the next three hundred years, while some projections suggest that perhaps a quarter of all insect species are under threat of imminent extinction (122). In Britain, butter-

flies are becoming locally extinct faster than plants or birds (195). Furthermore, some parasitic insects are becoming extinct with their vertebrate hosts (50), making a coextinction crisis.

## **CHALLENGES FOR INSECT CONSERVATION**

Only about 10% of all insects have scientific names, with many taxonomic revisions still required, and many species, even common ones, are multispecies complexes with the determination of their DNA (76). Describing all unknown species before they become extinct is the taxonomic challenge. Still, there are likely to be many extinctions, even of species that have never and will never be described

Addressing this taxonomic challenge is not an easy task, although several approaches are making this possible. These include undertaking full inventories of small but important and tractable geographical areas, such as the Seychelles with its high number of endemics (67), or undertaking a global assessment of a particular taxonomic group as is being done for dragonflies. These approaches are supplemented with user-friendly keys for nonspecialists engaged in conservation planning and with the deployment of computer recognition of specimens.

Another great challenge for insect conservation is the perception challenge. Even among some general conservation practitioners, insects are often considered insignificant or given scant attention. This lack of appreciation of insects can reach major proportions among some sectors of human society, who may only recognize the dirty cockroach and the nuisance fly. Yet there is a growing awareness and even fondness for some insects. The British society Butterfly Conservation currently has about 14,000 members, roughly 200 members per national species!

## THREATS TO INSECTS

### Insidious Impacts of Environmental Contamination

A combination of rising human population and more consumption of resources and energy has, as measured by gross domestic product, increased by 460% over the last century, with estimates that there will be a further rise of 240% by the year 2050 (129). Among the concerns is that this human pressure will have cascading effects on ecosystems, with loss of plant species leading to loss of insect species. Hawaii has lost five moth species because of plant extinctions (63). Simulations suggest that loss of just 5% to 10% of keystone members of food webs can radically alter ecosystem function. Many effects of environmental contamination are sublethal and not easily detected. The insecticide deltamethrin can reduce fitness of larval and adult butterflies when applied at only 1/640 of the field dose (25).

Despite the apparent importance of environmental contamination, little is known about its impact on insect species. Species respond differently to any particular contaminant and concentration. Furthermore, there can be adverse interactive effects between impacts of contamination and other forms of stress, such as habitat fragmentation.

Differences in the responses of species in the same feeding guild are seen on Mayotte Island in the Indian Ocean, where some dragonflies are much more susceptible to stream contaminants such as detergent than are others (163). Some insects are little affected by some pollutants, with some herbivorous insects even benefiting from low levels of sulfur dioxide and nitrous oxide (16). In contrast, although the larvae of the butterfly *Parnassius apollo* can excrete metals, it cannot tolerate high levels on its host plant. Relaxation of heavy metal pollution has enabled it to widen its geographical range once again (134).

### Loss of Natural Habitat: Prime Cause of Insect Extinctions

Tilman et al. (196) estimate that by 2050 another  $10^9$  ha of natural ecosystems will be converted to agriculture, with a 2.5-fold increase in nitrogen- and phosphorus-driven eutrophication. These changes will be synergistic with pollution, habitat fragmentation, impact of invasive alien organisms, and global warming. These impacts will not affect all species equally, with specialists likely to decline the most (99), although some common species may also decline dramatically (108), as did the Rocky Mountain locust, *Melanoplus spretus*. It was so abundant in the Midwest of North America in the late 1800s that it caused the wheels of locomotives to slip, yet by 1906 it was extinct (111). Some species even benefit from increased edge effects, such as aggressive ants at the interface between natural habitat and the agricultural matrix, where they heavily affect soil-dwelling arthropods of the transition zone (38).

Land transformation leads to a mosaic of landscape patches, which is highly isolating for many species. Less mobile species may be tolerant of such isolation, which may be the confined spatial environment in which they evolved (165). At the other end of the spectrum, highly mobile species may move across transformed patches, but for those with intermediate mobilities, the anthropogenic landscape mosaic may pose a major threat (191).

Not all aspects of human disturbance are harmful. For example, limestone quarries in the Czech Republic are beneficial for some species that enjoy locally warm and disturbed conditions, which simulate early successional habitats (9). Indeed, some rare insect species require disturbed conditions, such as slipping cliff faces (213).

Urban impact includes traffic, which can be particularly devastating for many Lepidoptera species (121). Furthermore, the materials used to build roads affect not only the immediate area but also many tens of meters into the surrounding area. As with many other

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#### Threats:

anthropogenic factors that reduce population viability and can lead to extinction of a species

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types of disturbance to natural systems, some specialist species are lost but some generalists, such as tramp ants, benefit (167). Similarly, canalization of rivers can encourage populations of certain resourceful species of black fly (*Simulium* spp.) (42).

Of greatest concern is the loss of tropical forests, where probably more than half of all insects live. Currently, 130,000 km<sup>2</sup> are lost annually, and in Southeast Asia it is estimated that by 2010 three quarters of the forests will be gone (175). Evidence is accumulating that forest-to-farmland conversion has a major effect on insect assemblages, particularly the primary forest specialists (39, 45, 51, 58, 80, 83, 92). As in some other ecosystems, it is the opportunist generalists, such as dung beetles and ants, that survive the transition (8, 41). Nevertheless, ecosystem function changes with the altered vegetational canopy (23, 109).

Other natural ecosystems are also losing species, with grassland insects (21, 137, 169, 189) and insects of Mediterranean-type ecosystems (73, 161) affected. The Satyr butterfly *Cercyonis stbenele stbenele* of San Francisco was the first recorded insect extinction in the United States, and the appropriately named katydid *Neduba extincta*, also formerly of San Francisco, was lost in 1937, and only scientifically named after it went extinct.

Of further concern is the loss of cave faunas (36, 86, 173) and island insects (67, 88, 91). Islands appear particularly prone to having their food webs altered, especially by invasive alien organisms (29), environmental changes, and, to some extent, lack of genetic variation (52).

### **Pervasive Effects of Invasive Alien Organisms**

Invasive alien organisms are a major threat to many indigenous and endemic species (28). Invasive alien plants can displace indigenous ones and overrun ecosystems, even affecting

local hydrology. Such impacts inevitably reduce local insect diversity (170), which can return when the alien plants are removed (171). Invasive insects are also posing a threat. In the United States, a new insect species is discovered on average every 54 inspections of maritime cargo (216).

Interestingly, the impacts of invasive alien plants are not always negative. Alien plants sometimes provide shelter when there otherwise might not be (22), and alien water weeds can provide increased habitat for some dragonflies, but only for already geographically widespread and generalist species (182).

Invasive alien vertebrates can have both direct and indirect effects on insects. On sub-Antarctic Marion Island, alien mice eat up to 194 g ha<sup>-1</sup> of invertebrate biomass (174), and alien rats have been implicated in local extinction of several insects including the Lord Howe Island stick insect, *Dryocelus australis*, on that island (148). The cane toad, *Bufo marinus*, was introduced into Australia to control certain beetle pests and is now having a major impact on many nontarget native insects, as are mosquitofish *Gambusia* spp. introduced into Hawaii to control mosquitoes but have since affected indigenous *Megalagrion* spp. damselflies (54).

Of the invasive species, ants have been the most resourceful. The bigheaded ant, *Pheidole megacephala*, and the Argentine ant, *Linepithema humile*, have affected ecosystems in many countries, including Hawaii, which originally had no ants (84). These ants out-compete local ants and can devastate local insect faunas, as has the fire ant *Solenopsis geminata* in the United States (33). On Christmas Island, the yellow crazy ant, *Anoplolepis gracilipes*, is changing the local ecosystem as it kills large numbers of crabs that take refuge on the island. Other hymenopterans can also have a major impact; for example, the common wasp, *Vespula vulgaris*, is having a major affect on New Zealand insects and spiders and is thus changing ecosystem processes (198).

## Side Effects of Classical Biological Control

Although the introduction of foreign biological control agents to control foreign pests has had economic and environmental benefits, inevitably it does carry some risks for nontarget organisms (87, 112, 132, 160). While adverse impact is likely species or genus specific, the main concerns are twofold: The activity of classical biological control is deliberate, and once control agents have been introduced and established, they cannot be recalled and are therefore a new and permanent feature of the host landscape, thus violating a sense of place (112). While the adverse impacts of classical biological control are often difficult to prove, there is nevertheless evidence that some facets of it are detrimental to indigenous biotas. For example, the tachinid fly *Compsilura concinnata*, which was introduced into the United States several times to control various pests, has been implicated in the decline of some local saturniid moths (14).

While the control of alien weeds with insect herbivores has in many cases been successful and has had economic and ecological benefits, there have also been some side effects. Indigenous prickly pear cacti (*Opuntia* spp.) in the United States and Mexico are currently threatened by the cactus moth, *Cactoblastis cactorum*, which is spreading in North America (79).

Even insect pathogens carry risks. The bacterium *Bacillus thuringiensis israelensis*, which is used to control mosquitoes, causes mortality in various aquatic insect larvae. Another form of *B. thuringiensis* used for controlling pest Lepidoptera has an impact on indigenous North American moths (123).

## The Pernicious Side of Genetic Engineering

Genetically modified organisms (GMOs), particularly transgenic plants, are increasingly used in integrated pest management programs. The use of GMOs can pose risks to

some indigenous insects (113), although it has been argued that these risks are considerably reduced at the large, regional spatial scale (135). Furthermore, GM plants are not a general answer for pest control, as there are transgenic plants with *B. thuringiensis* insecticidal toxins resistant to the diamond-back moth, *Plutella xylostella* (216a). For insect conservation, the real risk of GM crops is what Woiwod (214) has called the "pernicious side": An area the size of Wales is cleared annually in Amazonian Brazil to grow GM-free soya for the European market, thus devastating Amazonian insect diversity.

## Impacts of Global Climate Change

The phenology of British butterflies changed considerably between 1980 and 2000, with the first appearance of 13 species significantly advanced (157). Climate change is also affecting trophic interactions, with all components of food webs from pathogens and mycorrhizae to predators and parasitoids affected directly and indirectly (6, 66, 74). Insect herbivores in elevated carbon dioxide grew more slowly, consumed more plant material, took longer to develop, and suffered higher mortality compared with controls (210). Competitive interactions are also likely to be affected, as seen in *Drosophila* assemblages in which different species were favored by particular temperatures (40). Nevertheless, some interactions have remained in step with climate change, with the winter moth, *Operophtera brumata*, larvae tracking changed budburst (19) and the orange tip butterfly, *Antibocharis cardamines*, keeping pace with food plant phenology (176).

As insects typically migrate faster than trees, many temperate plant species are likely to have new encounters with particular herbivores shifting their geographical ranges from warmer areas. As each species responds to climate change in its specific way, there is likely to be a reshuffling of communities (37). This cautions the use of simple climatic models to predict future geographic range changes, as empirical evidence from ladybird range

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**Synergisms:** the interaction between factors where the outcome is a multiple of these factors

**Prioritizing:** the regional scale activity of selecting reserves and landscapes of conservation value

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extensions (through biocontrol activities) shows that many features of an insect's biology affect where and how it establishes more than simple thermal considerations (168).

Nevertheless, there is a salient warning from Kuchlein & Ellis's (103) study of microlepidoptera in the Netherlands, which suggests little point in monitoring individual species to assess the conservation status of specific ecosystems. This indicates that spatially fixed reserves of today may not necessarily be home to the same species in the future, with specialists ill-adapted to move through the fragmented landscape likely the first to suffer. This event is illustrated by British butterflies, in which 30 of 35 species have not tracked recent climate change owing to lack of suitable habitat (81). Indeed, for these butterflies the extensive alteration and destruction of natural habitats means that newly available, climatically suitable areas are too isolated to be colonized or do not contain some specific key elements for survival (209). Evidence suggests that it is only the more mobile generalist butterflies (43, 143, 142) and dragonflies (3) that are tracking climatic suitability.

It is conceivable that some species will adapt locally rather than move to geographically new and more suitable areas, the phenomenon of contemporary evolution. The brown argus butterfly, *Aricia agestis*, is now using an alternative host plant, enabling it to inhabit new localities (192). Nevertheless, there have been some dramatic geographical range changes, with the chequered skipper, *Cartrocephalus palaemon*, having disappeared from England and now restricted to Scotland (81). This finding is also in agreement with some butterflies having shifted their northern range margins more than their southern margins (142).

The greatest concern is that climate change will be interactive and synergistic with other adverse factors, leading to multiple impacts on species. Indeed, Travis (199) has called the synergism between climate change and habitat loss a "deadly anthropogenic cock-

tail" for biodiversity. This is borne out by British butterflies, of which 89% of the habitat specialists, compared with only 50% of the mobile generalists, have declined in geographical distribution (209). Similarly, since the 1950s there has been a 70% decline in the larger British moths, probably due to agricultural intensification and widespread and intensive use of insecticides coupled with climate change (31). Similar fate has befallen moths in the Netherlands, especially those of marshlands (70).

## **INSECT CONSERVATION PLANNING AT THE REGIONAL SCALE**

### **Systematic Reserve Selection**

Planning at the global scale has identified at least 25 areas that are hotspots of world biodiversity and that are also threatened (128). These are likely to be major areas for insect diversity but this still has to be demonstrated, with the proviso that there is likely little distributional concordance (i.e., their habitat preferences and geographical ranges do not coincide) between some taxa in some areas (107, 146).

At the regional scale, insects have a role in systematic conservation planning, which aims to identify locations and landscapes that are a priority for conservation action (i.e., prioritizing) (147). There are many ways to combine targeted sites or reserve areas, and the outcome must be flexible enough for practical conservation management, including making allowances for climate change. As some sites may be common and others rare or even unique, it is essential to include irreplaceability, which is a concept that embodies the potential contribution of a site to a particular conservation goal, combined with determining the extent to which the options for meaningful conservation are lost if the site is lost. While the focus may be primarily on endemic hotspots, it is essential to include areas that are typical, areas that are zones of ecological

transition (4), and areas that have evolutionary potential (177).

These reserve selection procedures are a coarse-filter or landscape approach. These should ideally be complemented with a fine-filter or species approach, in which particular, usually threatened, species of special conservation status are also built into the planning process. A shortcoming of systematic conservation planning for insect conservation is that when insect data are included, there are often taxonomic errors, poor distributional data, and a bias toward certain species. When actual intensive on-the-ground studies are made as part of the ground-truthing of the modeled reserve network, the insect fauna usually is richer than originally thought, much more so than for vertebrates or plants.

### Surrogates in Conservation Planning

In the case of insects, the reserve selection procedure has to operate on crude or incomplete data. This shortcoming can be addressed by using surrogates of insect species diversity. Such surrogates may be alternatives or complements, such as higher taxa, species richness, rarity, endemism, threat status, and/or alternative taxa. Other types of surrogates include vegetation types, land systems or classes, and environmental domains. However, none of these surrogates is perfect, and the risk of using them is that important or even critical aspects of regional insect diversity may be overlooked. For example, although British butterfly family richness may be a good indicator of species richness, rare and threatened species will go unrecorded. When different types of taxa are compared, there may not be concordance, leading to biases depending on which taxa are used (146), making it essential to use a broad selection of taxa (101). While use of environmental surrogates can embrace a range of taxonomic diversity, this broad-scale approach can overlook critical small-scale habitats and special features (such as large logs for certain saproxylic species, hills for hilltopping behavior, mud for mud-puddling, and sun-

basking sites) essential to small animals such as insects.

The consensus being reached is that it is best to combine both environmental and species surrogates for systematic conservation planning. The first studies in this field suggest that insects and plants are often, but not always, concordant and are represented by many environmental surrogates (159, 217), with due caution that there will not always be a perfect match (140). Where species and environmental surrogates have been combined, the alarming conclusion is that perhaps half the land surface needs to be conserved to maintain biodiversity at current levels (153).

This conclusion emphasizes that some creative approaches are needed for future insect conservation, and these may be divided into three broad categories: reserve selection, conservancies, and land sparing. Conservancies are areas of land, often adjacent to reserves, where there is reduced or minimal impact on the land surface. For certain species this means that there is some physical area outside a formal reserve which is their habitat, thus increasing their chances of long-term survival, which then become greater than if they were confined just to a reserve. In other words, the landscape contrast, which otherwise would have been great between the reserve area and the surrounding highly disturbed matrix, is dramatically reduced. Land sparing (119) is set-aside land that may not be a formal reserve. Usually it is strips (corridors, or linkages or greenways) and nodes of land that may be too small on their own for many species' long-term survival but nevertheless complement high-quality reserve areas. Such spared land may also have been disturbed land that has undergone restoration toward a more suitable state.

## INSECT CONSERVATION MANAGEMENT AT THE LANDSCAPE SCALE

In a recent overview of insect diversity conservation (164), it became apparent that some

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**Coarse-filter:** The landscape or community approach to conservation

**Fine-filter:** the species approach to conservation, in which the focus is on a particular species or small number of species

**Corridor:** a linear strip of land connecting one high-value conservation patch with another (also known as a linkage or greenway)

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**Synthetic management:** an overarching management approach which involves six principles of biodiversity management

**Metapopulation trio:** the combination of three landscape features that encourage metapopulation dynamics and hence optimal survival of populations and thus of species

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principles for insect conservation were beginning to emerge. These six basic principles are further developed here, bearing in mind the need for conservation managers to have guidelines for practical insect conservation (62, 98). They are interrelated and together provide guidelines for synthetic conservation management of insects, and also have broader applicability to biodiversity than just insects, emphasizing just how integral insect conservation is to biodiversity conservation. They also build on the threats listed above and their mitigation.

The six principles are maintain reserves as source habitats, particularly for specialists (principle 1); maintain as much quality landscape heterogeneity as possible (principle 2); reduce contrast between remnant natural patches and neighboring disturbed areas (principle 3); outside reserves, maintain as much undisturbed or minimally disturbed habitat as possible (land sparing) (principle 4); in transformed landscapes, simulate natural conditions and disturbance as much as possible (principle 5); and connect like patches of quality habitat as much as possible (principle 6) (**Supplemental Figure 1**, follow the Supplemental Material link from the Annual Reviews home page at <http://www.annualreviews.org>). These principles are discussed below. All six are coarse-filter, landscape approaches. Running throughout all six is the necessity for healthy population levels, bearing in mind that the extinction process is about loss of populations and declining population levels until a point is reached when the last individual has died. Healthy populations usually require the combined support of the metapopulation trio of large patch (habitat) size, good patch quality, and reduced patch isolation. As fragmentation and loss of habitat quality are felt most critically in the case of principle 4, the importance of maintaining this metapopulation trio is discussed below. Furthermore, in addition to the six coarse-filter principles, there is an overlay of the fine-filter, species approach, in which particular species in specific areas require focused attention.

## Maintain Reserves

Wildlife reserves are critical for many specialist organisms that cannot survive in transformed landscapes (27, 58, 110, 116, 179). A cautionary note is that reserves must be large enough to retain these species in the long-term and not lose them to ecological relaxation (114, 197) and global warming (103). Among such specialists are the birdwing butterflies (30) and Malaysian ants, which need over 40 km<sup>2</sup> (17). Size of reserve, however, is not necessarily a fixed entity, because in times of environmental adversity, larger areas may be required. This contributes to principle 3.

Such reserves are not necessarily simply ring-fenced and left as is. They may require some management to maintain natural processes, such as trampling and foraging by megaherbivores or fire, to simulate the natural precedent, at least since the last glacial in the Northern Hemisphere and perhaps deeper in time in the Southern Hemisphere. This principle thus sits closely with principle 6.

## Maintain as Much Quality Landscape Heterogeneity as Possible

Maintenance of a naturally heterogeneous landscape is essential for conserving a wide range of insects, from bumble bees (95) to dragonflies (183). British bumble bees need a variety of field and forest boundaries, while South African dragonflies need a variety of structural vegetation types. Such vegetation heterogeneity is three-dimensional and includes the vertical dimension. For Sulawesi butterflies, it is essential that the vertical structural layers of primary forest remain intact (59). Even on the ground it may be necessary to maintain a healthy, thick layer of deciduous leaf litter for insect and other arthropod diversity (118). Management for heterogeneity for insects in Britain (69) and Ireland (127) may involve letting in sunlight to encourage both plant and invertebrate diversity through

a variety of microhabitats. At the larger spatial scale of landscape elements, heterogeneity also encourages a variety of insect species on Swedish farms (212).

Temporal considerations overlay the spatial ones. While butterfly richness did not change with vegetation succession over time, species composition changed substantially (181). There have been similar findings for soil microarthropods (141). However, there must be adequate migration between like seral stages to avoid local extinction (20, 136). Such migration may not necessarily involve continuous habitat, so long as there are stepping-stone opportunities from one reasonably suitable habitat patch to another for individuals to reach an ideal patch (5, 32, 100, 151). Whether continuous habitat or stepping stone, it is essential in management terms to cater not simply for average environmental conditions but rather for adverse ones (96).

### **Reduce Contrast Between Remnant Patches and Neighboring Disturbed Ones**

As insects are small and plants are larger, insect populations are generally affected by the boundaries at distances beyond what humans perceive as the vegetation boundary (166a). The boundary between landscape elements then becomes an important feature in management planning. This emphasizes that management activities must focus on the wider landscape and not simply on individual patches. Nevertheless, as reserves are important source habitats (85, 133, 138, 202), the ideal situation is to reduce contrast between these source areas and their surroundings to encourage movement through the differential landscape filter (89). Results from heathland (211), forest (117), and agricultural patches (48) point to reducing the contrast between patches. This is underscored by Ricklefs' (154) appeal that ecologists should abandon circumscribed concepts of local communities where they are simply considered spatially explicit entities.

### **Outside Reserves, Introduce Land Sparing**

As small patches have a greater proportion of edge to interior than do larger patches, the quality of the patch generally decreases the smaller its size. This small patch size can lead to loss of populations of butterflies (82), katydids (97), and froghoppers (13). Conversely, large patches can be proportionately richer in species than small patches (49, 94) and suffer less emigration (207). Nevertheless, some small patches may still have important conservation value for certain species of butterfly (172, 200) and may also act as stepping-stone habitats for some species (1, 186, 187, 208). Outside reserves or outside large, good-quality patches in general, the transformed matrix may not necessarily be unsuitable for all species (132). Both metapopulation dynamics and island effects may be taking place (26, 194). The area surrounding a good patch can be viewed as a differential filter, favoring some species but not others, and even a certain sex, age, or ecotype (89), with specialists usually the most affected. Yet in the Southern Hemisphere, where there have been no glaciations for well over 200 million years, many species live in discrete, small populations that are virtually preadapted to fragmentation as long as the footprint of any severe impact does not land squarely on their total population (165). In the Northern Hemisphere, there is sometimes a related phenomenon in which an unsuitable matrix may encourage conservation of certain species that prefer to stay in a good patch rather than venture across a hostile matrix (104).

Habitat patches are usually variable in quality, with large patches sometimes acting as metapopulation units in their own right and small patches functioning only as temporary or semipermanent habitats (186), which are subject to changing environmental conditions and making them only differentially suitable for the suite of focal species (187).

For certain butterflies, habitat quality is more significant than patch isolation (193).

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**Adaptive management:** an approach in which there is not regimented rotational management, but rather there is spontaneous, irregular or variable management to simulate natural impacts

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This emphasizes that patch quality is the third parameter in metapopulation dynamics (in addition to habitat or patch area, and isolation). Indeed, these three factors (patch quality, patch size, and isolation) were by far the most important multiple driver for maintenance of populations of the large heath butterfly, *Coenonympha tullia* (44).

In the final analysis, large, good-quality, close-together remnants of natural habitat can play an important role as habitats (139) or as patches facilitating movement. Thus, set-aside land and the activity of land sparing (119) become an important feature of landscape management (203). However, land sparing is in need of much more development, as results from the disturbed British landscape illustrate that it is more complicated than just leaving parcels of land (57, 60). Thus, land sparing does not necessarily equate with no simulation of natural disturbance, the topic of principle 5.

### Simulate Natural Conditions and Disturbance

Any simulation of natural conditions has a temporal component as well as a spatial component. Management and restoration targets require knowledge of the character of the focal ecosystem at different times in the past and aim to simulate some time bracket. For the postglacial Northern Hemisphere, this is arguably the landscape immediately prior to the Neolithic clearances, at least in Europe. Elsewhere, where biotas were not eliminated by ice sheets, deeper time considerations may be necessary. Such simulations may not always be possible because of the current extensive and intensive landscape fragmentation and loss of certain ecological drivers such as megaherbivores. The remaining natural fragments may not be large enough to sustain the natural disturbance factors, such as herds of ungulates, or, in the case of fire, may present too much of a risk to real estate (131). This means that each reserve or set-aside piece of land generally requires a customized management strat-

egy that has clear conservation goals and is realistic and feasible. As not all options may be available, some sort of triage may be necessary, in which priority is given to the conservation goal rather than emulating what the ecosystem should look like (162), while remembering that no single management activity will suit all species (125) or all processes.

The conservation goal may be to maintain a range of ecological conditions (35, 126), ecological processes and trophic interactions (180), endemic species, or even typical species or landscapes (201). Accumulating evidence is suggesting that to address these conservation goals we need to employ adaptive management. This is illustrated by prairie butterflies (188, 190), in which most specialists increase with less frequent and/or less intrusive management. However, leaving habitat entirely unmanaged is rarely optimal, with the occasional wildfire generally more favorable for specialists than regimented rotational management. This approach also appears to suit grasshoppers in Africa, a range of North American arthropods in mixed forest (178), and butterflies in Borneo (72) and Britain (93). This adaptive management approach is an answer to the risks of applying a single management type, which would otherwise not benefit all the specialists. Swengel (188) concludes that both consistency of management type within site yet deliberate differences in management type between sites of like habitat is the best way forward. Indeed, patchy burns have the advantage that the resultant refugia become source habitats for dispersal (138), an important issue in general for insect conservation in various ecosystems (59, 152, 158).

Thus, the evidence points to retaining considerable spatiotemporal variation (which contributes to principle 2) among sites of the same ecosystem type, both in terms of megaherbivore grazing [for various taxa in various countries (7, 46, 53, 64, 65, 75, 102, 205, 219)] and fire (188, 204), as well as various special disturbance features such as tropical forest tree fall (15). In turn, domestic livestock may, in certain circumstances, be good disturbance

surrogates in the absence of indigenous mega-herbivores (155, 166, 218). A corollary is that we must never be too hasty in deciding what is appropriate for a species. After 18 years of work, it was found that fire was not necessary, as formerly thought, for the British rosy marsh moth, *Coenophila subrosea* (61), and that for some New Zealand tussock grass moths grazing is detrimental (144).

### Connect Like Patches of Quality Habitat

Corridors, or linkages, are continuous linear strips of habitat that connect and therefore improve the chance of survival of otherwise isolated populations (10). As insects are small and speciose, a landscape feature that is beneficial for a large mammal will not necessarily be beneficial for a particular insect species or even a particular individual.

Corridors have multiple roles depending on the focal organism(s) at any particular time. These roles include conduit (movement corridor), habitat, filter, barrier, source, and sink (77). Various studies (71, 149, 185, 206) have illustrated how insects move along corridors of remnant indigenous vegetation. Where these corridors are large, they may also be habitats where certain species can fulfill all their life functions (150) and where normal ecological interactions between plants and insects take place (18). Yet not all species or all individuals can move along these corridors with equal ease [or, conversely, move across the corridor (115)], making these corridors differential filters (156, 215). When dispersal along these corridors is effective, they can have an important function for population persistence (124), although such movement may not be in a straight line (11, 24, 184) nor necessarily down the middle (12). Furthermore, sensitively managed field margins (47, 56) can also encourage movement of insect species across the wider countryside (56).

Instigation and development of corridors involve not only the short-term, ecological scale of movement but also the long-term,

evolutionary scale of movement (90), which emphasizes the importance of developing ecological networks of corridors (and nodes) for conservation of both individual species (130) and biodiversity as a whole. For this function to take place, the network of corridors needs to be a source habitat. In turn, it is only acceptable as a link between habitats when it is a movement corridor or stepping stone to a new patch or habitat.

As reserves are unlikely to be enough to maintain insect species in a climatically dynamic era (103), a regional network of corridors (55) is likely to mitigate the effects of climate change. This also links with principles 3 and 4, in which reducing contrast between disturbed areas and adjacent natural areas along with land sparing all contribute to ameliorating the effects of landscape fragmentation. Although improving the landscape for population dispersal goes a long way to facing the “deadly anthropogenic cocktail” (199), it can also encourage other threatening factors such as invasive organisms, biocontrol agents pathogens, and GMOs. This means that a management program must consider all these factors as one holistic strategy while being sensitive to the nuances of individual species.

### SYNTHESIS

Threats to the world's insect fauna are often synergistic and repercussionary. Deforestation encourages weedy species, invasive aliens, and pathogens, which in turn further fragment populations, lessening their chances of moving across the landscape to survive climate change. Some principles are emerging from recent research on how we might manage the landscape for insect conservation. These principles similarly are positively synergistic and interrelated. An ideal management strategy is to maintain reserves and habitat heterogeneity while reducing the adverse impacts of the transformed matrix, setting aside quality stepping-stone habitats across that matrix, and introducing ecological and

evolutionary corridors. The outcome of this landscape management package cannot be left to its own devices, but must be adaptively managed to simulate a particular set of conditions that match the ecological conditions at some particular time in the past. This coarse-filter, landscape approach can then be overlaid with the fine-filter, species approach in spot locations to cater for in-

dividually threatened species. Such an approach always takes into consideration the importance of the combined positive effects of large patch size, good patch quality, and reduced patch isolation. Not all species will survive the current huge anthropogenic impact, and some difficult triage decisions are likely a part of future management planning for insect conservation.

#### SUMMARY POINTS

1. Threats to insect diversity are rapidly increasing, and many of these threats are synergistic.
2. Six, interrelated principles are emerging from recent research on how we might manage the landscape for insect and other biodiversity conservation.
3. An ideal management strategy is to maintain reserves (principle 1) and promote habitat heterogeneity (principle 2) while softening the disturbed matrix immediately surrounding the reserve (principle 3).
4. Outside reserves, set aside land for biodiversity (principle 4), and simulate natural conditions and disturbance (principle 5).
5. Link good-quality habitats with corridors (principle 6), which has both short-term ecological value and long-term evolutionary value and can be a buffer in the face of global climate change.
6. Permeating these six landscape principles is a population-level approach, involving the metapopulation trio, which are large patch (habitat) size, good patch quality, and reduced patch isolation.
7. Overlying these coarse-filter, landscape principles is the fine-filter, species approach, which recognizes the needs of particular species under threat.

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