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# Assessing the impact of forest disturbance on tropical invertebrates: some comments

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Hill & Hamer (1998) make the rational contention that species–abundance data relevant to selected invertebrate taxa, such as butterflies, might be used to monitor forest disturbance, but that the issue warrants further research. Nummelin (1998) shows cogently that fit of species–abundance data to the log-normal distribution to monitor forest disturbance is unlikely to apply universally. The debate is timely since studies of the impact of forest disturbance on invertebrates, particularly tropical insects, have increased substantially during the past 10 years (e.g. Holloway 1977; Nummelin & Hanski 1989; Verhaagh 1991; Holloway, Kirk-Spriggs & Chey, 1992; Belshaw & Bolton 1993; Schowalter 1994; Didham *et al.* 1996; Eggleton *et al.* 1996; Nummelin 1996; Brown 1997; Didham 1997; Intachat, Holloway & Speight 1997; Malcolm 1997; Ozanne *et al.* 1997; Spitzer *et al.* 1997; Watt *et al.* 1997; Holloway 1998; Lawton *et al.* 1998; Rodriguez, Pearson & Barrerea 1998). This results both from general concerns about the rapid modification of tropical habitats and the recognition that invertebrates are highly sensitive to such modifications and much more amenable to statistical analyses than vertebrates (e.g. Collins & Thomas 1991; Kremen 1992; Kremen *et al.* 1993).

Hill & Hamer (1998) refute the data of Nummelin (1998) as being inappropriate to discuss this issue, yet there are problems associated with both studies. The study of Hill *et al.* (1995) analyses a 'snap shot' of the butterfly community during the dry season, obtained during 40 days of field work in Indonesia. It is doubtful that most species present during the annual cycle at their sites would have been collected. This is of particular concern because some specialist insect herbivores are known to be more seasonal than those that are generalists (Novotny & Basset 1998) and these specialists may be particularly sensitive to forest disturbance. Whether butterflies represent appropriate taxa for monitoring forest disturbance is also commented on later. Nummelin (1998 and see references therein) used sweeping as a main method for collecting different insect taxa. Both the mesh size of the sweeping net and the experience of the operator may influence the results strongly (Hespenheide 1979). Notably, most of the larger and rapid insect flyers may escape. Furthermore, as Hill & Hamer (1998) state, adjusting sweeping results for different density and structure of vegetation at unlogged and logged forest sites may also be difficult. Standardization of sampling effort across habitats with different physical structures is likely to be a problem in studies of forest disturbance, but this may also apply to butterfly census transects. That said, both studies are to be commended since they promote tropical insects as indicators for monitoring forest disturbance and regeneration, but point to possible caveats in so doing.

In our opinion, the question as to whether the log-normal distribution is universal or useful in the present context should be part of a wider research agenda, with the intention of answering the following questions: (i) are species–abundance relationships useful for monitoring invertebrate responses to forest disturbance; (ii) assuming that they are, on which type of data should the analyses focus and how; and (iii) which invertebrate taxa should be considered for such analyses?

**1.** The answer here is affirmative, but with some caution. After serious disturbance, species disappear or their abundance is greatly modified, so species–abundance relationships should be an appropriate method to quantify these changes. Furthermore, patterns of species–abundance relationships are often more informative than species diversity indices (e.g. Novotny 1993; Tokeshi 1993).

However, in addition to species–abundance relationships, one must be aware that there is a panoply of statistical methods that may help to interpret better species–abundance plots and, ultimately, to comprehend the changes in invertebrate density/diversity that result from forest disturbance. Briefly, these promising methods can be classified as (a) considering species as mutually replaceable units, in a fashion analogous to species–abundance relation-

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ships: *k*-dominance curves (e.g. Lambshead, Platt & Shaw 1983; Warwick, Pearson & Ruswahyuni 1987), rarefaction and other related techniques (e.g. Hurlbert 1971; Colwell & Coddington 1994) or the new index of evenness developed by Bulla (1994); (b) using the information associated with the identity of the species: direct gradient analysis, for example CCA, Canonical Correspondence Analysis (e.g. Palmer 1993; see applications in e.g. Kremen 1992; Spitzer *et al.* 1997) or *R*-mode clustering (e.g. Holloway 1977); and (c) being associated with better design of field experiments: BACI analyses (Before-After/Control-Impact; Stewart-Oaten, Murdoch & Parker 1986). CCA offers the particular advantage that responses of invertebrates can be related directly to the degree of disturbance and this may be crucial for a sound interpretation of the data. Others also used OLS regressions to characterise the slope of the abundance ranked by species (e.g. Cotgreave & Harvey 1994), but this procedure may be statistically unsound as ranked data points are not independent from each other.

To turn now specifically to species–abundance plots, one major question is to decide against which theoretical distribution the data should be compared, since a variety of models exist (see review in Tokeshi, 1993). Ideally, the expectation to fit particular distributions should be based on biological arguments. Unfortunately, the biological reality of many theoretical distributions is not straightforward, and the log-normal is perhaps the best example in this regard (e.g. May 1975; Sugihara 1980; Ugland & Gray 1982; Pagel, Harvey & Godfray 1991; Gaston, Blackburn & Lawton 1993; Tokeshi 1993). Inference as to the mechanisms producing the observed log-normal pattern is not possible since the same distribution can result from various mechanisms. For example, species–abundance distributions in a climax and a highly disturbed community may be virtually identical in some situations (Novotny 1993). The difficulty of inferring mechanisms from patterns applies to all species abundance distribution models since no general theory exists that would allow specific predictions to be made (and tested) about the effects of disturbance. As long as theory is not reconciled with biological reality, erroneous concepts may move on unsuspected. Is there still time available for statisticians and ecologists to work together and devise specifically ecological studies to test and/or develop theoretical models that could be used in conservation studies? It would be preferable, but the urgency of the conservation crisis in the tropics commands that rapid progress is made from whatever framework has been acquired so far. One promising strategy may be to design studies so that the intensity of disturbance is known and the corresponding species–abundance distributions are measured as dependent variables. To illustrate these problems, Spitzer *et al.* (1997) reported that moderate levels of logging in Vietnam resulted in higher species richness and diversity of butterflies in gaps, a result opposite to that of Hill *et al.* (1995), who studied larger-scale disturbance.

**2.** For species–abundance plots to be representative of the study systems, sample size must be large enough to reveal most species present in the community and their relative abundance. For example, it may be unsound to attempt to fit a log-normal distribution to a set of data not revealing the mode of the distribution (see Preston 1962; Hughes 1986; Magurran 1988), as, indeed, is the case for most tropical insect data sets. Furthermore, once sampling size is judged to be large enough, whether the analyses should include rare species is highly debatable. One can argue that rare species are commonplace in pristine forests and generate the characteristic lower tail of log-normal distributions. Conversely, insect rarity in tropical rain forests may be an artefact resulting from a combination of high habitat diversity, contamination from these habitats and insufficient sampling effort (Basset 1997). Rare species may appear to be rare because they are sampled in 'marginal' habitats as opposed to their 'optimal' habitats (the 'mass effect' of Shmida & Wilson 1985). Since the impact on community structure of a high number of rare species is arguable, one may wish to restrict the analyses to common species (Tokeshi 1990, 1993). Typically, the boundaries of insect communities in highly heterogeneous environments such as tropical rain forests are difficult to define and more research should be invested to understand how we should limit such boundaries statistically, if this is possible at all (Tokeshi 1993; Basset 1997).

Usually, species–abundance plots are obtained from pooling data collected during protracted periods of time, to ensure sufficient sample size. Rarely, as in Tokeshi (1990), spatial or temporal replicates are available to test the consistency of the distribution and its shape. This may be one way to proceed for a sound comparison of the distributions obtained at sites experiencing different levels of disturbance. However, this is likely to require a considerable sample size and large amounts of work.

Whether abundance should be expressed in terms of the number of individuals, biomass or both represents the next uncertainty. Biomass data reflect the partitioning of resources within the community better than the number of individuals (Tokeshi 1990) and they are more sensitive than the number of individuals, particularly for species of lower occurrence (Jarosik 1992). In marine biology, biomass data have been successfully used to detect pollution effects on benthic communities (e.g. Warwick, Pearson & Ruswahyuni 1987). Furthermore, in recent years, body size has emerged as one of the key biological characteristic (e.g. Pagel, Harvey & Godfray 1991; Blackburn *et al.* 1993), so that biomass data may indeed reveal interesting patterns where number of individuals appears to show none (e.g. Basset 1997). How-

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ever, biomass data should, as far as possible, be derived from related taxa, to avoid inclusion of large versus minute species in the analyses, which would then be highly sensitive to chance events during the collecting protocols. Further, to avoid destruction of the specimens, biomass is often estimated using published regressions with body size as independent variable (e.g. Schoener 1980) and various inaccuracies may result from this approach (e.g. Hodar 1996).

The type of abundance data is also likely to require different methods of analyses. One can argue that very few sampling methods can estimate reliably invertebrate densities but, surely, data obtained with methods inferring abundance from activity, such as light or pitfall traps, as opposed to 'direct' density measurements, may need a different treatment. For light traps, samples including species drawn from different associations that may exhibit very different species–abundance relationships may be examined first by performing an *R*-mode cluster analysis of species across samples to identify associations, and then by looking at these as far as possible independently (e.g. Holloway 1977, 1998; Intachat, Holloway & Speight 1997).

To close on analyses, testing for differences in two species–abundance distributions is relatively straightforward, by using the Kolmogorov–Smirnov two sample test (Tokeshi 1993). Yet, since species–abundance relationships do not allow inference of disturbance levels from the empirical parameters calculated, it may not be easy to decide which type of curve may be classified as being representative of either undisturbed or disturbed habitat. Other statistical methods listed in (1) may help in this regard, but theoretical work should also proceed in that direction.

**3**. As far as possible, taxa included in the analyses should be representative of the invertebrate communities present in the study plots at large, to avoid the interpretation of the results becoming dominated by the idiosyncrasies of a few common species (but see below). Lawton *et al*. (1998) go further on suggesting that attempts to assess the impacts of tropical forest modification using changes in the species abundance of one or a limited number of indicator taxa to predict change in species richness or other taxa may be highly misleading. Hill & Hamer (1998) state that for the analyses, pooling together different taxa with different ecology may result in not so well-defined patterns and a log-normal distribution. However, this kind of problem is less likely if these taxa exploit (and share) a particular resource, likely to be strongly altered by forest disturbance (e.g. insect herbivores feeding on, or pollinators associated with, a particular tree species extracted by selective logging; insect detritivores associated with top soil horizons likely to be affected by soil loss or compaction, etc.). Although there is little theoretical justification for limiting research on resource utilisation patterns to taxocenoses, such as butterflies, this strategy is popular and probably reflects more the taxonomic expertise of ecologists than the real structure of ecosystems. Rather, a multispecies and, preferably, multifunctional (e.g. Eggleton *et al*. 1996) approach should be encouraged to improve the interpretation of the data, but data relevant to different trophic or functional groups should not be mixed together. Indeed, conservation studies focusing on a multifunctional approach have revealed interesting patterns of habitat degradation and their effects on invertebrate communities (e.g. Robinson *et al*. 1992; Didham *et al*. 1996; Eggleton *et al*. 1996).

However, given the time and budget limitations of the research, as well as personal expertise, it may still be preferable to focus on particular invertebrate taxa. For example, Pearson (1994) has elaborated much on Cicindelidae as being prime indicator taxa in either inventory or monitoring surveys (see also Rodriguez, Pearson & Barrerea 1998). It is important to know whether extrapolations can be made with confidence using results obtained with rather non-diverse taxa whose food resources are indirectly affected by forest clearance, such as tiger beetles (Cicindelidae), as opposed to mega-diverse taxa likely to be directly affected by forest clearance, such as many groups of insect herbivores. Note that this question is secondary if we wish to identify suitable indicator taxa at the local, rather than regional, scale. In this case, one may wish to focus solely on particular species whose idiosyncrasies represent good indicators of local disturbance. For example, in the Tam Dao mountains of northern Vietnam, the butterfly *Stichophthalma louisa* (Nymphalidae: Amathusiinae) is common in the understorey, but rarely found in small clearings and outside of the forest (Novotny, Tonner & Spitzer 1991). A local study focusing on this particular species may be more appropriate than community parameters based on anonymous species.

It is now time to discuss whether butterflies, as a whole, represent adequate indicator taxa to monitor forest disturbance. Detailed lists of desirable properties for indicator taxa exist (e.g. Sutton & Collins 1991; Pearson 1994; Brown 1997). Certainly, butterflies are convenient to study, being conspicuous and relatively easy to sample (during day-time); their taxonomy is often straightforward and identification of the species may give access to known ecological information, natural history and improved interpretation of the results (see e.g. Brown 1997). However, tropical entomologists are unlikely to be struck by the variety and/or abundance of butterflies in unlogged forests. Their attention is more likely to be caught by the myriad leaf beetles, weevils, leafhoppers, moths or wasps, not to mention the diversity of the litter fauna. The majority of species of butterflies are heliophilous as adults, and this makes the forest interior a marginal habitat for them as a group, despite the existence of species with strong crepuscular preferences, limited to

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this habitat. Still, heliophilous species are present in the undisturbed forest, flying in and above the canopy. When the forest is opened by logging, the subsequent invasion of heliophilous species from the canopy results in the understorey butterfly community being more diverse and abundant than the original. These differences are primarily caused by changes in the behaviour of butterflies, rather than changes in their abundance (see Spitzer *et al*. 1993, 1997).

Even if some butterfly species are restricted to pristine forests, and others to natural gaps inside those forests (e.g. Spitzer *et al*. 1997), this is certainly also true of many other insect taxa which are more diverse than butterflies and may be better indicators in this regard. For example, Watt *et al*. (1997) mention that in forest plots of different levels of disturbance in Cameroon, complete clearance of vegetation prior to replanting resulted in a 40–70% species loss for arboreal beetles and termites, but only in a 15% loss for butterflies. In the same vein, Kremen (1992) concludes that butterflies are limited indicators of anthropogenic disturbance.

In short, community analyses of butterflies may not be straightforward, but analyses of individual species may be more promising because of the considerable ecological information that may be associated with them. For example, there is a group of crepuscular species (e.g. some Amathusiinae and Satyridae) which never leave the shaded understorey and their disappearance can be a good indicator, but it will not influence any synthetic community characteristics (such as the total number of species) because they are a minority, and their disappearance will be more than compensated for by the invasion of heliophilous species from the canopy.

However, butterflies have the immense advantage of being well-known taxonomically and this is likely to be crucial over other less well-known taxa for two main reasons. First, sibling or morphologically highly variable species may greatly distort species–abundance relationships, if the taxonomy is poor (see discussion of related problems in, for example, New 1996). At least these difficult morphospecies should be checked by professional taxonomists, even if this does not result in formal species identification. Note that close collaboration with taxonomist colleagues is essential to ensure the robustness of the analyses, whether they focus on butterflies or other taxa. Secondly, some authors may be reluctant to publish anonymous data points, in the absence of proper identifications. This can be resolved by the deposition of voucher specimens at local and renowned institutions.

Among these indicators, Geometridae, and particularly their green forms, appear to be good indicators of closed forests (e.g. Intachat, Holloway & Speight 1997; Holloway 1998; S.E. Miller, personal observation, L.J. Orsak, personal communication). However, in this case, light-trapping of moths may be difficult to calibrate for different background illuminations in logged and unlogged plots and the resulting different trap efficiency at these locations.

It may be worth mentioning here that, as far as possible, monitoring should not be confined to diurnal invertebrates. Modifications of the soil characteristics following disturbance are also known to affect the litter fauna and certain soil taxa may be excellent indicators of forest disturbance (e.g. Eggleton *et al*. 1996). However, as pointed out by Eggleton *et al*. (1996) one must be aware that estimating representative abundance of social insects, such as termites or ants, is not straightforward because of the clumped distribution of these species. Such a task is likely to require considerable sample size and labour.

The richness and variety of invertebrate taxa is also such that we may have the opportunity to target invertebrate indicators of either pristine forests or highly disturbed forest plots, depending on the aims of the research. For example, Coccinellidae may respond to an increase of sap-sucking prey, sensitive to vegetation regrowth in logged habitats (e.g. Schowalter & Crossley 1988), as, for example, the data of Nummelin (1998) suggest. A variety of heliophilous taxa, such as Acrididae (see Nummelin 1988; E. Charles, personal communication) or certain butterflies (e.g. Spitzer *et al*. 1997), are also likely to fare better in natural or man-made forest gaps. Ultimately, the choice of the indicator taxa may be dictated by the goals of the research.

To summarize, community analyses target multispecies assemblages exploiting specific forest resources, but particular invertebrate taxa may be worthy of consideration if this appears to be more practical, particularly at the local scale (see review of promising indicator taxa in Sutton & Collins 1991). The moment is right for large and parallel studies of potential indicator taxa with sufficient sampling effort and adequate methodology at selected tropical locations.

Finally, it is obvious that who disappears or is greatly reduced in individuals/biomass in the logged plots should be more significant than a mere change in the rank order of an anonymous data point on a species–abundance plot. The need to recognize species and to preserve their identity throughout the analyses is crucial (see, for example Hengeveld 1996), since different species may have different response optima to different levels of disturbance. Seeking correlations between certain biological characteristics of species and their sensitivity to disturbance may, indeed, represent one key approach to this field of research. Changes in species–abundance distribution parameters cannot be interpreted causally without studying the species composition of the distributions. Taxonomy has again a vital role to play here. However, since many tropical insect species may remain unnamed for decades and perhaps for generations of taxonomists (e.g. Erwin 1995), the stage is also set for

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large-scale observations and experiments in the field, targeting the ecology and life-cycles of particular species, and careful deposition of voucher specimens at selected institutions. The task is daunting, but local parabiologists trained specifically for this purpose may certainly help with many aspects of the research agenda, particularly in increasing sample sizes above the minimum required for statistical analyses (e.g. Janzen *et al*. 1993; Beehler 1994; Novotny *et al*. 1997).

In conclusion, given all of the above, it is not surprising that studies such as those of Hill & Hamer (1998) and Nummelin (1998) reach conflicting results. We expect that present problems with the log-normal distribution and other species–abundance relationships will be solved when statisticians, taxonomists, ecologists and local parabiologists learn to collaborate on carefully constructed programmes of environmental monitoring and biodiversity assessment.

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