2 Insect Conservation in Tropical Forests

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1 Introduction

In comparison with most temperate ecosystems, tropical forests are characterized by extraordinarily high but poorly inventoried insect diversity (perhaps 5–10 million species, with less than 1 million of them described), and by an absence of basic biological and ecological information for all but a handful of non-pest species (Godfray *et al*., 1999; Novotny *et al*., 2002). Rates of tropical forest habitat degradation and destruction are higher than in almost any other biome (Sala *et al*., 2000; Pimm, 2001). In combination, these facts signal that the potential loss of insect diversity in tropical forests through human actions in the coming decades is enormous. In fact we are in danger of losing the vast majority of species before we have even documented them (Lawton and May, 1995).

Given the practical difficulties of gathering detailed ecological data in tropical environments where the species of interest may often occur at low levels of abundance (Folgarait *et al*., 1995; Basset, 1999), and where the nature of the habitat often makes sampling or observation difficult, it is perhaps inevitable that efforts to conserve insects in temperate and tropical regions have typically involved rather different approaches. In temperate countries, at least in the northern hemisphere, conservationists have often focused on gathering detailed autecological information on threatened species, including their precise habitat requirements, local and global distributions, interactions with other species and dispersal ability (Stewart and New, Chapter 1, this volume). On the basis of such information, priority areas for the conservation of individual species have been designated, and management or recovery plans have been drawn up and implemented, often with great success (e.g. Collins and Thomas, 1991; Samways, 1994; New *et al*., 1995). In contrast, there has been no consistent conservation approach for tropical insects. For a minority of rare, threatened or exploited tropical taxa we do have detailed ecological

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information that can help guide conservation practice. These species tend to be members of what might be called the 'charismatic microfauna' – insects that are large, attractive or ideally both (e.g. *Ornithoptera alexandrae*; New, Chapter 13, this volume). These exceptions are representatives of a very large constituency: since at least 50% of terrestrial diversity occurs in the tropical zone, and at least 50% of the earth's species are insects, and since tropical habitats are often more threatened than temperate ones, it follows that the majority of threatened species are likely to be tropical insects.

Such exceptions aside, conservation studies of tropical insects are generally focused at the assemblage rather than the species level. An increasing number of studies are investigating how insect taxa respond to habitat disturbance and fragmentation, in terms of species richness, diversity or taxonomic or ecological distinctiveness. In this chapter, we elaborate on the potential and pitfalls of some of these approaches, focusing on three questions that we feel are key to tropical insect conservation: (i) How can we accurately make an inventory of insect diversity in tropical forests? (ii) What are the effects of human habitat exploitation or degradation on tropical insects? (iii) How critical are insects for ecosystem integrity in tropical forests? We conclude by considering some of the practical and methodological barriers to progress in answering these questions, and suggest some potential solutions; and we highlight additional areas of uncertainty, which may be fruitful areas for future investigation. Our focus is on humid tropical forests, the habitats with which we are most familiar, but many of our comments will be equally applicable to poorly studied, species-rich insect assemblages throughout the tropics and elsewhere at higher latitudes.

2 How Can We Accurately Make an Inventory of Insect Diversity in Tropical Forests?

A good understanding of the spatio-temporal distribution of insect biodiversity in tropical forests is fundamental information needed to guide conservation action. There are far too many tropical insect species to study them all, and so the goal of most conservation biology for tropical insects is to document patterns in diversity and community structure, and to assess the effects of anthropogenic disturbance on these patterns (Basset *et al*., 1998). Such assessments can be undertaken at a hierarchy of spatial scales, from studies of vertical gradients from soil to canopy (Basset *et al*., 2003b), through trends in richness along elevational gradients (e.g. Lewis *et al*., 1998) to 'hotspots' analysis on a national or international scale (Bibby *et al*., 1992). Depending on the spatial scale at which they are carried out, such studies may be used to identify the key habitat zones to conserve within a tropical forest, or to rank competing sites or regions in terms of conservation 'value'. Similar approaches can also be used to assess the effects of habitat fragmentation on tropical forest insect assemblages (Brown and Hutchings, 1997; Didham, 1997a, 1997b), and the relative importance of 'undisturbed' or less-disturbed forests (Hamer *et al*., 1997; Lawton *et al*., 1998; Lewis, 2001), issues we discuss

in more detail below. Whatever the precise goal of the investigation, the fundamental task for insect conservation biologists in tropical forests is to document the magnitude and spatial distribution of insect diversity; in essence, to produce comparable and representative inventories.

Conservationists interested in compiling species inventories for tropical forest sites face several major challenges. The very factor that makes tropical insect assemblages of such interest and concern – their extraordinary diversity – creates enormous practical and analytical difficulties. The long tail of species-abundance distributions typical of tropical forest habitats (Novotny and Basset, 2000) mean that many species are encountered only infrequently, but the rare species least likely to be recorded in rapid assessments are often those of most conservation concern. Furthermore, if the pattern of species accumulation with sampling effort varies among habitats or sites, comparisons of diversity, species richness or other measures of conservation value based on restricted sampling may be unreliable. This makes ranking and comparing sites and treatments in terms of species richness or diversity problematic, unless intensive and long-term monitoring programmes are undertaken. Furthermore, the physical complexity of tropical forest habitats brings difficulties in sampling associated insects in a comprehensive or at least unbiased fashion (Kitching *et al.,* 2001). Finally, the challenge of identifying the material (Kitching, 1993) means that once the samples are collected the hard work is only just beginning.

Faced with these problems, there remains an urgent need to inform conservation decisions with data on species composition, species richness and diversity from tropical sites, without the need for expensive long-term and labour-intensive sampling. It is little wonder that (with some notable exceptions, e.g. Lawton *et al*., 1998 (Fig. 2.1); project investigating the biodiversity of soil and canopy arthropods (IBISCA): Didham and Fagan, 2003) the vast majority of such studies focus on a single taxon (e.g. Belshaw and Bolton, 1993; Eggleton *et al*., 1996; Hill, 1999; Intachat *et al*., 1999; Vasconcelos *et al*., 2000; Davis *et al*., 2001). Diurnal Lepidoptera are the most frequently studied group, by a substantial margin (e.g. DeVries *et al*., 1997; Hamer *et al*., 1997; Lewis, 2001; Ghazoul, 2002; Cleary, 2003; Cleary and Genner, 2004). Perhaps 80–90% of tropical taxa have never been the focus of tropical conservation studies, and it is an open question what the consequences of this taxonomic selectivity are likely to be. A full discussion of the choice of indicator taxa (and the question of what we might expect them to indicate) is beyond the scope of this chapter, but some key issues were covered in detail by Brown (1991) and are discussed by McGeoch (Chapter 7, this volume). More often than not the choice is more a function of the interests of the researchers involved, combined with selection of a group that has manageable levels of diversity, rather than 'megadiverse' taxa, such as weevils, leafhoppers and moths. An additional key reason for choosing a limited set of groups for study is the practical difficulties in identifying (even to morphospecies level) most taxa. In the tropics, insect surveys are continually hampered by the 'taxonomic impediment', something we return to later.

However, the single-taxon approach may be misleading: it is by no means certain that other insect taxa will show congruent patterns (Lawton *et al*.,

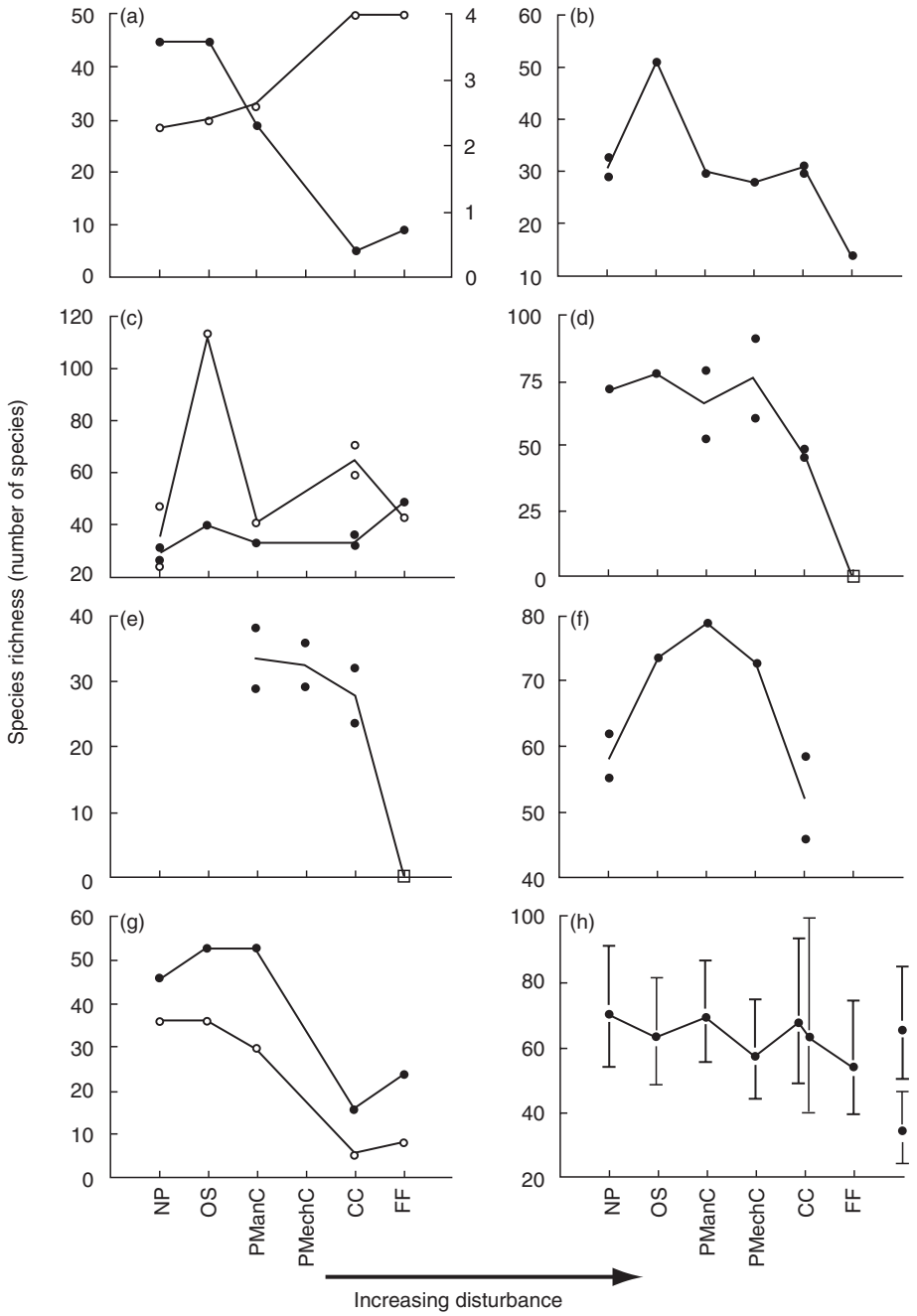

Fig. 2.1. Species richness of animal groups along a gradient of increasing habitat modification (left to right) in the Mbalmayo Forest Reserve, south-central Cameroon. (a) Birds (with mean habitat scores (open circles) on right ordinate); (b) butterflies; (c) flying beetles – malaise traps (filled circles); flight-interception traps (open circles); (d) canopy beetles; (e) canopy ants; (f) leaf-litter ants; (g) termites; (h) soil nematodes (with 95% confidence). (Reprinted from Lawton *et al*., 1998, with permission from Macmillan Publishers.)

1998: Fig. 2.1). There is little consensus on the appropriate choice of 'indicator' species, especially in the tropics (Prendergast *et al*., 1993; Hammond, 1994; Landres *et al*., 1998; Lawton *et al*., 1998; McGeoch, 1998; Kotze and Samways, 1999; Basset *et al*., 2001b; Moritz *et al*., 2001). A minority of tropical insect studies have a wider taxonomic focus, including whole orders or a few families from different orders, so that representatives of different guilds are included (e.g. Kremen, 1992; Didham *et al*., 1998b; Kotze and Samways, 1999; Chung *et al*., 2000; Kitching *et al*., 2000). These studies may provide more representative results. Kitching (1993, 1996) and Didham *et al*. (1996) have advocated a more formal approach to widening the set of taxa included in such assessments through the use of 'predictor sets', including taxa from multiple functional groups or guilds (see also Kremen *et al*., 1993). Such predictor sets are selected following statistical analysis of a larger data-set, including a wide range of taxa from multiple complementary sampling methods, and may give more reliable and general results.

Even for the best-studied taxa, little information is available to assess how much sampling is sufficient to provide a reliable indication of a site's conservation value. It would be extremely useful to generate 'rules-of-thumb' that may allow conservationists working on species-rich tropical assemblages to assess the completeness of their inventories, and whether a 'rapid' inventory approach can provide reliable information. Furthermore, guidelines on how best to employ the available effort would also be of value. For example, given a fixed period of time available to carry out surveys, is it more useful to concentrate sampling over a short period (perhaps during the season when abundance of the studied species is highest); or is it important to spread survey work throughout the year? Similarly, how useful is it to use multiple sampling methods, as opposed to a single method (Stork, 1994); and are comparisons among sites reliable if carried out at different times of year? We can start to answer some of these questions using the relatively restricted set of studies that have intensively surveyed particular taxa at individual sites. Structured inventories (Longino and Colwell, 1997) and the use of morphospecies or 'Recognizable Taxonomic Units' as surrogates for species level identifications (e.g. Netuzhilin *et al*., 1999) provide a practical way forward, but additional work in this area is urgently needed. Although in many cases a morphospecies approach will be the only practicable way forward, we join the appeal for specimens to be assigned to morphospecies based on sound taxonomic methods (Wilson, 2000).

A related issue is the choice of metrics in such assessments. Diversity or species richness may seem a sensible metric to measure, but in practice in both tropical and temperate environments these measures often increase with disturbance, concurrent with a *decrease* in conservation value (Basset *et al*., 1998). In many butterfly assemblages, for example, forest disturbance allows a suite of mobile, widespread and generalist taxa to colonize and coexist with much of the existing fauna (Thomas, 1991; Hamer *et al*., 1997; Spitzer *et al*., 1993, 1997; Lewis *et al*., 1998), enhancing overall diversity. These newcomers are typically species of low conservation concern, and it does not make sense to

give them equal weighting to restricted range habitat specialists in conservation assessments. One solution is to restrict analysis to endemics (e.g. Lewis *et al*., 1998); or it may be possible to weight the conservation value of a species to reflect its geographic range or rarity, in a similar way to indices that take into account the taxonomic similarity of species for conservation assessments (Erwin, 1991c; Vane-Wright *et al*., 1991; Williams *et al*., 1991). Alternatively, measuring the ratio of 'wider countryside' to forest specialist species might provide a rapid and approximate measure of human impacts on tropical forest ecosystems, although we are unaware of such studies. Of course, in order to use these approaches we do need some basic biological information in order to categorize taxa a priori as 'endemic' or widespread. Such information may be available for a surprisingly wide range of taxa, if the number of literature or museum localities for a taxon provides an approximate indication of its geographic range, although it is worth remembering that taxa can be both widespread and rare (Rabinowitz, 1981). It is quite uncertain how many tropical insect species are widespread yet rare: because of low levels of sampling for most taxa, if a species is locally rare then its recorded range is almost inevitably likely to be small. Many widespread and 'rare' species may prove to be much more common than has been assumed. A related issue concerns specialist versus generalist species: specialists will often (but not always) have relatively small geographic ranges (Gaston *et al*., 1997; Gaston, 1999), but endemic generalists certainly exist, for example, many island taxa. If sufficient information is available to categorize species on both counts then specialists (in terms of food or habitat use) might perhaps be accorded more weight in conservation assessments than endemics, since they may be the species most endangered by habitat disturbance.

3 What Are the Effects of Human Habitat Exploitation or Degradation on Insects?

Approximately half of the earth's closed-canopy tropical forest has already been converted to other uses (Wright, 2005), and the population of tropical countries, having almost trebled since 1950, is projected to grow by a further 2 billion by 2030 (Wright, 2005). Inevitably, anthropogenic pressures mean that it will only ever be possible to maintain a small fraction of the world's tropical forests as reserves or parks, free from human disturbance. Most tropical forests are likely to remain subject to varying intensities of disturbance, which takes numerous interacting forms. Each year, approximately 5.8 million hectares of tropical forests are destroyed completely through conversion to pasture and plantation, habitats that are unlikely to support more than a fraction of the insect fauna present earlier. An equivalent area is degraded annually, to varying degrees and with less clear-cut effects on biodiversity (Mayaux *et al*., 2005). Small-scale (often subsistence) agriculture is, in terms of the area affected, the most important single cause of tropical forest degradation, accounting for around 60% of deforestation. Commercial logging also typically results in [AU1]

degraded forest, rather than total forest loss since, with the exception of certain dipterocarp forests in south-east Asia, only a minority of tropical trees is economically viable for exploitation as timber. All of these human impacts, individually or in isolation, can result in a fragmented network of relatively intact patches, separated by a matrix that may vary from 'recovering' secondary forest, apparently rather similar to the pre-disturbance state of the system, through to pasture devoid of woody vegetation, or plantation monocultures. Few tasks can be more important for conservationists than assessing the impact of such human activities on tropical forest biodiversity. In order to minimize species extinctions globally, we need to know how we are altering the structure of these tropical communities, what degree of disturbance is consistent with the persistence of acceptable levels of tropical forest biodiversity and which groups of organisms are most seriously affected. Here, we consider disturbance and fragmentation separately, although one will rarely act entirely without the other.

3.1 Logging and other forms of disturbance

Can commercial timber extraction and other forms of tropical forest disturbance be reconciled with the maintenance of insect diversity? A growing set of studies throughout the tropics has investigated how human disturbance, in various forms and at varying intensities, is affecting the species richness or diversity of particular insect groups. The results of such studies have proved highly unpredictable, with disturbance shown to have a positive, negative or no effect on species richness in individual studies. Individual studies will be of local value, but generalizations are proving difficult to extract from the existing data. Are there general factors influencing whether species richness is observed to increase or decrease following disturbance? In particular, to what extent is the variability among studies real, and to what extent does it reflect variability in the sampling methods used, or idiosyncratic characteristics of individual study locations?

Replication is a troublesome issue for researchers trying to assess the effects of disturbance on tropical insect communities. Tropical rain forests have high spatial heterogeneity, which generates high beta diversity (Wolda, 1996; Vasconcelos *et al*., 2000), so protocols should ideally partition the variance in insect response between forest disturbance and faunal turnover with increasing distance between study sites. Typically, researchers will compare insect diversity in a single area of 'disturbed' forest with diversity in a nearby 'less-disturbed' forest. If there are multiple sites within each habitat these are likely to be pseudoreplicates (Hurlbert, 1984) because they are clustered in space and effectively represent multiple samples from the same habitat unit: the true sample size for each habitat type is in fact one. When differences are detected between such areas, it is difficult to determine whether these are a consequence of disturbance, or if they simply reflect pre-existing differences in topography or geography. Such differences are likely to exist for practical reasons. For example, areas of forest are unlikely to be logged if they include

steep slopes, major watercourses or low densities of timber trees, all factors that are likely to affect species composition in the absence of disturbance effects. There is no simple solution to this problem since the spatial scale necessary to sample truly replicated disturbed and undisturbed habit units is likely to be large and logistically challenging.

One opportunity for genuinely replicated sampling that has been taken advantage of rather rarely by tropical insect conservation biologists is the availability of silvicultural and logging plots in many tropical forests. These are typically set up by foresters to provide information on the effects of forest management on growth and yield of timber trees, and include before-after control-impact (BACI) designs, which allow robust comparisons in the face of spatial and temporal variability (Stewart-Oaten and Murdoch, 1986). Such experiments provide excellent opportunities for insect conservation biologists to ask how the experimental treatments (which by definition are those under consideration for wider application in the area concerned) affect insect assemblages. A crucial advantage of such studies is that treatments have been allocated at random to experimental units, avoiding the risk of pseudoreplication. Basset *et al*. (2001a, b) provide an example of this approach for an unreplicated BACI protocol in Guyana. Experimental plots also provide an opportunity to assess the extent to which new logging protocols, such as 'Reduced Impact Logging', affect insect diversity, relative to conventional approaches. These protocols are typically designed with at least one of the following goals in mind: to reduce biodiversity loss from logging, to enhance sustainability of timber extraction, or to promote carbon sequestration by increasing the density of the residual stand (e.g. Bird, 1998; Davis, 2000). We have recently made use of such an experiment in Belize to assess the effects of an experimental selective logging regime on butterfly (Lewis, 2001) and dung beetle assemblages (R. Pateman, O. Lewis and E. Slade, unpublished data), [AU2] and found that logging treatment effects were small relative to spatial block effects, highlighting the danger that spatial heterogeneity in species richness and species composition will generate misleading results in similar but non-experimental studies.

In reaching more general conclusions about the likely global effects of habitat modification on tropical insect assemblages it will be valuable to draw together information from many studies through meta-analysis. Individual studies in the literature should represent independent replicates, even if they are in themselves pseudoreplicated (Cottenie and De Meester, 2003). For the most widely studied taxon (Lepidoptera), sufficient studies are now potentially available to allow such analyses (Hamer and Hill, 2000; Hill and Hamer, 2004). Unfortunately and perhaps inevitably, because individual authors have had their own aims and methods specific to their particular studies, collating published investigations in a way that allows a meaningful meta-analysis is difficult. For example, the Lepidoptera studies vary considerably in the methods used to measure 'diversity'. Most present results for either species richness or for a diversity index, and rarely for both. Species richness is highly sensitive to sample size and many studies present 'raw' species richness values that have not been corrected for sample size.

Many of these problems could be avoided, and syntheses of published information could be made more rigorous and effective if individual authors included more information about their studies. The wider value of future individual studies can be increased through careful description of the methods employed and through consistent reporting of results. In Box 2.1 we present a 'wish list' for studies of the effects of disturbance on tropical insects. There are very many permutations in possible metrics for analysis, and some will be more appropriate than others for individual studies. Thus, rather than striving for standardization, we encourage authors to publish (perhaps as electronic appendices) summary tables of counts of species in each sampling unit. Analyses should take into account the numerous pitfalls inherent in comparisons of diversity measures (Gotelli and Colwell, 2001). In the tropics, insect species accumulation curves rarely saturate, but rarefaction or Coleman curves allow comparisons of species richness taking into account variations in sample size among sampling units. Where available, information on the nature, spatial extent and intensity of disturbance should be reported. In the context of logging, for example, Greiser Johns (1997) recommends a simple and consistent means of reporting the intensity of logging in terms of the percentage of the stand harvested and the time elapsed since harvesting. Disturbance from human activities other than logging may also vary markedly in its form and intensity, but this will be more difficult to quantify unambiguously and consistently. Additional complications are that the spatial scale of observation, sampling effort and sampling techniques may explain a large proportion of the

Box 2.1. A 'wish list' for studies of the effects of disturbance on tropical insects.

1. Take into account the geographical distribution/endemicity of taxa, rather than focusing solely on overall species richness or diversity values
2. Report both species richness and diversity measures, and control for the critical influence of sample size on species richness values through rarefaction
3. Be explicit about the nature of replication in the investigation
4. Document clearly the forms of habitat disturbance, and the time since disturbance events
5. Document the history of human and natural disturbance in the studied areas
6. To avoid publication bias, publish negative results (where no significant disturbance effect is found), as well as positive ones; this plea is addressed to editors, as well as authors
7. Consider employing or exploiting experimental protocols, such as before-after-control-impact (BACI)
8. Use sound concepts of taxonomy (where morphospecies correspond to unnamed species, rather than fuzzy groupings of unidentified specimens)
9. Use a multi-taxon approach to reach more general conclusions as to the impacts of disturbance on diversity; where this is not possible recognize clearly the limitations associated with individual study taxa
10. Include summary data on numbers or individuals of each species recorded from individual sampling locations (perhaps as electronic appendices), to facilitate subsequent meta-analyses

variation in outcomes observed across studies (Hamer and Hill, 2000; Hill and Hamer, 2004), and that sites that have a long history of 'natural' disturbance may be relatively insensitive to subsequent human disturbance (Balmford, 1996; Lewis, 2001).

Whether or not in a designed experiment, the scale of the study areas relative to the dispersal ability of the organisms studied is critical, and it may be important to take this into account when assessing the impacts of disturbance. Human-modified habitats are sometimes deemed to support a high proportion of the insect fauna associated with nearby, less-disturbed habitats. It is of course possible that these species have self-supporting breeding populations in disturbed habitats. However, if 'disturbed' sites are well within the dispersal range of 'less-disturbed' sites then for mobile insects like adult tropical butterflies, the nature of the surrounding habitat will almost inevitably influence the taxa recorded. Many may be 'tourists' from neighbouring, less-disturbed forest, which are not breeding in these habitats; others may breed there, but persist solely as 'sink' populations, dependent on repeated immigration for local persistence.

3.2 Habitat fragmentation

The creation of a patchwork landscape of forest fragments embedded in a matrix of habitats degraded to varying degrees is an inevitable consequence of deforestation (Wright, 2005). What effect does fragmentation have on tropical forest insect diversity? Habitat fragmentation has been a key focus of conservation research in temperate ecosystems over the last two decades, and insect studies have been key to the development, testing and application of metapopulation models in particular (Hanski and Poyry, Chapter 8, this volume). Fewer studies have investigated the effects of fragmentation on insect assemblages in tropical forests. A notable exception, on a large scale, is the experimental Biological Dynamics of Forest Fragments (BDFF) project in the Brazilian Amazon. The BDFF study is one of the most intensive habitat fragmentation assessments ever undertaken, and although much of the work there has focused on vertebrates, there has been intensive study of certain insect taxa, notably beetles (Didham *et al*., 1998a; Didham *et al*., 1998b) and butterflies (Brown and Hutchings, 1997). In fact there are compelling reasons to select insects as focal species in such studies. In particular, the relaxation period between fragmentation and species reaching equilibrium densities in the fragmented landscape is much lower for short-lived insects, allowing more rapid conclusions to be drawn about the true impacts of fragmentation. Existing data suggest that fragmentation has effects on insect communities that mirror in many ways the effects of logging and other forms of habitat degradation. [AU3]

It remains to be seen how relevant single-species studies of fragmentation are to tropical situations. In particular, it is uncertain how many tropical insects have population structures that approximate to metapopulations, with local populations in patches of habitat subject to periodic extinction and colonization events, and a dependence on recolonization for long-term regional persistence. As for temperate insects, some tropical taxa may be forced into metapopulation-like

situations by habitat fragmentation. Furthermore, tropical insects with high host specificity have breeding habitat that is defined by the spatial availability of host plants, which may represent patches of suitable habitat in a sea of unsuitable foliage. Resource fragmentation thus arises from two main factors: high host specificity (Janzen, 1973; Gilbert and Smiley, 1978; Basset, 1992; Marquis and Braker, 1993; Basset *et al*., 1996; Barone, 1998) and high plant diversity (Novotny *et al*., 2002, 2004). Individual plants of any one species are isolated in space, so host plant-specific tropical insects may occur as patchy populations or metapopulations on fragmented resource patches. Similarly, specialized predators or parasitoids will have a patchy spatial distribution determined by the distribution of their host herbivores. Will such fragmented populations act like 'true' metapopulations (Levins, 1969), with relatively independent demography in individual patches, and persistence dependent on dispersal among empty patches? Or will they operate more like 'patchy populations' (Harrison, 1991), where dispersal is high relative to the typical isolation between patches? If the former, then metapopulation models may be relevant to conservation planning; for example, selective logging, which removes individual trees may serve to increase patch isolation within the metapopulation. Since population densities for individual insect species are typically very low in tropical forests, establishing occupancy and local extinction of herbivores on whole trees is difficult, so it will be challenging to assess how widespread this type of population structure is in these habitats, and perhaps impossible to parameterize predictive, spatially explicit metapopulation models. However, many of the more general insights that have emerged from metapopulation biology may prove helpful in a tropical forest context, for example, the requirement for a landscape perspective, the importance of 'unoccupied' habitats and the fact that extinctions may be long delayed following fragmentation.

4 How Critical Are Tropical Insects for Ecosystem Integrity?

Whether humans alter insect assemblages through habitat modification or through fragmentation, then the consequences for ecological processes are of considerable interest, as are the likely direct and indirect effects of changes in the insect fauna on the wider community.

4.1 Ecosystem function

The relationship between biodiversity and ecosystem function has become a major preoccupation among ecologists and conservation biologists (e.g. Loreau *et al*., 2002; Hooper *et al*., 2005), and provides a widespread justification for conservation. The literature on this topic is dominated by studies of the relationship between diversity and productivity in temperate plants (e.g. Hector *et al*., 1999), and studies of organisms at higher trophic levels (e.g. insects) are few. We join the call for an increasing emphasis on the impact of insect biodiversity loss on ecosystem processes (e.g. Didham *et al*., 1996). Are insects really the 'little things that run the earth' (Wilson, 1987) by providing services that maintain the

'health' of ecosystems? A strong case can certainly be made for the key importance of several guilds, including dung beetles, termites and other arthropods involved in decomposition. More generally, insects play a key role in pollination (Kremen and Chaplin-Kramer, Chapter 15, this volume) and nutrient cycling via herbivory (Frost and Hunter, 2004). These and related topics are covered in more detail by Memmott *et al*. (Chapter 10, this volume) and Kremen and Chaplin-Kramer (Chapter 15, this volume), but here we briefly highlight tropical examples for a well-studied and ecologically important taxon: scarabaeid dung beetles.

The movement and burial of animal faeces by dung beetles for feeding and ovipositing results in soil fertilization and aeration, as well as nitrogen and nutrient cycling (Estrada *et al*., 1999; Davis *et al*., 2001; Andresen, 2002, 2003). The burial of dung also helps control important parasites of vertebrates, such as flies and hookworm. Furthermore, dung movement and burial is important for secondary seed dispersal: removing seeds from the surface of the soil protects seeds from predation and so is important for rainforest regeneration. The rate at which dung is buried can be measured in the field, and the correspondence between dung burial rates and diversity or species richness calculated. Klein (1989; see also Didham *et al*. 1996), working in Amazonia, found a strong positive relationship between dung beetle diversity and rates of dung burial, and between fragmentation and diversity, such that forest fragments were characterized by low dung beetle diversity and reduced ecosystem function, compared to continuous forest (Fig. 2.2; see also Quintero and Roslin (2006) for recovery of these communities following [AU4]

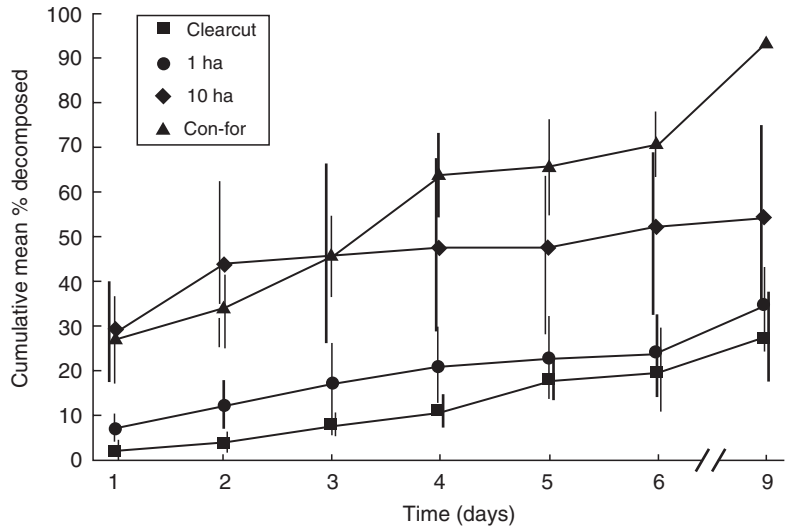

Fig. 2.2. Cumulative mean (n = 9, ± s.e.) percentage dung removal from experimental piles of cattle dung in Amazonian forest fragments of different areas, and in adjacent clear-cuts and continuous forest. (Reprinted from Klein, 1989, with permission from the Ecological Society of America.)

re-growth of secondary forests between fragments). However, Klein's (1989) methods appear not to rule out dung beetle abundance as the casual factor linking diversity and function (e.g. Andresen, 2003), and subsequent studies of dung beetle assemblages elsewhere in the tropics have found less clear-cut diversity–function relationships (R. Pateman, O. Lewis and E. Slade, unpublished data). In general, the field is ripe for further experimental and manipulative investigations of ecosystem processes (e.g. decomposition within litter bags) (Fagan *et al*., 2005) in relation to the diversity of the insect guilds involved in carrying out these functions.

[AU5]

[AU6]

4.2 Food webs and community interactions

Linked to ecosystem function is the study of trophic interactions among species. All species are embedded in complex webs of mutualistic and antagonistic interactions, and nowhere are these webs more complex and diverse than in tropical forest ecosystems (Janzen, 1983). Trophic interactions have been described as the glue that holds together ecological communities, and several authors have called for the conservation of trophic interactions as a goal for conservationists (Gilbert, 1980; Janzen, 1983; Memmott *et al*., 2006). Through their high diversity and wide variety of feeding niches, insects are a key component of all tropical forest food webs. The effects of losing individual species from food webs can be unpredictable and may propagate some distance through interlinked chains of trophic linkages ('indirect effects'). One recent study of a tropical forest host-parasitoid community suggests that removal of a single species can have widespread cascading indirect effects through apparent competition (Morris *et al*., 2004; Morris *et al*., 2005). Similarly, alterations in herbivore abundance can lead to trophic cascades (Letourneau and Dyer, 1998; Dyer and Letourneau, 1999). Given the major effects that insects can have on plant fitness (Marquis and Braker, 1993; Marquis, 2005) and potentially plant diversity (Janzen, 1970; Connell, 1971), alterations in insect assemblages may have major repercussions for the wider tropical ecosystem.

5 Unknowns, Practical Problems and Potential Solutions

5.1 The taxonomic impediment, and a role for parataxonomists

The 'taxonomic impediment' refers to the gaps of knowledge in our taxonomic system, the shortage of trained taxonomists and curators, and the impact these deficiencies have on our ability to manage and use biological diversity (Anon., 1998). The taxonomic impediment is perhaps at its greatest for tropical invertebrates, where the mismatch between taxonomic effort and biological diversity is at its greatest, and it greatly inhibits tropical insect conservation biology by making even the most taxonomically restrictive inventory a major undertaking.

Meeting the taxonomic challenge will require the use of new technologies (e.g. DNA barcoding and digital imaging) and the transfer of technologies and training to tropical countries, which harbour most biodiversity. Making taxonomic information available to entomologists around the world is increasingly possible with advances in information technology, but access to information in itself does not reduce the need for well-trained taxonomists and field workers.

Over the last decade or so, a new model has proved very successful in speeding the flow of biodiversity information from tropical ecosystems: working with parataxonomists (Janzen *et al*., 1993; Basset *et al*., 2000). Parataxonomists stand 'at the side' of conventional taxonomists: they collect specimens, prepare them, carry out preliminary sorting into morphospecies and enter the associated information onto databases. They are not an alternative to professional taxonomists in the field or laboratory, but enhance their activities and capacities. The advantages of working with local parataxonomists in the tropics were summarized by Basset *et al*. (2000, 2004) and include: (i) increased efficiency and replication of sampling with year-round activity in the field; (ii) rapid preparation of high quality specimens at low cost; (iii) enhanced integration of local ecological information associated with collected specimens; and (iv) enhanced public outreach and local interest in biodiversity. Parataxonomists may reduce greatly the time-lag between the initiation of the study and the publication of results, a particular advantage for conservation studies where there may be urgent need for action. With the help of parataxonomists, it may become feasible to include several taxa or guilds within the sampling protocol. As discussed in Section 2, we believe that this represents a promising alternative to the monitoring of species-poor taxa over relatively short periods. Training and employment of parataxonomists could profitably be put to use in conservation biology and in subsequent biodiversity management throughout the tropics.

5.2 The canopy

The tropical forest canopy – consisting of all the tree crowns in a forest stand – supports a diverse and poorly studied assemblage of insects, and has been described as the 'last biotic frontier' (Erwin, 1982a, 1982b). At least 20% of tropical arthropods, most of them insect herbivores, are confined to the upper canopy (the canopy surface and the volume of vegetation within a few metres below it; Basset *et al*., 2003b), where biotic and abiotic conditions contrast markedly with conditions in the understorey. Consequently, canopy insect assemblages are expected to show considerable differences in their composition, structure and function, compared with those in the understorey. The responses of canopy insects to anthropogenic habitat change are also likely to differ. Sound estimates of the effects of disturbance cannot be inferred from ground-based studies alone; data on the distribution and ecology of canopy arthropods are essential (e.g. Willott, 1999; Basset *et al*., 2003b). Furthermore, most of the key ecosystem processes in which insects are involved (herbivory, parasitism, pollination) occur largely in the canopy.

A few conservation studies in tropical rainforests have specifically targeted canopy arthropods. The results of such studies have been mixed, a point that we illustrate with two recent examples, both from Malaysia, and both focusing on beetles sampled by insecticide knockdown ('fogging'). Speight *et al*. (2003) reported that loss of diversity in human-modified forests was small, compared with primary forests. They found that alteration in guild structure and loss of species was obvious only in plantations of exotic trees, and even these acted as partial refugia for the fauna, provided that the understorey was well developed (unlike in oil palm plantations). In contrast to this rather optimistic scenario, Floren and Linsenmair (2003) reported strong effects of anthropogenic disturbance. For example, 40 years after disturbance, the fauna of the disturbed forest they studied, including canopy inhabitants, still differed from that in the primary forest. They found a transition from deterministically structured communities to randomly assembled ones along a succession or disturbance gradient. In particular, assemblages of Coleoptera (and also Formicidae) showed patterns that were deterministic in disturbed forests, but random in primary forests, where non-equilibrium conditions may mediate species coexistence. Such conflicting results may result, in part, from the focus on beetles rather than a multi-taxa, multi-guild approach, and because of limited sampling of the fauna of the upper canopy, which may be rather specialized and therefore sensitive to disturbance (Basset, 2001). Future studies of the effects of disturbance on canopy arthropods should ideally address these two concerns.

What are the likely effects on arboreal arthropods of the opening of the canopy, after the creation of natural or anthropogenic gaps? Do the upper canopy and its fauna 'fall' to the ground? As far as insect herbivores are concerned, the short answer to this is most likely 'no', since forest gaps typically include sets of plant species (largely pioneers) different from those present in the mature canopy (largely shade-tolerant species), and many insect herbivores are relatively specialized. In addition, herbivores foraging on mature trees in Guyana tend not to attack conspecific seedlings in light gaps resulting after logging (Basset, 2001). Taxa less tied to resources occurring specifically in the upper canopy, such as dung beetles, may suffer less from canopy loss and survive well in the understorey of disturbed forests (Davis and Sutton, 1998). This and related issues warrant further investigation.

5.3 Climate change

Climate change remains a major unknown in the context of tropical insects, but the response of tropical forest insects to climate change is of some significance. Recent predictions that up to 15–37% of all biodiversity may be committed to extinction by climate change by 2050 (Thomas *et al*., 2004) rely implicitly on tropical insects (which constitute the bulk of biodiversity) responding in a similar manner to better-studied temperate taxa (Lewis, 2006). It is debatable whether they will: most assessments suggest that tropical environments will be less affected by climate change than temperate biomes (Sala *et al*., 2000),

[AU7]

with habitat fragmentation and destruction rated as much greater threats. The steep environmental gradients from canopy to understorey in tropical forests may in part buffer populations against changes in climate. For example, specialized species of the upper canopy may move down to lower, cooler strata, although their resources are less abundant in their new microhabitats, then extinctions are still likely (Basset *et al*., 2003a). Certainly, we should not be complacent: the fact that existing examples of species responding to climate change are drawn entirely from temperate regions (e.g. Wilson *et al*., 2006) should not be surprising, given the limited monitoring data for tropical insects. Although predicting how tropical insects will respond to a warmer world is difficult, we may at least soon be in a position to detect the 'footprint' of climate change without the need for long time-series of survey data: recent work suggests that shortcuts may allow changes in species' status to be detected even from snapshot surveys (Wilson, 2004 #10862). [AU8]

6 Conclusions

The challenge to insect conservation biologists in the tropics is rather different from that facing many conservation biologists working on better-known taxa in better-studied parts of the world. In an influential paper, Caughley (1994) identified two paradigms in conservation biology: the small population paradigm (where conservationists seek to identify the measures needed to prevent small populations from going extinct) and the declining population paradigm (where conservationists seek to identify declining species and the causes of their decline). Conservation biology for the vast majority of tropical insects falls into neither category comfortably. We are not in a position to carry out – or act on – detailed population studies for the vast majority of rare tropical insects; and although we know that many species are likely to be declining, we rarely have information on rates of population or distribution decline. But the sheer magnitude of tropical insect diversity should not be allowed to stifle progress.

We have identified three main interlinked issues that we believe are fundamental to integrating insects fully into the conservation of tropical forests: undertaking reliable and comparable inventories, assessing the effects of disturbance and quantifying the wider role of insects within tropical forest ecosystems. We have also identified a series of challenges, which may impede progress towards these goals. These include the very diversity that we value, and the problems of identification, sampling and replication that it brings. Our suggested solutions are pragmatic ones: to design our studies more robustly to answer criticisms about replication; to improve reporting of results to allow more informative integration across studies and to speed the flow of biodiversity information from field to decision-maker through the work of parataxonomists.

As entomologists, we naturally rate the conservation of insects as an important goal; but we appreciate that, in practice, tropical insects will rarely, if ever, be the targets of conservation action in their own right. However, the

danger is that they will be overlooked in setting conservation priorities and guiding habitat management practice. We feel that tackling the issues surrounding inventory, impacts and function should go a long way towards ensuring that the use of insects in conservation assessments in the tropics moves a step further towards reflecting their numerical and ecological importance in tropical forest ecosystems.

References

Andresen, E. (2002) Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecological Entomology* 27, 257–270.

Andresen, E. (2003) Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. *Ecography* 26, 87–97.

Anon. (1998) *The Darwin Declaration*. Available at: http://www.deh.gov.au/biodiversity/abrs/publications/other/darwin/

Balmford, A. (1996) Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends in Ecology and Evolution* 11, 193–196.

Barone, J.A. (1998) Host-specificity of folivorous insects in a moist tropical forest. *Journal of Animal Ecology* 67, 400–409.

Basset, Y. (1992) Host specificity of arboreal and free-living insect herbivores in rainforests. *Biological Journal of the Linnean Society* 47, 115–133.

Basset, Y. (1999) Diversity and abundance of insect herbivores foraging on seedlings in a rainforest in Guyana. *Ecological Entomology* 24, 245–259.

Basset, Y. (2001) Communities of insect herbivores foraging on saplings versus mature trees of Pourouma bicolor (Cecropiaceae) in Panama. *Oecologia* 129, 253–260.

Basset, Y., Samuelson, G.A., Allison, A. and Miller, S.E. (1996) How many species of host-specific insect feed on a species of tropical tree? *Biological Journal of the Linnean Society* 59, 201–216.

Basset, Y., Novotny, V., Miller, S.E. and Springate, N.D. (1998) Assessing the impact of forest disturbance on tropical invertebrates: some comments. *Journal of Applied Ecology* 35, 461–466.

Basset, Y., Novotny, V., Miller, S.E. and Pyle, R. (2000) Quantifying biodiversity: experience with parataxonomists and digital photography in Papua New Guinea and Guyana. *Bioscience* 50, 899–908.

Basset, Y., Charles, E., Hammond, D.S. and Brown, V.K. (2001a) Short-term effects of canopy openness on insect herbivores in a rain forest in Guyana. *Journal of Applied Ecology* 38, 1045–1058.

Basset, Y., Charles, E., Hammond, D.S. and Brown, V.K. (2001b) Short-term effects of canopy openness on insect herbivores in a rain forest in Guyana. *Journal of Applied Ecology* 38, 1045–1058.

Basset, Y., Horlyck, V. and Wright, S.J. (eds) (2003a) *Studying Forest Canopies from Above: The International Canopy Crane Network*. Smithsonian Tropical Research Institute and UNEP, Panama City.

Basset, Y., Novotny, V., Miller, S. and Kitching, R. (2003b) *Arthropods of Tropical Forests – Spatio-temporal Dynamics and Resource Use in the Canopy*. Cambridge University Press, Cambridge.

Basset, Y., Novotny, V., Miller, S.E., Weiblen, G.D., Missa, O. and Stewart, A.J.A. (2004) Conservation and biological monitoring of tropical forests: the role of parataxonomists. *Journal of Applied Ecology* 41, 163–174.

Belshaw, R. and Bolton, B. (1993) The effect of forest disturbance on the leaf litter ant fauna in Ghana. *Biodiversity and Conservation* 2, 656–666.

Bibby, C.J., Collar, N.J., Crosby, M.J., Heath, M.F., Imboden, C., Johnson, T.H., Long, A.J., Stattersfield, A.J. and Thirgood, S.J. (1992)

Putting Biodiversity on the Map: Priority Areas for Global Conservation. International Council for Bird Preservation, Cambridge.

Bird, N.M. (1998) *Sustaining the Yield. Improving Timber Harvesting Practices in Belize 1991–1998*. Natural Resources Institute, Chatham, UK.

Brown, K.S.J. (1991) Conservation of neotropical environments: insects as indicators. In: Collins, N.M. and Thomas, J.A. (eds) *The Conservation of Insects and Their Habitats*. Academic Press, London.

Brown, K.S.J. and Hutchings, R. (1997) Disturbance, fragmentation, and the dynamics of diversity in Amazonian forest butterflies. In: Laurence, W.F. and Bierregaard, R.O. Jr. (eds) *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, Illinois, pp. 91–110.

Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology* 63, 215–244.

Chung, A.Y.C., Eggleton, P., Speight, M.R., Hammond, P.M. and Chey, V.K. (2000) The diversity of beetle assemblages in different habitat types in Sabah, Malaysia. *Bulletin of Entomological Research* 90, 475–496.

Cleary, D.F.R. (2003) An examination of scale of assessment, logging and ENSO-induced fires on butterfly diversity in Borneo. *Oecologia* 135, 313–321.

Cleary, D.F.R. and Genner, M.J. (2004) Changes in rain forest butterfly diversity following major ENSO-induced fires in Borneo. *Global Ecology and Biogeography* 13, 129–140.

Collins, N. and Thomas, J.A. (eds) (1991) *The Conservation of Insects and Their Habitats*. Academic Press, London.

Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Boer, P.J.D. and Gradwell, G.R. (eds) *Dynamics of Populations*. PUDOC, Wageningen, The Netherlands, pp. 298–312.

Cottenie, K. and De Meester, L. (2003) Comment to Oksanen (2001): Reconciling Oksanen (2001) and Hurlbert (1984). *Oikos* 100, 394–396.

Davis, A.J. (2000) Does reduced-impact logging help preserve biodiversity in tropical rainforests? A case study from Borneo using dung beetles (Coleoptera: Scarabaeoidea) as indicators. *Environmental Entomology* 29, 467–475.

Davis, A.J. and Sutton, S.L. (1998) The effects of rainforest canopy loss on arboreal dung beetles in Borneo: implications for the measurement of biodiversity in derived tropical ecosystems. *Diversity and Distributions* 4, 167–173.

Davis, A.J., Holloway, J.D., Huijbregts, H., Krikken, J., Kirk-Spriggs, A.H. and Sutton, S.L. (2001) Dung beetles as indicators of change in the forests of northern Borneo. *Journal of Applied Ecology* 38, 593–616.

DeVries, P.J., Murray, D. and Lande, R. (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* 62, 343–364.

Didham, R.K. (1997a) The influence of edge effects and forest fragmentation on leaf litter invertebrates in central Amazonia. In: Laurece, W.F. and Bierregaard, R.O. Jr. (eds) *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, Illinois, pp. 55–70.

Didham, R.K. (1997b) An overview of invertebrate responses to forest fragmentation. In: Watt, A.D., Stork, N.E. and Hunter, M.D. (eds) *Forest and Insects*. Chapman & Hall, London, pp. 303–320.

Didham, R.K. and Fagan, L.L. (2003) Editorial: IBISCA – Investigating the biodiversity of soil and canopy arthropods. *The Weta* 26, 1–6.

Didham, R.K., Ghazoul, J., Stork, N.E. and Davis, A.J. (1996) Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution* 11, 255–260.

Didham, R.K., Hammond, P.M., Lawton, J.H., Eggleton, P. and Stork, N.E. (1998a) Beetle species richness responses to tropical forest fragmentation. *Ecological Monographs* 68, 295–323.

Didham, R.K., Lawton, J.H., Hammond, P.M. and Eggleton, P. (1998b) Trophic structure

stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences* 353, 437–451.

Dyer, L.A. and Letourneau, D.K. (1999) Trophic cascades in a complex, terrestrial community. *Proceedings of the National Academy of Sciences of the United States of America* 96, 5072–5076.

Eggleton, P., Bignell, D.E., Sands, W.A., Mawdsley, N.A., Lawton, Wood, T.G. and Bignell, N.C. (1996) The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences* 351, 51–68.

Erwin, T.L. (1982a) Tropical forests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin* 36, 74–75.

Erwin, T.L. (1982b) Tropical forests: their richness in Coleoptera and other arthropods. *Coleopterists' Bulletin* 36, 74–75.

Erwin, T.L. (1991c) An evolutionary basis for conservation strategies. *Science* 253, 750–752.

Estrada, A., Anzuras, D.A. and Coastes-Estrada, R. (1999) Tropical forest fragmentation, howler monkeys (*Alouatta palliata*) and dung beetles at Los Tuxtlas, Mexico. *American Journal of Primatology* 48, 353–62.

Fagan, L.L., Didham, R.K., Winchester, N.N., Behan-Pelletier, V., Clayton, M., Lindquist, E. and Ring, R.A. (2005) An experimental assessment of biodiversity and species turnover in terrestrial vs canopy leaf litter. *Oecologia* October 15, 1–13 (Epub ahead of print).

Floren, A. and Linsenmair, K.E. (2003) How do beetle assemblages respond to anthropogenic disturbances? In: Basset, Y., Kitching, R., Miller, S. and Novotny, V. (eds) *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy*. Cambridge University Press, Cambridge, pp. 190–197.

Folgarait, P.J., Marquis, R.J., Ingvarsson, P., Braker, H.E. and Arguedas, M. (1995) Patterns of attack by insect herbivores and a fungus on saplings in a tropical tree plantation. *Environmental Entomology* 24, 1487–1494.

Frost, C.J. and Hunter, M.D. (2004) Insect canopy herbivory and frass deposition affect soil nutrient dynamics and export in oak mesocosms. *Ecology* 85, 3335–3347.

Gaston, K.J. (1999) Implications of interspecific and intraspecific abundance-occupancy relationships. *Oikos* 86, 195–207.

Gaston, K.J., Blackburn, T.M. and Lawton, J.H. (1997) Interspecific abundance range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology* 66, 579–601.

Ghazoul, J. (2002) Impact of logging on the richness and diversity of forest butterflies in a tropical dry forest in Thailand. *Biodiversity and Conservation* 11, 521–541.

Gilbert, L. (1980) Food web organization and the conservation of neotropical diversity. In: Soulé, M.E. and Wilcox, B.A. (eds) *Conservation Biology*. Sinauer, Sunderland, Massachusetts, pp. 11–33.

Gilbert, L.E. and Smiley, J.T. (1978) Determinants of local diversity in phytophagous insects. In: Mound, L.A. and Waloff, N. (eds) *Diversity of Insect Faunas*. Blackwell Scientific, London.

Godfray, H.C., Lewis, O.T. and Memmott, J. (1999) Studying insect diversity in the tropics. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences* 354, 1811–1824.

Gotelli, N.J. and Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4, 379–391.

Greiser Johns, A. (1997) *Timber Production and Biodiversity Conservation in Tropical Forests*. Cambridge University Press, Cambridge.

Hamer, K.C. and Hill, J.K. (2000) Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conservation Biology* 14, 1435–1440.

Hamer, K.C., Hill, J.K., Lace, L.A. and Langan, A.M. (1997) Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba, Indonesia. *Journal of Biogeography* 24, 67–75.

Hammond, P.M. (1994) Practical approaches to the estimation of the extent of biodiversity in

speciose groups. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences* 345, 119–136.

Harrison, S. (1991) Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society* 42, 73–88.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S. and Lawton, J.H. (1999) Plant diversity and productivity experiments in European grasslands. *Science* 286, 1123–1127.

Hill, J.K. (1999) Butterfly spatial distribution and habitat requirements in a tropical forest: impacts of selective logging. *Journal of Applied Ecology* 36, 564–572.

Hill, J.K. and Hamer, K.C. (2004) Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology* 41, 744–754.

Hooper, D.U., Chapin, F.S.I., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setaelae, H., Symstad, A.J., Vandermeer, J. and Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75, 3–35.

Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54, 187–211.

Intachat, J., Holloway, J.D. and Speight, M.R. (1999) The impact of logging on geometroid moth populations and their diversity in lowland forests of Peninsular Malaysia. *Journal of Tropical Forest Science* 11, 61–78.

Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist* 104, 501–28.

Janzen, D.H. (1973) Comments on host-specificity of tropical herbivores and its relevance to species richness. In: Heywood, V.H. (ed.) *Taxonomy and Ecology*. Academic Press, London, pp. 201–211.

Janzen, D.H. (1983) Food webs: who eats what, why, how, and with what effects in a tropical forest? In: Golley, F. (ed.) *Tropical Rain Forest Ecosystems*. Elsevier Scientific, Amsterdam, The Netherlands, pp. 167–182.

Janzen, D.H., Hallwachs, W., Jimenez, J. and Gamez, R. (1993) The role of the parataxonomists, inventory managers, and taxonomists in Costa Rica's national biodiversity inventory. In: Reid, W.V., Laird, S.A., Meyer, C.A., Gamez, R., Sittenfeld, A., Janzen, D.H., Gollin, M.A. and Juma, C. (eds) *Biodiversity Prospecting: Using Generic Resources for Sustainable Development*. World Resources Institute, Washington, DC, pp. 223–254.

Kitching, I.J. (1996) Identifying complementary areas for conservation in Thailand: an example using owls, hawkmoths and tiger beetles. *Biodiversity and Conservation* 5, 841–858.

Kitching, R.L. (1993) Biodiversiy and taxonomy: impediment or opportunity? In: Moritz, C. and Kikkawa, J. (eds) *Conservation Biology in Australia and Oceania*. Surrey Beatty, Chipping Norton, New South Wales, Australia, pp. 253–268.

Kitching, R.L., Vickerman, G., Laidlaw, M. and Hurley, K. (2000) *The Comparative Assessment of Arthropod and Tree Diversity on Old-World Rainforests: The Rainforest CRC/Earthwatch Manual*. Technical Report, Cooperative Research Centre for Tropical Rainforest Ecology and Management, Cairns, Queensland, Australia.

Kitching, R.L., Li, D.Q. and Stork, N.E. (2001) Assessing biodiversity 'sampling packages': how similar are arthropod assemblages in different tropical rainforests? *Biodiversity and Conservation* 10, 793–813.

Klein, B.C. (1989) Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* 70, 1715–1725.

Kotze, D.J. and Samways, M.J. (1999) Invertebrate conservation at the interface between the grassland matrix and natural Afromontane forest fragments. *Biodiversity and Conservation* 8, 1339–1363.

Kremen, C. (1992) Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* 2, 203–217.

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F. and Sanjayan, M.A. (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* 7, 796–808.

Landres, P.B., Verner, J. and Thomas, J. (1998) Ecological uses of vertebrate indicator species: a critique. *Conservation Biology* 2. [AU9]

Lawton, J.H. and May, R.M. (eds) (1995) *Extinction Rates*. Oxford University Press, Oxford.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A. and Stork, N.E. (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391, 72–76.

Letourneau, D.K. and Dyer, L.A. (1998) Experimental test in lowland tropical forest shows top-down effects through four trophic levels. *Ecology* 79, 1678–1687.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15, 237–240.

Lewis, O.T. (2001) Effect of experimental selective logging on tropical butterflies. *Conservation Biology* 15, 389–400.

Lewis, O.T., Wilson, R.J. and Harper, M.C. (1998) Endemic butterflies on Grande Comore: habitat preferences and conservation priorities. *Biological Conservation* 85, 113–121.

Longino, J.T. and Colwell, R.C. (1997) Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. *Ecological Applications* 7, 1263–1277.

Loreau, M., Naeem, S. and Inchausti, P. (eds) (2002) *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*. Oxford University Press, Oxford.

Marquis, R.J. (2005) Impacts of herbivores on tropical plant diversity. In: Burslem, D.F.R.P., Pinard, M.A. and Hartley, S.E. (eds) *Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity*. Cambridge University Press, Cambridge, pp. 328–346.

Marquis, R.J. and Braker, H.E. (1993) Plant-herbivore interactions: diversity, specificity, and impact. In: McDade, L.A., Bawa, K.S., Hespenheide, H.A. and Hartshorn, G.S. (eds) *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. University of Chicago Press, Chicago, pp. 261–281.

Mayaux, P., Holmgren, P., Achard, F., Eva, H., Stibig, H. and Branthomme, A. (2005) Tropical forest cover change in the 1990s and options for future monitoring. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences* 360, 373–384.

McGeoch, M.A. (1998) The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews of the Cambridge Philosophical Society* 73, 181–201.

Memmott, J., Carvelheiro, L., Gibson, R., Henson, K.E., Huttel R., Lopezaraiza, M.E. and Pearce, S. (2006) The conservation of ecological interactions. In: Lewis, O.T., New, T.R. and Stewart, A.J.A. (eds) *Insect Conservation Biology*. CAB International, Wallingford, UK.

Moritz, C., Richardson, K.S., Ferrier, S., Monteith, G.B., Stanisic, J., Williams, S.E. and Whiffin, T. (2001) Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a tropical rainforest biota. *Proceedings of the Royal Society of London Series B – Biological Sciences* 268, 1875–1881.

Morris, R.J., Lewis, O.T. and Godfray, H.C.J. (2004) Experimental evidence for apparent competition in a tropical forest food web. *Nature* 428, 310–313.

Morris, R.J., Lewis, O.T. and Godfray, H.C.J. (2005) Apparent competition and insect community structure: towards a spatial perspective. *Annales Zoologici Fennici* 42, 449–462.

Netuzhilin, I., Chacon, P., Cerda, H., López-Hernández, D., Torres, F., Paoletti, M.G. and Reddy, M.V. (1999) Assessing agricultural impact using ant morphospecies as

bioindicators in the Amazonian savanna-forest ecotone (Puerto Ayacucho, Amazon State), Venezuela. In: Reddy, M.V. (ed.) *Management of Tropical Agroecosystems and the Beneficial Soil Biota*. Science Publishers, Enfield, New Hampshire, pp. 291–352.

New, T.R., Pyle, R.M., Thomas, J.A., Thomas, C.D. and Hammond, P.C. (1995) Butterfly conservation management. *Annual Review of Entomology* 40, 57–83.

Novotny, V. and Basset, Y. (2000) Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos* 89, 564–572.

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. and Drozd, P. (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature* 416, 841–844.

Novotny, V., Miller, S.E., Leps, J., Basset, Y., Bito, D., Janda, M., Hulcr, J., Damas, K. and Weiblen, G.D. (2004) No tree an island: the plant-caterpillar food web of a secondary rain forest in New Guinea. *Ecology Letters* 7, 1090–1100.

Pimm, S. (2001) *The World According to Pimm: A Scientist Audits the Earth*. McGraw-Hill, New York.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. and Gibbons, D.W. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365, 335–337.

Rabinowitz, D. (1981) Seven forms of rarity. In: Synge, H. (ed.) *The Biological Aspects of Rare Plant Conservation*. Wiley, New York.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. and Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.

Samways, M.J. (1994) *Insect Conservation Biology*. Chapman & Hall, London.

Speight, M.R., Intachat, J., Chey, V.K. and Chung, A.Y.C. (2003) Influences of forest management on insects. In: Basset, Y., Kitching, R., Miller, S. and Novotny, V. (eds) *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource use in the Canopy*. Cambridge University Press, Cambridge.

Spitzer, K., Novotny, V., Tonner, M. and Leps, J. (1993) Habitat preferences, distribution and seasonality of the butterflies (Lepidoptera, Papilionoidea) in a montane tropical rain forest, Vietnam. *Journal of Biogeography* 20, 109–121.

Spitzer, K., Jaros, J., Havelka, J. and Leps, J. (1997) Effect of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. *Biological Conservation* 80, 9–15.

Stewart-Oaten, A. and Murdoch, W.W. (1986) Environmental impact assessment: pseudo-replication in time? *Ecology* 67, 929–940.

Stork, N.E. (1994) Inventories of biodiversity: more than a question of numbers. In: Forey, P.I., Humphries, C.J. and Vane-Wright, R.I. (eds) *Systematics and Conservation Evaluation*. Clarendon Press, Oxford, pp. 81–100.

Thomas, C.D. (1991) Habitat use and geographic ranges of butterflies from the wet lowlands of Costa Rica. *Biological Conservation* 55, 269–281.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. and Williams, S.E. (2004) Extinction risk from climate change. *Nature* 427, 145–148.

Vane-Wright, R.I., Humphries, C.J. and Williams, P.H. (1991) What to protect? Systematics and the agony of choice. *Biological Conservation* 55, 235–254.

Vasconcelos, H.L., Vilhena, J.M.S. and Caliri, G.J.A. (2000) Responses of ants to selective logging of a central Amazonian forest. *Journal of Applied Ecology* 37, 508–514.

Williams, P.H., Humphries, C.J. and Vane-Wright, R.I. (1991) Measuring biodiversity: taxonomic relatedness for conservation priorities. *Australian Journal of Systematics and Botany*, 665–679.

Willott, S.J. (1999) The effects of selective logging on the distribution of moths in a Bornean rainforest. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences* 354, 1783–1790.

Wilson, E.O. (1987) The little things that run the world: the importance of conservation of invertebrates. *Conservation Biology* 1, 344–346.

Wilson, E.O. (2000) On the future of conservation biology. *Conservation Biology* 14, 1–4.

Wilson, R.J., Davies, Z.G. and Thomas, C.D. (2006) Insects and climate change: processes, patterns and implications for conservation. In: Lewis, O.T., New, T.R. and Stewart, A.J.A. (eds) *Insect Conservation Biology*. CAB International, Wallingford, UK.

Wolda, H. (1996) Between-site similarity in species composition of a number of Panamanian insect groups. *Miscellánia Zoològica* 19, 39–50.

Author Queries

[AU1] Wright, 2005 not in Reference list.
[AU2] Pl provide place and year of unpublished data.
[AU3] Wright, 2005 not in Reference list.
[AU4] "Quintero and Roslin (2006)" has not been listed in the Reference list. Please provide reference
[AU5] Pl provide place and year of unpublished data.
[AU6] Closing parenthesis has now been inserted after the word "bags" please check.
[AU7] Lewis, 2006 not in Reference list.
[AU8] Wilson, 2004 not in Reference list.
[AU9] Please provide page nos. for the reference "Landres, P.B. et al. (1998)".