How and why butterfly communities are changing

Declining butterfly communities in a changing world can be mitigated by science-informed conservation

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Thanks to their popular appeal, butterflies are better documented and monitored worldwide than any other non-pest taxon of insects[1]. In the UK alone, weekly counts of every individual seen are made on >1200 fixed routes from April to October, in a scheme whose volunteer recorders have collectively sampled more than 750,000 km of repeat transects since 1976, equivalent to walking to the moon and back counting butterflies[2]. Such programmes are revealing unsuspected declines across Europe - losses that began before 1900 in the UK and Netherlands[3,4]. A recent study of inventories of butterflies and burnet moths since 1840 in Bavaria exposes a comparable story, not only of severe species losses but of a dismal pattern of change in which scarce specialised butterflies have largely disappeared leaving ecosystems dominated by common generalist ones, and where Protected Areas failed to conserve many species for which they were famed[5]. Similar depressing trends are echoed from across Europe in 120 papers and posters presented in 2016 at the *Future4Butterflies In Europe* Conference[6].

The severity of butterfly declines is worth stressing. On the Bavarian reserve, 71 species survive compared with 117 in 1840[5], while in the Netherlands and the English county of Suffolk, 24% and 42% respectively of resident breeding species became extinct during the late 19th and 20th centuries. In contrast, declines of native vascular plant and breeding bird species were an order of magnitude lower in Holland and the UK[4]. Base-line data for insects are sparse outside Europe; nevertheless, similar declines are indicated from North America, Japan and such hotspots of butterfly endemism as Brazil, South Africa and Australia, not least among the iconic Birdwings of the Indo-Australian tropics[7-11].

Although butterflies comprise just 2% of the world's 950,000 described insect species, it is increasingly evident that their rates of loss are matched – and even exceeded - by other groups, including bumblebees, dragonflies, moths and ladybirds, whose respective social, aquatic, nocturnal and predatory life-styles make them additionally susceptible to anthropogenic environmental changes[4,13]. This matters because bees and moths are essential pollinators of numerous plants, including crops, whilst ladybirds are valued predators of insect pests. Butterflies, by comparison, contribute little to landscape functioning or ecosystem services – their value is aesthetic and as indicators of diversity – yet even here there are exceptions such as the Mountain Pride *Aeropetes tulbaghia*, the sole known pollinator of ~20 endemic plant species of southern Africa[10].

The intensification of human land-use, especially for agriculture, is the key cause of butterfly declines and of changes in community composition[2,3,6,10,12]. The main processes are illustrated in the figure. First is the fundamental loss of breeding areas, in which the essential larval foodplant(s) of almost every species are replaced by crops, sown grass leys, exotic plantations, urbanisation and other land-use changes. This has eliminated the large majority of ‘unimproved’ lowland grasslands in developed countries, a process that has started, and is often advanced, in developing ones. But butterflies (and other taxa) have also declined and changed on the fragments that survive as isolated islands of semi-natural habitats in modern landscapes, shifts that are attributable to two constraints in their population dynamics[12].

One is low adult dispersal. About 80% of known butterfly species live in ‘closed’ populations supported by small (often <2ha), discrete patches of breeding habitat, with surprisingly little migration between sites separated by >1-2km of inhospitable ground. Consequently, when populations go extinct from time to time on isolated sites – as they always have, but now do with increased frequency due to the deteriorating quality and small size of many sites – it becomes progressively less likely that vacant or new patches will be recolonised soon enough for a meta-population of interlinked populations to persist in a landscape. This unravelling leads to the disappearance of many sedentary butterflies from modern landscapes, and to a preponderance of mobile species in their depleted assemblages (see the figure).

The other constraint is the narrowness of the larval niche. Whereas the resources utilised by adult butterflies are generally catholic, exchangeable and (the Monarch apart) seldom limit numbers, the quality of caterpillar habitats is the major determinant of population densities[12]. Most larvae eat just one or a few related species of plant, but whether a butterfly is mono- or polyphagous, only a subset of potential foodplants is useable on most sites, defined by their growth form, water or nutrient quality, local microclimate or other attributes specific to the butterfly in question[12]. Furthermore, perhaps ~25% of species’ young stages interact with ants, and some require high densities of particular ant species to co-occur with the foodplant. Almost every butterfly niche studied was found to be more critical than had been supposed, although in conservation it is still convenient to class species into two types: specialists (~60% species) and the common ‘wider countryside generalists’. The former group live predominantly in closed populations whereas roughly half the latter are more mobile.

A less conspicuous process that drives change in butterfly assemblages is a shift or subtle degradation of these larval habitats within surviving fragments of ecosystem (see the figure) [2,6,12]. Many unproductive grasslands, especially hillsides, that once experienced intermittent low-intensity grazing are today abandoned as uneconomic to farm, whilst much woodland management has shifted to produce mature crops of (often exotic) tree species, very unlike the frequent small-scale disturbances generated by coppicing and other defunct practices. Both processes lead to greater uniformity in the habitats available to butterfly larvae, and typically to a shift from early and mid-successional stages of vegetation to taller, denser, shadier ones. This may benefit a few common generalist species, but again at the expense of numerous specialists. More insidious still are landscape-scale degradations from pollution (especially increased Nitrogen), drainage schemes, and climate change. The last is considered to have had a largely neutral impact on butterfly populations to date, enhancing numbers and expansions in the cooler sectors of species’ climatic ranges whilst depleting them in warmer parts[14]. However, the increased frequency of extreme weather, especially drought, and projections for future climate impacts are universally harmful[2,6,12].

It is disappointing that many Protected Areas (PAs) have failed to conserve their butterfly assemblages despite their plant diversity being unchanged[6,12]. Encouragingly, a better understanding of different species' ecologies and of the processes driving population changes makes it possible to restore appropriate management or hydrological regimes. In practice, restoration plans are often biased towards a few Endangered Species that nevertheless prove to be sensitive umbrellas for a diversity of other rarities that thrive under their treatments[6,15]. Consequently, four of the six nationally threatened butterflies that became extinct on all or most of their UK reserves in 1960-89 have now returned to a greater representation on PAs than ever before[12]. The most ambitious of these was the reintroduction in 1982 -91 of the previously extinct specialist *Maculinea arion*, which has already spread to a third of the ~100 PAs that receive targeted management for it, and which today support some of the world's largest known populations of this iconic, globally threatened species (see picture and caption)[12,15].

Although the factors driving change in butterfly assemblages are best understood in Europe, there is evidence of similar processes occurring in developed and developing nations worldwide, for example in Brazil's surviving fragments of Atlantic Forest[7] and in USA prairie grassland[8]. Equally disturbing is the decline of the north American Monarch *Danaus plexippus*, from 1 billion to 33 million adults in the past 25 years: this however is a highly atypical species, made doubly vulnerable by possessing specialised larvae, exceptional in a migrant, and by the adult trait of congregating overwinter in mainly one vast Mexican roost[9].

It is reassuring that some of the most challenging species' declines can, and have been, reversed by new conservation practices informed by ecological study[2,6,12,15], but such measures are expensive. A higher priority is to assess and protect the remaining global hotspots for butterfly diversity[10]; to establish a comprehensive suite of more local reserves; and to understand and conserve the historical successions and dynamics of their ecosystems, whether these be primary forest, natural grasslands, or the low-input pastoral landscapes that survive in many developing nations, including eastern Europe[6]. Monitoring change in butterfly assemblages is an essential first step[4]: it is thus encouraging that the rigorous schemes in Europe are being extended to richer regions such as South Africa, China and Australia[10]. Urgent too is the need for further research, to explore how well the drivers of declines identified in temperate regions apply to the tropics, and to assess the plasticity of butterfly phenotypes to adapt to future climatic and land-use changes.

REFERENCES AND NOTES

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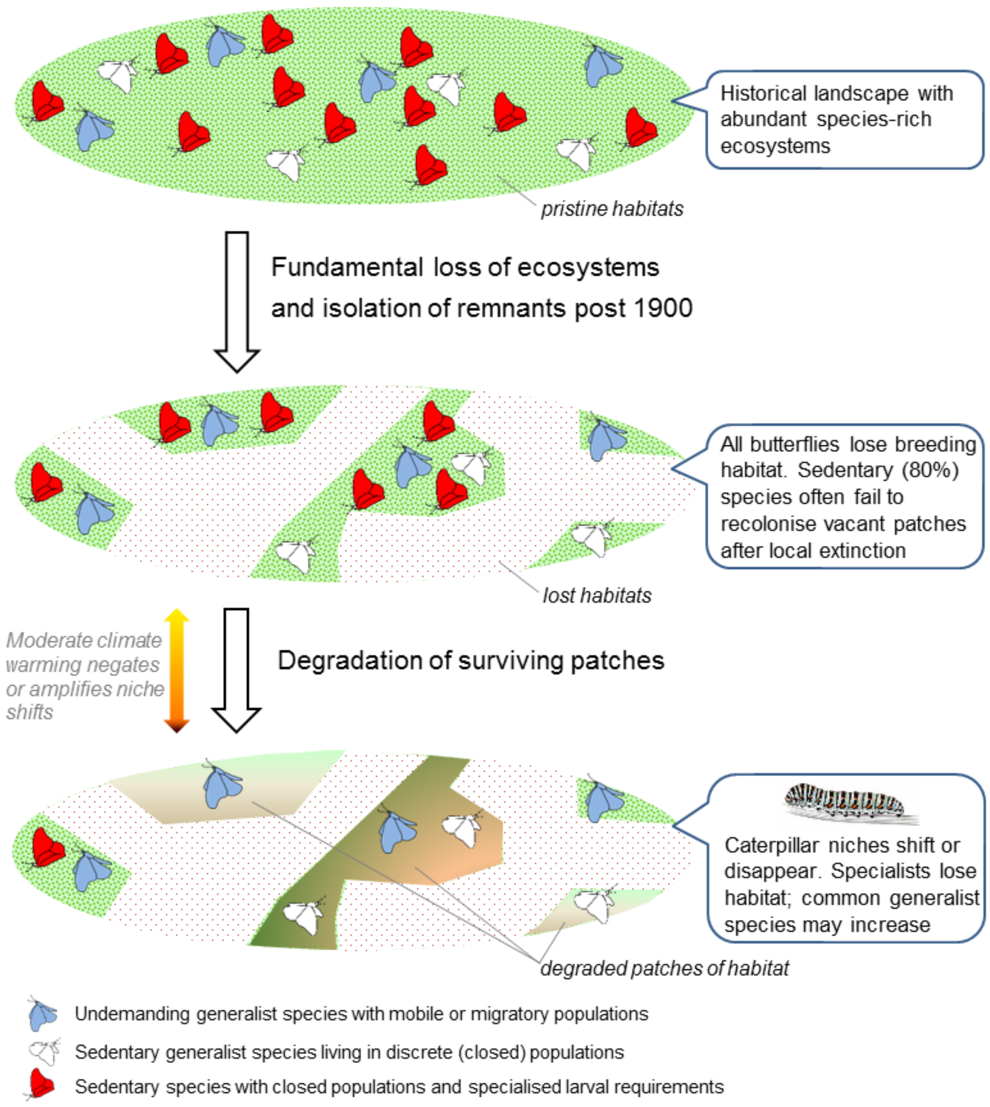
Main figure



Trends in butterfly assemblages during a century of anthropogenic change. Modern land-use destroys most ecosystems as breeding areas for butterflies. The surviving remnants are typically isolated and also experience degradations in the range and quality of their habitats. The net impact is the loss of the more specialised sedentary rarities that once dominated species-rich ecosystems, with surviving fragments supporting a subset of common generalist species, especially those with mobile or migratory adults. Many of the detrimental changes in surviving habitats can be reversed by targeted, science-based conservation management.

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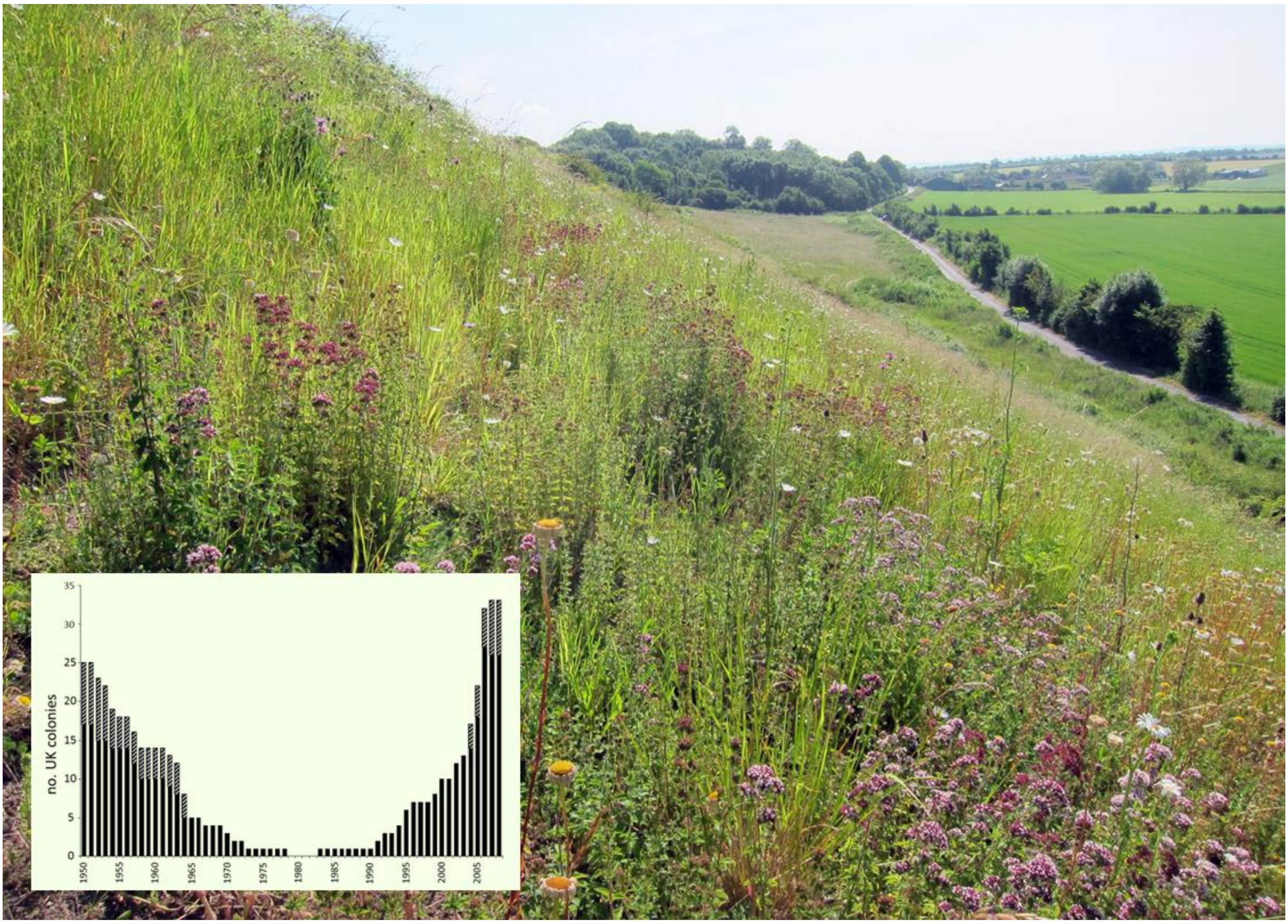

Following extinction in the UK in 1979, the globally threatened butterfly *Maculinea arion* was successfully re-introduced using a similar genotype from Sweden and has now spread to ~35 sites (inset), each specifically managed to contain the optimum larval habitat and also located within the quinquennial adult colonisation ranges of 5-11 other populations[15]. New sites include this 5ha railway embankment, designed and created from scratch in 2004.