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Insects on the brink of a major discontinuity

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Population surges and local extinctions are not uncommon among insects. In response to climatic changes in the past, insects have often shifted their ranges. This long-term range shifting and the vagaries of short-term weather makes reserve selection unrealistically rigid for many species. Although some insect species are surviving in reserves, others have disappeared from such small areas because of adverse weather. In contrast, many other insects depend on localized disturbance for survival. In response to anthropogenic disturbance, some native insects have become more abundant and widespread, such as Orthoptera in response to grazing and burning, and some Odonata in response to aquatic weeds and water impoundment. The effect of some exotic invasive insects on some native ecosystems is of major concern. Human-induced insect population crashes and species extinctions are becoming more common and widespread, and exacerbated by the synergistic effect of the various local impacts with global changes. A major insect population and species extinction discontinuity is beginning to take place. Yet, there is also an increase in range and abundance of some other insects. The world is becoming increasingly species-poorer and more homogenous in its insect fauna.

Keywords: insects; populations; landscapes; conservation; discontinuity.

Introduction

Fragmentation of landscapes into mosaics is a vast unplanned experiment. As insects are a major component, both as individuals and as species, it is likely that this landscape change is having a major impact on their population levels, patterns and distributions.

I review here the question of whether these changes are linear and gradual or non-linear and sudden, i.e. discontinuous. Such discontinuities, may be defined as 'environmental responses disproportionate to changes in stimuli, with scope to threaten adaptive capacities of both biotas and ourselves' (Myers, 1996).

I first ascertain whether such discontinuities occur in the absence of anthropogenic impact, before conclusions can be drawn on how humans have discontinuously disrupted insect populations. This overview makes a first assessment.

The situation without humans

Natural insect-population surges and range increases

Whittaker (1975) identified three hypothetical types of population fluctuation. The first fluctuates near carrying capacity, the second fluctuates more widely at a range of densities between lower and upper carrying capacity limits, and the third fluctuates near the lower limit, usually being rare but showing occasional or periodic outbreaks.

Some insects which inhabit fairly constant environmental conditions and with finite resources, follow the first model (e.g. cave insects (Carchini *et al.*, 1983)). Population stability also occurs in many insect herbivores utilizing rapidly-growing and juvenile plant modules, and is determined by the low but persistent generation of such modules in a host–plant population (Price *et al.*, 1995a).

For insect populations, the second two models are mostly appropriate, especially the third, with population surges being most common (e.g. moths (Varley *et al.*, 1983), acridids (Uvarov, 1977; Lockwood and Schell, 1995), a seed-feeding bug (Solbreck, 1995), hoverflies (Owen, 1991) and ladybirds (Majerus, 1994), and various tropical insects (Wolda (1983 *et ante*)).

As widespread insects tend to be locally more abundant (Lawton, 1993), temporal surges may also be associated with increases in range. Indeed, range increase is a hallmark of new pest insects, especially those that have been accidentally introduced and have spatially escaped natural enemy regulation. However, some insects have naturally increased their range (e.g. the small skipper butterfly *Thymelicus sylvestris* in England (Pollard and Yates, 1993) and the monarch butterfly *Danaus plexippus* reaching the Canaries and Spain (Vane-Wright, 1986)). However, with the huge human traffic worldwide, some range expansion is both natural and artificial (e.g. the ladybird, *Chilocorus nigritus* (Samways, 1984)).

Natural crashes in insect populations

Insect populations often become extinct (Dempster, 1989), and, long-term survival of a species at a locality may rely on a flux of individuals (Ehrlich and Murphy, 1987). Such metapopulations provide novel patterns of genetic variation associated with short bottlenecks (Brakefield, 1991). However, bottlenecks extending over many generations may lessen the population's chance of adapting to future environmental perturbations.

Coope's (1995) evidence from Quaternary fossil insects suggests that, in the past, many insect species altered their geographical ranges by tracking climatic changes, with species extinctions on a global scale being uncommon. Although, in the last century two species of South African lycaenid butterflies may have become extinct naturally: *Deloneura immaculata* was last seen in the East Cape in 1864, and *Lepidochrysops hypopolia* was last recorded from the central savanna area in 1879 (Henning and Henning, 1989).

Necessity of natural disturbance

Many insects need periodic natural disturbance. The southern pine beetle (*Dendroctonus frontalis*) in the USA (Schowalter, 1985) and many savanna insects (Warren *et al.*, 1987) as well as some ecosystems (Stein *et al.*, 1992) need fire, while the forest gap-inhabiting grasshopper, *Microtylopteryx hebardi*, requires tree falls for sunny patches (Braker, 1991). Fire, as with other destruction of mature plant growth, also results in rapid regeneration of plant modules to which many insect herbivores are adapted (Price *et al.*, 1995b). These disturbances are relatively localized and the insects mobile. Even the flightless *M. hebardi* soon finds light gaps in the forest, while grasshoppers readily fly away from the advancing fire. These disturbances may provide for growth of a foodplant, change in microclimate for development, or avoidance of disease and parasitoids, among other subtle life-support requirements. Indeed, many insects need change, with the various morphs (especially developmental morphs) sometimes requiring quite different disturbances (Samways, 1993).

Human-induced booms

Agriculture and forestry

Replacement of natural vegetation by an irrigated and fertilized monocrop can cause insect population surges with loss of other species. In the dry savanna of South Africa, islands of citrus produce high resident populations of the indigenous thrips *Scirtothrips aurantii* (Samways *et al.*, 1987) and the psyllid *Trioza erytraea* (Samways, 1987), while reducing, for example, the epigaeic ant fauna (Samways, 1989a). Such thrips and psyllid populations are notoriously difficult to control biologically, which encourages the use of pesticides. This in turn, is further damaging to other insects (e.g. ants in citrus: Samways, 1981). In contrast, other approaches such as polycropping (Andow, 1991), and chemically untreated conservation headlands (Dover, 1991) and the planting of habitat islands to encourage natural predators (Wratten and van Emden, 1995), can lessen these discontinuous population upsurges.

There is also a time factor. Andow and Imura (1994) suggest that although Japanese arthropod species numbers equilibrate with crop area, the communities appear to become more specialized over a long time (<2400 years).

The resultant impacts from agricultural development can be enormous. Ngxongo (1993), for example, showed that rice paddies cause an instantaneous and huge increase in the number of people with malaria, through an increase in breeding sites for the vector *Anopheles arabiensis*.

The response of some insect parasites of birds is complex once the forests are fragmented and bird population levels change (Loye and Carroll, 1995). This results in rare birds, which are already threatened, being put under even more pressure from an increased ectoparasite load.

Grazing by livestock

Grazing alters vegetation physiognomy and species composition, which, in turn, influences the abundance, both negatively and positively, of various insect taxa (Morris, 1991; Thomas, 1991). Overgrazing, besides depauperating fauna, can cause a population surge in some species, sometimes resulting in swarming behaviour when a mosaic of bare ground and vegetation is created (e.g. Orthoptera species: *Dociostaurus maroccanus* (Dempster, 1957), *Stenobothrus lineatus, Omocestus haemorrhoidalis* and *Chorthippus dorsatus* (Bei-Bienko, 1970)).

Exotic invasives and damming of waterways

Wildlife and invasion of exotic annual vegetation can cause outbreaks of the grasshopper *Melanoplus sanguinipes* (Fielding and Brusven, 1993). Exotic invasives generally reduce insect diversity (Samways *et al.*, 1996) but invasive waterweeds such as *Eichhornia crassipes* and *Pistia stratiotes* can increase Odonata species richness and abundance on rivers (Stewart, 1993), while establishment of the water weed *Salvinia auriculata* on Lake Kariba instantly provided conditions for the now-common damselfly *Pseudagrion nubicum* (Balinsky, 1967).

Dragonflies are good indicators of landscape change. In South Africa, farm dams increase the area of occupancy (*sensu* Gaston, 1994) of many species, but these are mostly eurytopic and vagile (Samways, 1989b), with a succession of species as the body of water matures (Moore, 1991; Osborn and Samways, 1996). Stenotopic and locally rare species are slow to appear, and only when biotic and abiotic conditions are exactly suitable (Steytler and Samways, 1995).

Similarly, creating stands of water, even small ones in cans, bags and tyres, can increase the range and population level of certain medical insects (Craig, 1993).

Forest clearing

Forest clearances, combined with a cooling of 2–3°C over the last 4500 years in Britain, may have prevented some butterflies, which are restricted to warm microclimates, from becoming extinct. Two points are significant here: (1) forest clearances are not necessarily detrimental to all species, and (2) time since the clearance allows some sort of modified plagioclimax to occur (Thomas, 1991). Without management of clearances however, succession occurs, which encourages a range of insect communities (Usher and Jefferson, 1991). The impact of management is seen with the Lulworth skipper butterfly, *Thymelicus lineola*, which is probably as abundant as it always has been in historic times through fairly regular and intense grassland management (especially grazing) in southern England (Morris, 1991).

Exotic invasives

Invasives spreading across native ecosystems are of particular concern (New, 1994a). Even a single invasive species can threaten a whole ecosystem, such as the Argentine ant, *Iridomyrmex humilis*, which is displacing the native myrmecochorous ants of the South African fynbos (Bond and Slingsby, 1984).

Exotic invasives can be most abundant at the first point of establishment, e.g. *Chilocorus nigritus* occurs in highest numbers where it was first discovered in the southern lowveld of South Africa (Samways, 1984).

Exotic invasives are one of the greatest threats to ecosystem integrity. Some invasives, such as aphids in Australia, cause such an impact that their arrival can be pin-pointed to within a few months (New, 1994a). Indeed, exotic invasives, of taxa besides insects, are highly threatening to biodiversity conservation, especially on islands (Howarth and Ramsay, 1991).

Not all new insect arrivals are invasive and abundant. Some tend to remain at relatively low, stable levels through suppression by native parasitoids, as with the European moth *Phyllonorycter messaniella* in Melbourne, Australia (New, 1994a).

Human-induced crashes

Population extinction

Insect population extinction from human activity is now common, and can be instantaneous or extended. One population of the katydid *Platycleis fedtshenkoi azami* was obliterated by the dumping of dredged silt in Southern France, while another population was gradually eliminated by increasing fragmentation of its habitat with the development of Montpellier airport (Samways, 1989c). Also, Kindvall and Ahlén (1992) have shown that, for a closely-related species, *Metrioptera bicolor*, small (<0.5 ha) and isolated patches (>100 m from source patches) cannot sustain populations.

Some fragmentation (McCauley, 1993) and short and small genetic bottlenecks (Brakefield, 1991) might actually enhance evolutionary adaptiveness. Certainly, some species thrive on landscape disturbance provided it is not too severe or frequent (Turner and Gardner, 1991). Also, some species, such as the grasshopper, *Chorthippus brunneus* in Britain, have benefitted from disturbed land and roadside verges (Port and Thompson, 1980).

The initial picture from fragmentation may not be the final one. Tilman *et al.* (1994) point out that habitat destruction may cause time-delayed but deterministic extinction of the dominant competitor in remnant patches. More species may then become extinct, in order from the best to poorest competitors, as habitat destruction increases. The models of Tilman *et al.* (1994) also suggest that the more fragmented the habitat already is, the greater is the number of population extinctions caused by added destruction, even many generations later. Where mutualists are involved, this could have even further repercussions (Bond, 1994). Then, when habitat destruction brings a community below its critical spatial size, the system may collapse (Hassell *et al.*, 1994).

Species extinction

Occasionally a narrow endemic taxon becomes extinct because the anthropogenic impact coincides exactly and strongly with the exact locality of the species. The Antioch Dune katydid *Neduba extincta* was last seen in 1937 before its demise came with expanding San Francisco (Rentz, 1993)

Although 71% of threatened species (Groombridge, 1993) are confined to one country, the converse (having a large geographical range) does not always guarantee survival. The Rocky Mountain grasshopper *Melanoplus spretus* which, in the mid 1800s, was a widespread agricultural pest in the western North America, was extinct by 1902 (Lockwood and De Brey, 1990). This was a single species discontinuity, from pest status to non-existence in three decades.

Loss of species from reserves – the risk of gap analysis for insect conservation

Gap analysis ascertains which species are in reserves and where reserves should be sited, whether for richness or for endemism (Lombard, 1995). Gap analyses have been used to determine endemism hotspots in insects and to establish whether threatened insects are situated in reserves or not (e.g. butterflies (Rebelo, 1992)).

Some insects, such as the dung beetle *Circellium bacchus*, once widespread in Southern Africa, is now restricted to one small area of the Eastern and Southern Cape (Scholtz and

Chown, 1993) where umbrella vertebrate species accord it protection in reserves. But for some other insects, presence in a reserve does not guarantee survival. The rare South African dragonflies *Orthetrum robustum, O. brachiale, O. guineense* and *O. hintzi* were in Kwazulu-Natal reserves in 1990, but by 1994, with intervening dry years, they disappeared.

Generalizations however, are difficult. Certain species, such as some lycaenid butterflies, may survive in a small reserve. The creation of the 12 ha Ruimsig Entomological Reserve in South Africa (Henning and Henning, 1985) for the threatened lycaenid *Aloeides dentatis dentatis* has been a success. In short, gap analysis is worthwhile providing there is some knowledge of how the species will respond to a remnant patch of a particular size and quality. This, however, is a circular argument, because success cannot be determined until the reserve is created.

Discussion

Mawdsley and Stork (1995) suggest that between 100 000 and 500 000 species of insect may become extinct in the next 300 years. On a geological time-scale, this is instantaneous. In short, the biotic world, as manifested by its most speciose component, the insects, is undergoing rapid change (Table 1). The effect is also compound, as insects are involved in so many multi-species interactions (Price, 1988; Miller, 1993), whether as prey, predator, parasite, pollinator or herbivore.

Even vertebrate extinctions can lead to insect extinctions. At least two species of lice became extinct with the passenger pigeon *Ectopistes migratorius* (Stork and Lyal, 1993). Then, in about the last 1000 years, 2000 species of birds have become extinct by humans (Pimm, 1995). Similar situations probably also occurred with extinction of the dinosaurs (Price, 1988). So how many insects may have vanished without a trace?

Table 1. Magnitude of insect response to anthropogenic changes to ecosystems

	Situation	
Variable	Without humans	With humans
Population surges	Common	Common
Range increase	Rare	Common (often species reach pest status) (N.B. Some range increases are deliberate, especially biocontrol agents)
Population fragmentation (through landscape fragmentation, habitat loss, impact of exotic invasives, etc.)	Rare	Very common
Population crashes	Fairly common	Common (N.B. Closely related with 'population fragmentation')
Species extinctions	Occasional	Becoming common and widespread
Loss of species from reserves	N/A	Does occur occasionally

There is also the possibility that 60 000 plant species will become extinct or threatened by the year 2050, and as there are about 30–40 animal species per plant species, and possibly about 10 species directly or indirectly dependent on any particular plant species, there is going to be a cascade through habitat loss and landscape fragmentation. There may also be more pervasive, synergistic interactions (Myers, 1993), such as interactive global climate changes on plants (Caldwell *et al.*, 1995), phenological asynchrony between plant host and insect in an elevated CO_2 environment (Watt *et al.*, 1995), range changes in response to elevated global temperatures (Dennis and Shreeve, 1991; Harrington and Stork, 1995), and delayed intrinsic factors associated with landscape fragmentation (Hassell *et al.*, 1994; Tilman *et al.*, 1994).

Possibly a discontinuity has already begun. The county of Suffolk in England has already lost 42% of its butterfly species this century (Thomas, 1989). And as tropical insects are so sensitive, especially to drought (Parsons, 1989) and to temperature changes (Greenwood, 1987), there is almost certainly going to be a major loss in the tropics.

Conserving ecosystems of which insects are parts of the processes

With the loss of about 20% of insect species, yet some thriving in the changed environment, which are the ones we should conserve? New (1994b) proposed concentrating on a restricted 'umbrella suite' of ecologically important taxa. But it might be more effective to conserve examples of choice, as well as typical, *landscapes* and *all* their processes (Samways, 1994). Insects and other invertebrates, in view of their sensitivity to ecosystem change, can then be used to monitor the success of the conservation effort. This landscape approach can be supplemented with conservation of certain threatened taxa or phenomena. The large-scale landscape approach coupled with a few flagship autecological programmes may ameliorate this inevitable discontinuity.

Conclusions

Insect population losses and species extinctions are common in nature. Range shifts and population booms also occur. However, through deliberate and accidental human agency, there is now a hugely increased world-wide movement of insects. In addition, at least in agro-ecosystems, there are also outbreaks of *indigenous* insects. Yet, much more significantly, many other indigenous insects are becoming extinct. Clearly, insects are undergoing major change in two areas: (1) the world insect fauna is becoming more homogeneous, and (2) insect extinction rates are becoming very high.

The evidence so far does *not* indicate a current major insect discontinuity in the strict sense of Myers (1996). However, as insects are often keystone in ecological processes (hence their successful use in biological control), it is probable that the current changes in insect populations will become more acute, and in the near future undergo a major discontinuity, as are many ecosystems (Fig. 1). Amelioration of this insect discontinuity would be best achieved by keeping as many and as large as possible tracts of undegraded land.

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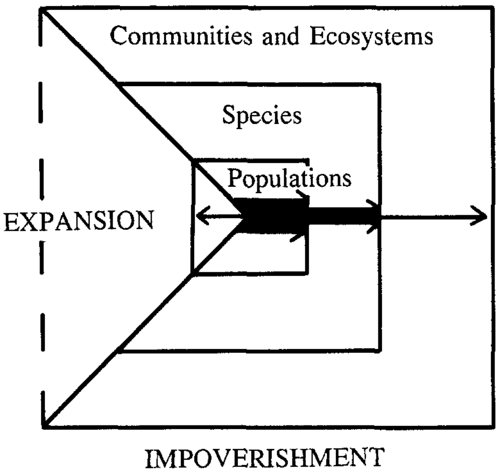

Figure 1. Insect discontinuities today. Discontinuities (arrows) may be considered at three levels: populations, species and communities and ecosystems. Extent of the discontinuities (width of arrow shafts) is already great for insect populations, many of which are becoming impoverished, but some also are expanding. Species discontinuities (i.e. species extinction rates) are also just beginning. In turn, communities and ecosystems are similarly starting to show discontinuities, and as insects are a major component of these systems, they are integral to those discontinuities. (N.B. Species are not 'expanding', i.e. species richness is not increasing beyond the background rate.) Many anthropogenically-disturbed communities and ecosystems, e.g. cattle-grazed grassland, are expanding (dotted line).

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