

## Insects in fragmented forests: a functional approach

Raphael K. Didham  
Jaboury Ghazoul  
Nigel E. Stork  
Andrew J. Davis

**Insects are highly susceptible to the adverse effects of forest fragmentation. It is now beyond any doubt that fragmentation-induced changes in abundance and species richness occur in many insect groups. However, the study of insects in fragmented forests is still in its infancy and lacks real direction. Simple empirical studies are not answering the questions we most want to answer about fragmented systems. Are we in the midst of a mass-extinction crisis? What is the functional significance of the immense insect biodiversity? Does biodiversity loss affect ecosystem functioning? A more focused, functional approach to the study of forest fragmentation is required to move beyond the description of pattern and to determine how changes in insect communities affect ecosystem processes in fragmented forests.**

Raphael Didham and Jaboury Ghazoul are at the Biodiversity Division, Dept of Entomology, The Natural History Museum, Cromwell Road, London, UK SW7 5BD;

Raphael Didham is also at the NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, UK SL5 7PY;

Nigel Stork is at the Cooperative Research Centre for Tropical Rainforest Ecology and Management, James Cook University, PO Box 6811, Cairns, Queensland 4870, Australia;

Andrew Davis is at the Danum Valley Field Centre, Rakyat Berjaya, Sdn Bhd PO Box 282, 91108 Lahad Datu, Sabah, Malaysia.

The nature of land-use change in recent decades has not only resulted in a dramatic decrease in total forest cover, but also in an increasingly skewed size-distribution of forest remnants. Forest fragmentation is an important process contributing to the present-day concern over the loss of biodiversity and rates of species extinction. There is now an urgent need to identify the key effects of forest fragmentation on biotic systems and to find management solutions.

It is widely speculated, through extrapolation from the limited data available, that isolation and fragmentation-induced changes in forest structure may cause the disruption of those biological processes that maintain biodiversity and ecosystem functioning, such as pollination, seed dispersal and nutrient recycling. To a large degree these processes are mediated by insects<sup>1</sup>. What is known, at least in very general terms (detailed below), is that forest fragmentation not only influences the abundance and diversity of insects, but also modifies higher-order interactions between insects and other organisms, both directly and indirectly.

While the ecological roles of insects are occasionally well-documented, the effects of forest fragmentation on insect populations are poorly understood and

the empirical data diffuse and contrasting. Here, we take a functional approach to what is known of the effects of forest fragmentation on insects in order to develop a clearly defined focus to future research. In particular, we look at four functional groups of insects representing processes that are critical for the maintenance of forest ecosystems: pollinators, seed predators, parasitoids and decomposers. We are concerned with fragmentation of all forest types, but emphasis is placed on tropical forest systems, which support a large proportion of the earth's terrestrial biodiversity and where the greatest complexity of biotic interactions occurs. Evidence from non-forest systems is also used where appropriate. The main processes affecting biotic communities in forest fragments (area, degree of isolation, edge effects, fragment shape and habitat connectivity) have been reviewed elsewhere<sup>2-4</sup>. While this discussion centres largely around the biological impact of forest fragmentation, there is evidence to suggest that abiotic factors (particularly edge effects) are one of the main driving forces behind changes in insect population levels in forest fragments<sup>5</sup>. Abiotic factors will have differential effects on different species, leading to important impacts on ecosystem functioning.

### Pollinators

Fragmentation-induced changes in the structure of the pollinator guild may have far-reaching consequences for gene flow in plant populations and for plant and animal community dynamics. Many groups of insects are known to pollinate plants, but bees are probably the most important pollinator group in number and diversity of plant species pollinated<sup>6</sup>. Pollination has been shown to be directly affected by fragmentation through a reduction in the abundance and species richness of pollinators, and also indirectly by the alteration of their behaviour and flight patterns. For example, both the abundance and species richness of euglossine bees declines in small forest fragments<sup>7,8</sup> (Fig. 1a), resulting in reduced flower pollination<sup>9</sup>. Such losses might be ameliorated to some extent by replacement with generalist foragers<sup>9,10</sup>, but these foragers are frequently less efficient pollinators than the oligolectic bees that visit a few closely related plants<sup>11</sup>. This is particularly true in habitats where many of the biotic components are part of co-evolved mutualistic interactions. Results from studies of hummingbird-pollinated plants support the prediction that generalized plants are less affected by a reduction in pollinator diversity than specialized plants<sup>12</sup>. However, there have been few studies that have demonstrated changes in pollinator diversity and abundance that cause a reduction in plant reproductive success in small isolated fragments<sup>9,13,14</sup> (Fig. 1b).

Insect-mediated pollen transfer between forest islands might be facilitated by long-distance foragers, such as bees<sup>11</sup> and butterflies<sup>15</sup>. Powell and Powell<sup>7</sup> showed that male euglossine bees failed to cross narrow (100 m wide) cleared areas, possibly because of altered microclimatic conditions, and Chan<sup>16</sup> suggested that fruit production was lower on isolated than non-isolated trees (although the sample size for isolated trees was low). There is some evidence to suggest that fruit set may be resource-limited rather than pollination-limited, and thus reduced pollination may have little impact on plant population dynamics<sup>17</sup>. Nonetheless, restricted pollen flow resulting from fragmentation may reduce both the genetic variability of progeny and the effective genetic neighbourhood size (particularly of woody species) causing inbreeding depression and changes in the long-term stability of insular populations<sup>18</sup>, though there have been too few large-scale and long-term studies to draw firm conclusions.

The evolutionary responses of isolated plant populations to a changing pollinator guild have been poorly documented. Plant species on islands tend to be more readily self-fertile and to have more generalized

pollination systems than their mainland counterparts, because of decreased pollinator availability<sup>19</sup>. Plants that increase their attractiveness to pollinators may overcome problems associated with a depauperate pollinator community, but possibly at the expense of other plants competing for the same pollinators. Such responses may be crucial in understanding the stabilization of a community following disturbance.

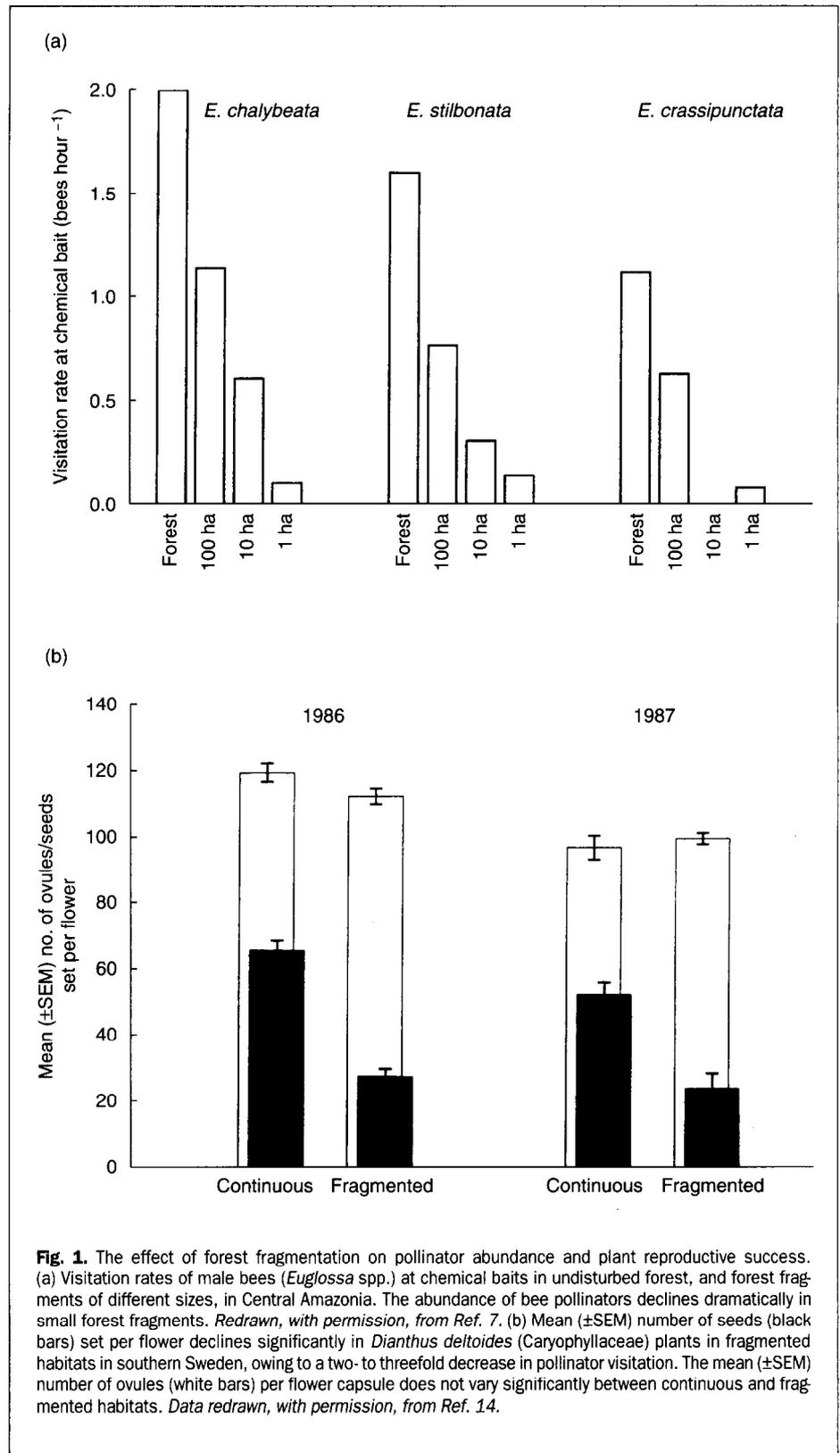
**Seed predators**

The impact of pre-dispersal seed predation by insects has rarely been quantified<sup>20</sup>, although studies have shown that seed-feeding insects do limit the recruitment and abundance of their host tree<sup>21</sup>. A decline of the insect seed-predator community following disturbance, therefore, may lead to an increased dominance of the predators' host plants. Sork<sup>22</sup> showed that the distribution of hickory plants (*Carya glabra*) was greatly affected by seed predation and seedling recruitment along a forest-edge-to-interior gradient. In the only experimental study of seed predation in fragmented forest, Burkey<sup>23</sup> showed that seed predation was significantly lower near the forest edge (Fig. 2), even though this edge was only a minor forest road. Unfortunately these results combine seed predation by all animals, not just insects, making inferences about the effect of forest fragmentation on insect seed predation impossible. Seedling survival to germination may be greater at the forest edge, although this may be offset by adverse microclimatic influences. The differential responses of seed predators to edge conditions may lead to changes in the spatial heterogeneity and/or survivorship of their host plants in forest fragments.

**Parasitoids**

Fragmentation is unlikely to affect all insects equally. Natural enemies of phytophagous insects are thought to be more susceptible to extinction or population decline than the insects they prey on<sup>24</sup>. The loss of parasitic Hymenoptera may release herbivore populations from parasitoid control, with detrimental effects on plant fitness<sup>24,25</sup>. Experimental removal of just two parasitoid species from citrus trees resulted in the defoliation and death of the trees<sup>26</sup>. LaSalle and Gauld<sup>25</sup> suggest that several hundred arthropods dependent on citrus trees might be affected by the removal of these two parasitoid species, and that such effects would be particularly pronounced in fragmented habitats.

The only study to date on the effects of fragmentation on parasitoid-herbivore interactions showed that on isolated clover islands, parasitoid diversity and the rate of parasitism of herbivores were reduced<sup>24</sup>



**Fig. 1.** The effect of forest fragmentation on pollinator abundance and plant reproductive success. (a) Visitation rates of male bees (*Euglossa* spp.) at chemical baits in undisturbed forest, and forest fragments of different sizes, in Central Amazonia. The abundance of bee pollinators declines dramatically in small forest fragments. Redrawn, with permission, from Ref. 7. (b) Mean (±SEM) number of seeds (black bars) set per flower declines significantly in *Dianthus deltoides* (Caryophyllaceae) plants in fragmented habitats in southern Sweden, owing to a two- to threefold decrease in pollinator visitation. The mean (±SEM) number of ovules (white bars) per flower capsule does not vary significantly between continuous and fragmented habitats. Data redrawn, with permission, from Ref. 14.

(Fig. 3). By maintaining its host at low numbers, an effective parasitoid may itself be rare<sup>25</sup>, thus making it more susceptible to extinction in the face of fragmentation and habitat disturbance.

**Decomposers**

To a large extent decomposer organisms control nutrient supply and, since this supply is limiting, strongly influence pri-

mary productivity<sup>27</sup>. Perturbation of the decomposer community has far-reaching impacts on nutrient supply and retention and hence on the stability of the ecosystem. The few studies that have investigated the responses of decomposers to habitat fragmentation and isolation have revealed marked changes in decomposer abundance and species diversity, but the quantitative impact of loss of biodiversity

on decomposition processes has rarely been measured.

Termites are arguably the most important insect decomposer group in tropical forests. Some estimates suggest that termites process 40–50% of total litterfall in some areas<sup>28</sup>. The sensitivity of termite communities to habitat disturbance has been well documented<sup>29</sup>. In Central Amazonia, Souza and Brown<sup>30</sup> found a dramatic two- to threefold decrease in termite species richness and a higher proportion of rare species in small (1 ha and 10 ha) forest remnants than in continuous forest. The loss of species in small fragments may be attributed to highly patchy species distributions<sup>30</sup> and a 'sample effect'. However, the differential responses of different trophic groups to fragmentation suggest that species loss may also be due to a lack of suitable resources, changes in microclimate, and stochastic extinction events resulting from low population sizes. Although all trophic groups decline in species richness, soil-feeders appear to be more susceptible to fragmentation than either litter-feeders or 'intermediate' litter- and soil-feeders<sup>30</sup>. This may result from the more sclerotized, desiccation-resistant nature of litter-feeders or the disproportionate increase in food resources (fine litterfall) in small forest fragments<sup>30</sup>. In addition, habitat-use patterns of termites change in small fragments, with a greater preference for rotting logs rather than living trees or epigeous termitaria (nest sites that are close to the ground)<sup>30</sup>.

Termites use resources in a variety of ways, and nutrient cycling activities differ between species<sup>31</sup>. Shifts in species composition, therefore, are likely to have a great impact on nutrient cycling processes in forest fragments, as in other disturbed habitats<sup>32</sup>. While this can be inferred from knowledge of the biology of the species in question, it has never been experimentally tested in any system.

Excreta and carrion represent rich but highly ephemeral nutrient sources. Decomposer organisms associated with dung and carrion breakdown are important in nutrient recycling, seed dispersal and control of vertebrate parasites, and some are thought to be good indicators of habitat disturbance<sup>33</sup>. Klein<sup>34</sup> found an almost complete turnover of dung beetle species (Scarabaeinae) between forest and clear-cut areas, and demonstrated that species richness in forest fragments was much lower than in continuous forest. Correlated with the decline in dung beetle species-richness was a sharp decrease in the rate of dung decomposition with increasing fragmentation (Fig. 4). However, the decline in decomposition rate was greater than expected from the observed decline in

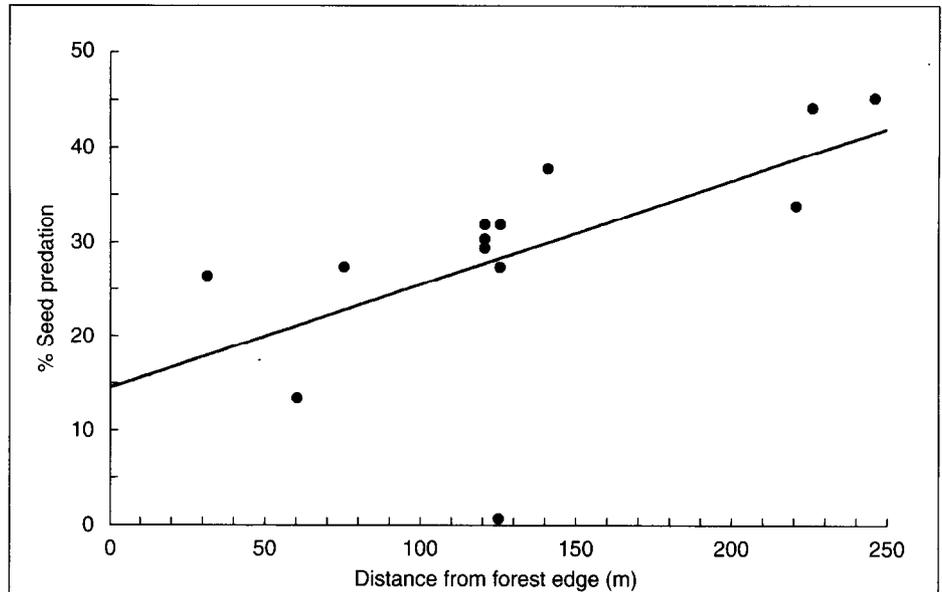


Fig. 2. Decline in seed predation rate (proportion of experimental *Brosimum alicastrum* seeds eaten by all insect and non-insect seed predators) as a function of distance from a forest edge in fragmented forest, Los Tuxtlas, Mexico. Redrawn, with permission, from Ref. 23.

species richness. Perhaps of greater functional significance is the dramatic decline in the abundance of primary forest species in forest fragments (Fig. 5). Although present, these species may be so rare as to be functionally extinct.

Springett<sup>35</sup> showed a significant decrease in the rate of leaf litter decomposition with declining species-richness (see also Ref. 36) (Fig. 6). Naem *et al.*<sup>37</sup> also found a change in decomposition rates with reduction in species richness, although in this study, rates were inconsistently re-

lated to species richness. Interestingly, decomposition rates may be only weakly correlated with the total abundance of decomposer organisms<sup>34,35</sup>, suggesting that some species are far more important than others in organic decomposition. Also, decomposition rates appear to decline dramatically at critical levels of biodiversity, with an apparently small change in actual species-richness. This supports the idea of a built-in functional redundancy in decomposer communities<sup>38</sup>. However, the critical species-richness at

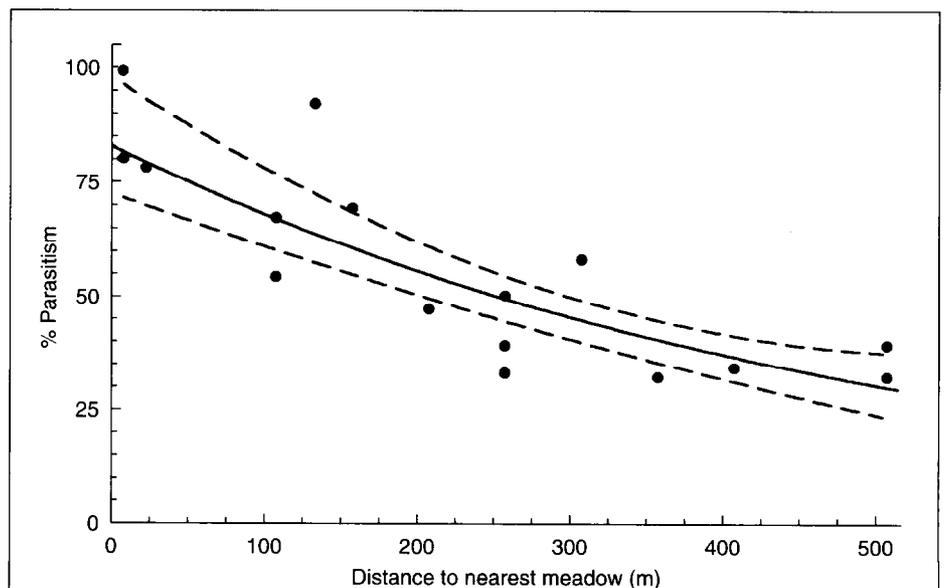
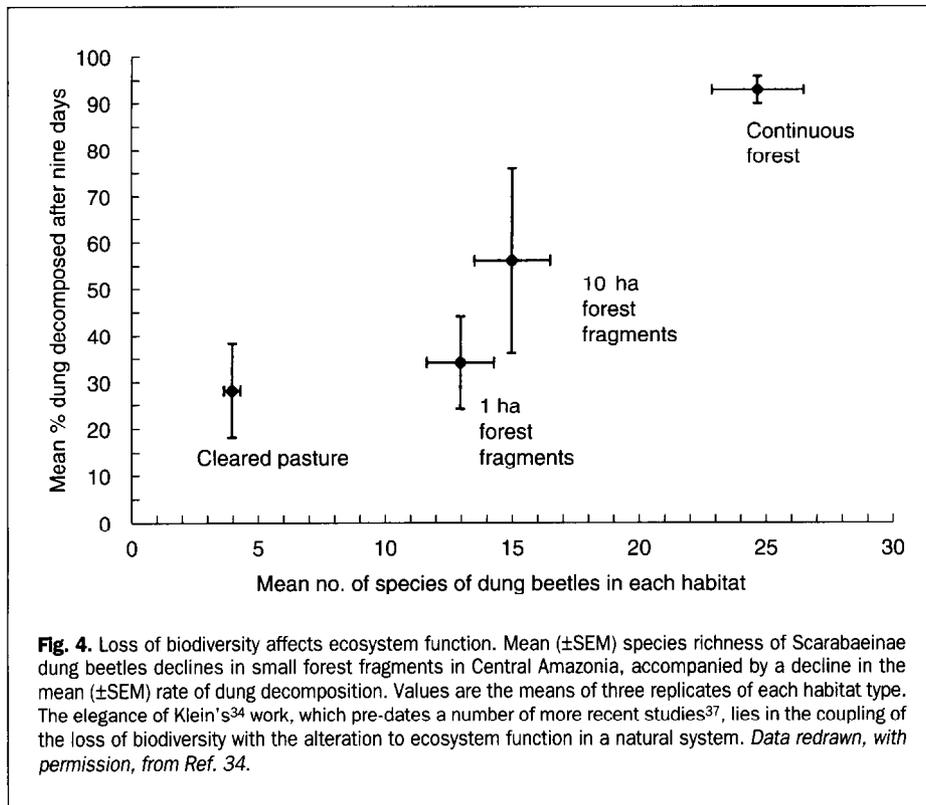
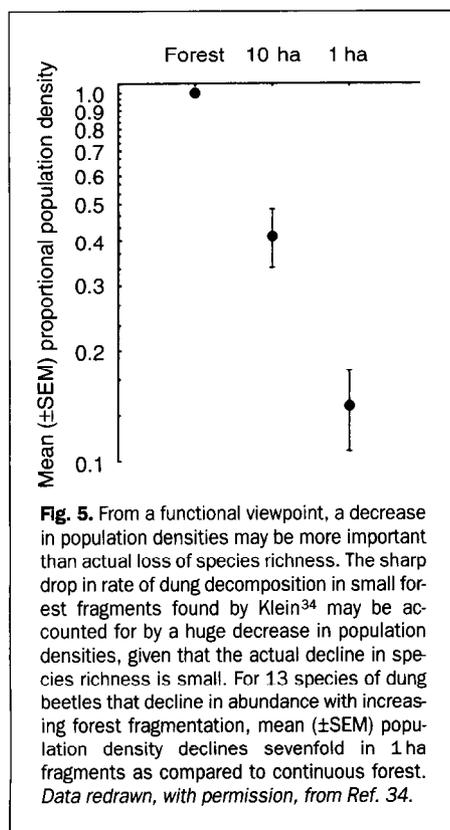


Fig. 3. Decline in percentage parasitism of the stem-boring weevils, *Apion seniculus* and *A. virens* (combined) in isolated clover (*Trifolium pratense*) meadows in Germany. With increasing isolation of clover patches, percentage parasitism decreases dramatically, releasing herbivores from parasitoid control. Natural enemies may be more affected by habitat fragmentation than are their phytophagous hosts. Redrawn, with permission, from Ref. 24.



**Fig. 4.** Loss of biodiversity affects ecosystem function. Mean ( $\pm$ SEM) species richness of Scarabaeinae dung beetles declines in small forest fragments in Central Amazonia, accompanied by a decline in the mean ( $\pm$ SEM) rate of dung decomposition. Values are the means of three replicates of each habitat type. The elegance of Klein's<sup>34</sup> work, which pre-dates a number of more recent studies<sup>37</sup>, lies in the coupling of the loss of biodiversity with the alteration to ecosystem function in a natural system. Data redrawn, with permission, from Ref. 34.

which ecosystem function appears to break down may be variable (i.e. not deterministic for a given community) as it will depend largely on when the key (functional) decomposer organisms are lost. This will almost certainly be context-sensitive for different types and degrees of habitat disturbance.



**Fig. 5.** From a functional viewpoint, a decrease in population densities may be more important than actual loss of species richness. The sharp drop in rate of dung decomposition in small forest fragments found by Klein<sup>34</sup> may be accounted for by a huge decrease in population densities, given that the actual decline in species richness is small. For 13 species of dung beetles that decline in abundance with increasing forest fragmentation, mean ( $\pm$ SEM) population density declines sevenfold in 1 ha fragments as compared to continuous forest. Data redrawn, with permission, from Ref. 34.

Hobbs *et al.*<sup>39</sup> caution against assuming a link between biodiversity and ecosystem function. In many cases, the relationship between ecosystem process rates and species richness may be obscured by abiotic processes, making causal links difficult to establish. For example, in Fig. 6, species richness is confounded with stand age, thus decomposition may be varying as a function of physical or chemical changes in stand structure, rather than as a function of species richness<sup>39</sup>. In practice it may be difficult to separate the two effects.

**Conclusions**

The potential for fragmentation-induced modification of the entire forest ecosystem is real<sup>40</sup>, although the implications of such changes are poorly known. A more focused approach to the problem of fragmentation and its effects on insect communities is required to fill the numerous gaps in current knowledge.

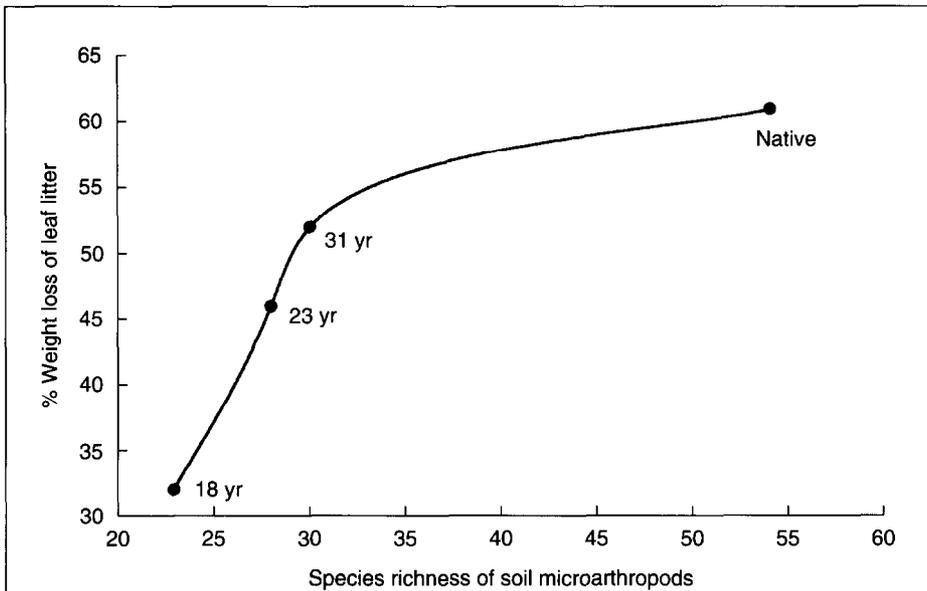
One important consideration is that spatio-temporal scale effects<sup>41,42</sup> have rarely been applied to fragmentation studies. Revealing patterns may be found through the study of small-scale dynamics (i.e. a mechanistic, or possibly experimental, approach)<sup>42</sup>, though conclusions derived from such studies may not be applicable to real large-scale systems. There are clearly practical and experimental difficulties in undertaking large-scale field research, and insights into the process of fragmentation might be enhanced by combining carefully designed field experiments with theoretical modelling of scale.

Furthermore, a functional approach to the study of invertebrates in fragmented forests may lend a more general relevance to the results than would a similar approach to the study of individual taxa.

There are a number of striking deficiencies in the study of the functional roles of insects in fragmented forest, in addition to a basic lack of primary data. Rates of herbivory (other than seed predation) in fragmented versus intact systems have never been investigated, despite the widespread study of herbivory rates and the impact of herbivory on plant community dynamics<sup>43</sup>. Indirect evidence from canopy dieback in *Eucalyptus* trees in Australia suggests that localized anthropogenic increases in soil fertility near forest remnants enhance foliar nutritional quality, resulting in an increased susceptibility to defoliation by insect herbivores<sup>44</sup>. Other forms of plant stress common in fragmented forests (e.g. water, fire, wind and temperature) may also alter plant nutrient content, both positively and negatively, and hence palatability<sup>44</sup>. Fragmentation may influence herbivory by altering herbivore communities, as well as their predators and parasitoids, potentially causing complex multi-trophic level interactions<sup>45</sup>. Predators themselves are an important component of insect communities for which there are few data available in fragmented forests<sup>45</sup>.

Many studies suffer from drawing weak functional inferences from empirical data on insect species-richness and abundance, without measuring the functional process directly. For example, it is known that seed predators affect seedling recruitment, so it is tempting to infer that a change in the seed-predator assemblage will result in changes in seedling recruitment and plant community dynamics. This kind of inference is no substitute for simple experimental manipulation of the system under investigation<sup>46</sup>. Such experimentation adds immeasurably to an understanding of fragmented ecosystems. For example, Klein<sup>34</sup> found that species richness of dung beetles declined in small forest fragments, yet total abundance (summed across all species) remained approximately the same. One could argue equally for or against a decline in the rate of dung decomposition. Through experimentation, Klein<sup>34</sup> showed that the rate of dung decomposition did in fact decline with increasing fragmentation, clearly indicating the important functional roles of different species.

An important consideration for all functional groups is the degree of specialization of different species. It appears that more-specialized species may be (directly or indirectly) more susceptible to forest fragmentation than generalist species, because, by definition, they are more closely linked to a particular host-, prey- or



**Fig. 6.** Rate of leaf litter decomposition (percentage weight loss of litter bags after 30 months) as a function of soil microarthropod species richness in Western Australia. Reduced subsets (of the same species composition) of the native forest soil microarthropod fauna are found in *Pinus pinaster* plantations of decreasing age, with a corresponding decline in the rate of leaf litter decomposition. Redrawn, with permission, from Ref. 36.

habitat-type and have little flexibility to cope with a changing environment. As with other aspects of insect responses to fragmentation, the importance of specialization has the potential to be context-sensitive and difficult to interpret. Nevertheless, this is a useful place to begin to look for assembly rules<sup>47</sup> for insect communities in forest fragments.

Choosing which are the key insect groups to study in fragmented systems is not self-evident. To some extent, at this early stage of investigation, any group will provide valuable information. Nevertheless, some groups are functionally more important than others. The concept of ecosystem engineers<sup>48</sup>, organisms that cause physical changes in their environment and modulate the availability of resources to other species, may provide a useful platform from which to launch future studies. Insect ecosystem engineers potentially have a far greater impact on subsequent ecosystem processes and species interactions than do non-engineers. Once again the main point is that the functional role of the insect should be quantified directly, along with changes in abundance and diversity caused by fragmentation. We must move beyond simple descriptions of patterns toward a more complete understanding of the effect of a loss of biodiversity on ecosystem function in fragmented forests.

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## Conservation needs ethology

Eberhard Curio

**With the number of species and near-to-natural habitats rapidly dwindling, conservation has become an undebatable necessity. There have been some laudable, successful species conservation projects but there have also been many deplorable failures. The failures are exacerbated by limited funding. Conservationists depend on funding by national government organizations (NGOs) and by private sponsors, more than other practitioners of organismic biology do. To maximize their success, conservationists would be well advised to heed the messages resulting from animal behaviour study (i.e. ethology) and/or to involve ethologists in their projects. Here, I illustrate how ethology can benefit both *in situ* and *ex situ* conservation measures; the need for conservation-oriented behaviour research is paramount.**

Eberhard Curio is at the Arbeitsgruppe für Verhaltensforschung, Fakultät für Biologie, Ruhr-Universität Bochum, D-44780 Bochum, Germany.

The well-being of a species is best served by protecting it in the wild, nevertheless *ex situ* measures (e.g. captive breeding) have often been resorted to when living conditions in the wild no longer guarantee survival. The harmful neglect of a species' natural behaviour is highlighted by the numerous failures of captive breeding and subsequent release into the wild. Managers of such captive individuals, in addition to falling short of their conservation aims, have had to face damaging criticisms for squandering funds, often in excess of millions of dollars. For many years, the small captive flock of the endangered Puerto Rican amazon parrot (*Amazona vittata*) on

its native island did not increase in size because the advice of aviculturists, long versed in the husbandry of amazon species, was rejected for subtle reasons<sup>1</sup>. Only in the recent past have numbers in captivity increased markedly to lift the captive flock from a dangerous low of 13 birds<sup>2</sup>. Similarly, severe and avoidable mistakes, largely in ethological husbandry, have prevented the small captive herd of a single-island endemic, the Philippine tamaraw (*Bubalus mindorensis*), from prospering<sup>3</sup>.

Captive-bred animals face a similar plight when released into the wild. Lack of familiarization with the area of release (e.g.

bald ibis, *Geronticus eremita*, see below<sup>4</sup>), neglect of the species' migratory habits (e.g. trumpeter swan, *Olor buccinator*<sup>5</sup>), or a combination of reasons, apparently including (behavioural) deficiencies that result from captive breeding *per se*, can prove fatal. Release of captive animals (birds and mammals) has proved half as successful as that of wild-caught ones<sup>6</sup>. Furthermore, apart from captivity-based phenotypic modifications of behaviour, genetic adaptations of behaviour to the captive environment are of even greater concern. These adaptations may prove maladaptive in the wild and, given some survival after release, they may potentially disrupt and genetically pollute the wild community. Studies of captive-bred fish released from hatcheries<sup>7</sup> reveal the magnitude of this threat. Furthermore, nutrition during early development has been shown to have an affect on reproductive physiology and behaviour in adulthood (see below). Hence, food choice and parental feeding assume a crucial role for proper behaviour of both wild and captive stock.

In spite of its multiple-cause effects in conservation, animal behaviour has received short shrift even in books on conservation biology and related areas<sup>8–10</sup>, an exception being one chapter in the recent book, *Creative Conservation* (see Ref. 11), or in the leading journals (*Conservation Biology*, *Biological Conservation*, *Oryx*). Instead, ecology is hailed as the major field that will enable us to cope with the crisis that is encroaching on us. In a disturbed state, a species' decline is often brought about