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PERSPECTIVES

ECOLOGY

Butterfly communities under threat

Butterfly populations are declining worldwide as a result of habitat loss and degradation

By **Jeremy A. Thomas**

Butterflies are better documented and monitored worldwide than any other nonpest taxon of insects (*1*). In the United Kingdom alone, volunteer recorders have sampled more than 750,000 km of repeat transects since 1976, equivalent to walking to the Moon and back counting butterflies (*2*). Such programs are revealing regional extinctions and population declines that began before 1900 (*3, 4*). In a recent study, Habel *et al.* report a similar story based on inventories of butterflies and burnet moths since 1840 in a protected area in Bavaria, Germany (*5*). The results reveal severe species losses: Scarce, specialized butterflies have largely disappeared, leaving ecosystems dominated by common generalist ones. Similar trends are seen across Europe (*6*) and beyond, with protected areas failing to conserve many species for which they were once famed.

The butterfly losses are severe. On the Bavarian reserve, Habel *et al.* found that 71 species survive compared with 117 in 1840 (*5*). 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—an order of magnitude more than the population declines and regional and national extinctions of native vascular plant and breeding bird species (*4*). Baseline data for insects are sparse outside Europe. Nevertheless, there is evidence for similar declines in North America, Japan, and hotspots of butterfly endemism such as Brazil, South Africa, and Australia, not

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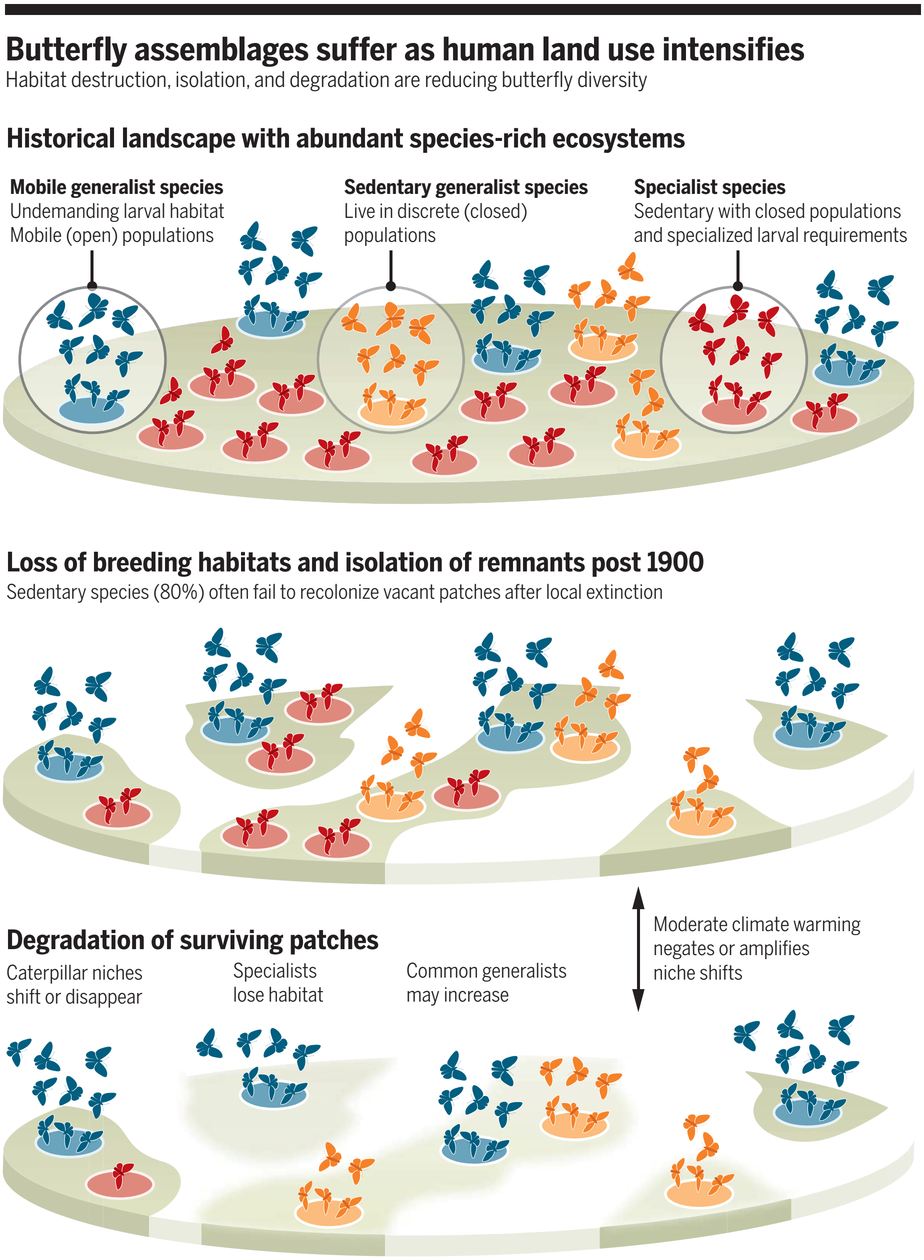
Following extinction in the United Kingdom in 1979, the globally threatened large blue (*Maculinea arion*, see photo) was successfully reintroduced using a similar genotype from Sweden. It has now spread to about 35 protected areas (*16*).



least among the iconic birdwings of the Indo-Australian tropics (*7–11*).

Butterflies constitute just 2% of the world's 950,000 described insect species, but 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 lifestyles make them particularly susceptible to environmental changes caused by humans (*4, 12, 13*). This matters because bees and moths are essential pollinators of numerous plants, including crops, while ladybirds are valued predators of insect pests. Butterflies, by comparison, contribute little to landscape functioning or ecosystem services. Their value for humans is largely aesthetic and as indicators of diversity. Yet, even here there are exceptions, such as the mountain pride (*Aeropetes tulbaghia*), the sole known pollinator of about 20 endemic plant species of southern Africa (*10*).

LOSS OF BREEDING AREAS

The intensification of human land use, especially for agriculture, is the main cause of butterfly declines and of changes in community composition (see the figure) (*2, 3, 6, 10, 14*). One process that drives changes in butterfly assemblages is a fundamental loss of breeding areas as essential larval food plants are replaced by crops, sown grass leys, exotic plantations, urbanization, and other land-use changes. These changes have eliminated most traditional, species-rich lowland grasslands in developed countries, a process that has started and is often advanced in developing ones. Butterflies and other taxa have, however, also declined and changed on the fragments that survive as isolated islands of seminatural habitats in modern landscapes. These shifts are attributable to two constraints in their population dynamics (*14*).

One constraint is low adult dispersal. About 80% of known butterfly species live in closed populations supported by small (often less than 2 ha), discrete patches of breeding habitat, with little migration between sites separated by more than 1 to 2 km of inhospitable ground. When populations go extinct from time to time on isolated sites—as they always have, but now do with increased frequency owing to the deteriorating quality and small size of many sites—it becomes progressively less likely that vacant or new patches will be recolonized quickly enough for a metapopulation of interlinked populations to persist in a landscape. This process 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 specialism of the larval habitat or niche. Whereas adult butterflies generally use wide-ranging, exchangeable resources that (the monarch apart) seldom limit their numbers, the quality of caterpillar habitats is the major determinant of population densities (*14*). Most larvae eat just one or a few related plant species, of which only a subset is palatable on most sites, defined by their nutrient quality, growth form, microclimate, or other attributes specific to the butterfly in question (*14*). Furthermore, about 25% of butterfly species interact with ants in their young stages; some require high densities of particular ant species to co-occur with the food plant. Almost every butterfly niche studied has been found to be more fastidious than had been supposed (*14*), but it is still convenient to class species into two types: specialists (~60% species) and the common wider countryside generalists. The former live mainly in closed populations, whereas roughly half of the latter are more mobile.

HABITAT DEGRADATION

The second, less conspicuous process that drives change in butterfly assemblages is a shift or subtle degradation of larval habitats

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in surviving fragments of ecosystem (see the figure) (*2, 6, 14*). Many unproductive grasslands, especially hillsides, that once experienced intermittent low-intensity grazing are today abandoned as uneconomic to farm. At the same time, much woodland management has shifted to producing mature crops of (often exotic) tree species, very unlike the frequent small-scale disturbances generated by coppicing (in which trees or shrubs are periodically cut back to ground level to stimulate growth) 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 is landscape-scale degradation from pollution (especially increased nitrogen concentrations), 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 while depleting them in warmer parts (*15*). However, the increased frequency of extreme weather and projections for future climate impacts, including increased droughts, are universally harmful (*2, 6, 14*).

It is disappointing that many protected areas have failed to conserve their butterfly assemblages despite unchanged plant diversity (*6, 14*). A better understanding of species ecologies and of the processes that drive population changes makes it possible to restore suitable conditions. In practice, restoration often focuses on a few endangered species that nevertheless prove to be umbrellas for numerous other rarities that thrive under their treatments (*6, 16*). Thus, four of the six nationally threatened butterflies that became extinct on all or most of their UK reserves between 1960 and 1989 have now returned to a greater representation in protected areas than previously recorded (*12*), including the large blue *Maculinea arion*, an iconic habitat specialist (see the photo) (*14, 16*).

A WORLDWIDE PROBLEM

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 U.S. prairie grasslands (*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 specialized larvae, exceptional in a migrant, and by the adult trait of overwintering mostly in one vast Mexican reserve (*9*).

It is reassuring that some of the most challenging species' declines can be reversed by conservation practices informed by ecological study (*2, 6, 14, 16*), 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, be they 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 other regions such as South Africa, China, and Australia (*10*). Urgent, too, is the need for 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. ■

> ***"...many protected areas have failed to conserve their butterfly assemblages despite unchanged plant diversity."***

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GENE EXPRESSION

Chromatin controls behavior

Dynamic regulation of chromatin remodeling controls learning and memory

By **J. David Sweatt**

Chromatin structure stabilizes and compacts the genome to package it within the nucleus. This structure also serves as a dynamic regulator of gene expression, silencing or activating transcription depending on molecular signals impinging upon it. It has been understood for the past two decades that chromatin stabilizes gene readout after cell-fate determination, establishing and perpetuating the precise pattern of genes transcribed in a given cell to maintain its phenotype (*1, 2*). But what about dynamic regulation of chromatin structure and its biological role? On page 300 of this issue, Yang *et al.* (*3*) describe how dynamic regulation of chromatin remodeling controls cerebellar circuit development, function, and cerebellum-dependent learning and memory, and challenge prevailing epigenetics dogma in the central nervous system.

One process that controls chromatin structure and transcription is chromatin remodeling by energy-dependent protein complexes (*4*). Such complexes that depend on adenosine 5′-triphosphate (ATP) can control gene expression by moving, ejecting, or restructuring nucleosomes, the scaffolds around which DNA wraps. Each nucleosome contains a core particle of eight histone protein subunits (*5*). Remodeling events include posttranslational modifications, swapping individual histone subunit isoforms into and out of the core particle, and facilitating the unbinding of DNA from the core particle.

The nucleosome remodeling and deacetylase (NuRD) complex catalyzes dynamic ATP-dependent nucleosome remodeling (*6, 7*). Among its constituent subunits are histone deacetylases (HDACs), chromodomain helicase DNA binding protein 3 or 4 (CHD3/4), and methyl-CpG binding domain protein 3 (MBD3). CHD4 is necessary for

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