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From communities to continents: beta diversity of herbivorous insects

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Recent progress in molecular systematics that assists species identifications, and in on-line databases of ecological and museum collections that enable the integration of insect distribution data represent important developments facilitating beta diversity studies. The increase in alpha and gamma diversities of insect herbivores from temperate to tropical communities is driven largely by a parallel increase in plant diversity while the diversity of insect herbivores per plant species remains constant. Likewise, the high beta diversity of insect herbivores along altitudinal gradients is only partially explained by changes in plant diversity, while abiotic factors and the abundance of natural enemies may also be important. The high alpha diversity of insect herbivores in lowland tropical forests is not matched by beta diversity as locally co-existing species represent a large proportion of regional species pools. The role of dispersal limitation in the distribution of herbivorous insects in tropical forests could be minor, as short-lived insects are efficient colonisers of their mostly long-lived woody hosts.

Introduction

Beta diversity, or diversity among ecological communities, is a Cinderella among biodiversity parameters, overshadowed by her more popular sisters, alpha and gamma diversities. While alpha, the local diversity of a community, and gamma, the regional diversity of species pools from large geographic areas, are simply counts of species from a particular territory, beta diversity is a more abstruse concept measuring change in species composition between communities. The difficulty of surveying species from more than one area is undoubtedly responsible for the scarcity of beta-diversity studies. Ecologists have not consistently applied standardised survey protocols to multiple sites and the study of changes in diversity among sites is impeded by incomplete taxonomy for many insect groups. Despite these problems there are new data (Stork *et al*. 1997, Asher *et al*. 2001, Basset 2001, Benes *et al*. 2002, Basset *et al*. 2003) and theoretical developments (Hanski 1999, Hubbell 2001) that improve our understanding of insect distribution. The present review uses this information to examine the factors that prevent species from being distributed everywhere, and tries to identify promising approaches to future beta diversity studies.

Defining and measuring beta diversity

Alpha diversity characterises species richness in communities, assemblages of species potentially involved in ecological interactions such as competition or predation, while the term gamma diversity is usually applied to species pools at large spatial scales, formed primarily by speciation and dispersal (Ricklefs 1987). Spatial resolution is necessarily defined rather vaguely and may vary among species. Some authors use the terms alpha and gamma diversities even more loosely to distinguish between point (alpha) diversity and the gamma diversity of any larger area, often obtained from a collection of multiple point estimates. For instance, Gering and Crist (2002) contrasted point and population samples of insects from a single tree, multiple trees at a single site, and multiple sites within a larger area. Koleff and Gaston (2002) and Arita and Rodriguez (2002) explored the effect of spatial resolution on beta-diversity estimates. At low resolution, high beta diversity can reflect local environmental heterogeneity. As sampling grain increases, biotic assemblages appear more homogeneous as each of the study areas encompasses a wider range of the available environments (Mac Nally *et al.* 2004). Alpha, beta and gamma terminologies and analytical approaches have further served the study of changes in diversity among microhabitats within communities and through time (de Vries *et al.* 1997). Vellend (2001) noted a distinction between the concept of beta diversity as among-plot variability in species composition independent of the position of individual plots on spatial or environmental gradients, and the concept of turnover in species composition along predefined gradients. The former can be measured by the partitioning of regional diversity, the latter using matrices of compositional similarity and physical or environmental distances among pairs of study plots.

Regional gamma diversity can be partitioned into the average local alpha diversity (α_{avg}) and between-site beta diversity (β) in either a multiplicative or additive fashion. Whittaker (1972) originally defined beta diversity as $\beta = \gamma/\alpha_{avg}$, a dimensionless number that relates gamma diversity to alpha diversity, each measured in numbers of species. As recently argued by Loreau (2000), Gering and Crist (2002) and Veech *et al.* (2002), the additive partitioning of gamma diversity $\gamma = \alpha_{avg} + \beta$ is more practical as all three parameters, including beta diversity, can be measured in the same unit, the number of species.

The change in species composition from community A to community B is fully described by three parameters: the number of species lost (present in A but not B), species gained (present in B but not A), and species shared (present in A and B). Nested communities where A is a subset of B represent a special case with no species loss. There are at least 24 measures of beta diversity based on these parameters (Koleff *et al.* 2003a) including those sensitive only to compositional differences between communities and those sensitive also to their differences in alpha diversity.

The differences in species composition between two communities can also be quantified using similarity measures sensitive to species abundance (Colwell & Coddington 1994). Condit *et al.* (2002) used the probability $P(r)$ that two randomly selected individuals separated by distance r were conspecific. An important application of this approach in beta diversity studies is to examine the decay of conspecific probability with increasing geographic distance between communities (Condit *et al.* 2002, Ricklefs 2004). Chao *et al.* (2005) proposed estimators for the classical Jaccard and Sørensen similarity indices based on species abundance data that include the effect of shared species missed by the sampling.

The probability that two individuals drawn from different communities are conspecific can be standardised by the analogous probability for two individuals drawn from the same community. This is the principle of Morisita's index, a special case of the normalized expected species shared index, NESS(m) (Grassle & Smith 1976). NESS(m) estimates the number of common species for random draws of a particular number of individuals m from two different communities and compares this estimate with the number of common species resulting from random draws from the same community. It ranges from 0 (no common species) to 1 (samples are random samples from the same community). NESS(m) is a more general case of Simpson's index. The sum of the squared proportional abundances is the probability that two individuals drawn at random belong to the same species. The complement of Simpson's index, also known as the Gini coefficient, is the probability that two individuals drawn at random belong to different species. Robinson and Tuck (1993), Frenzel and Brandl (2001) and Walla *et al.* (2004) used similar approaches relating observed differences between two communities to probabilistic estimates of the expected number of shared species between two samples drawn from the same community.

The complete census of species in many insect communities is very difficult to achieve due to numerous rare species (Novotny & Basset 2000) that can be discovered only in very large samples (Longino *et al.* 2002). Relying on NESS(m) or other probabilistic measures avoids the often serious overestimation of beta diversity based on simple comparisons of incomplete species lists. Although NESS(m) is more robust to biases in sample size than some measures of dissimilarity, it requires an arbitrary decision on the value of m. This parameter determines the relative importance of dominant and rare species in estimating beta diversity and NESS estimates are increasingly influenced by dominant species as m decreases.

Beta diversity can be also quantified using multivariate methods partitioning changes in species abundance into spatial and environmental components (Leps & Smilauer 2003, Borcard *et al.* 2004). For instance, Brehm and Fiedler (2004) explored the performance of correspondence analysis (CA), detrended correspondence analysis (DCA), and nonmetric multidimensional scaling (NMDS) in the analysis of species turnover along an elevation gradient.

There are two conceptually different approaches to measuring beta diversity with respect to environmental gradients (Fig. 1; *see* also Koleff *et al.* 2003b). Using a latitudinal gradient as an example, beta diversity can be calculated either between pairs of sites at different latitudes, or between pairs of sites from the same latitude that are themselves distributed along the latitudinal gradient. The former approach relates the change in latitude to the change in the species composition of insect communities (community composition gradient), measured as beta diversity, while the latter approach relates beta diversity of insect communities to particular latitudes (beta diversity gradient). The distinction between measuring change in species composition and change in beta diversity along environmental gradients is not always made and rarely has the latter pattern been studied.

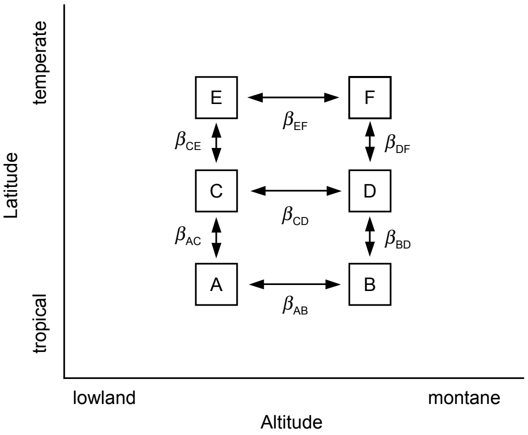

Fig. 1. Two approaches to measuring beta diversity with respect to environmental gradients: (i) The analysis of latitudinal gradients in community composition relates the change in latitude, from tropical to temperate, to the change in the species composition of insect communities, measured as beta diversity β_{AC}, β_{CE} in the lowlands and β_{BD}, β_{DF} in the mountains; (ii) The analysis of a latitudinal gradient in beta diversity relates the change in latitude to the change in beta diversity between insect communities from the same latitude (β_{AB}, β_{CD}, β_{EF}). The present example illustrates the analysis of latitudinal gradients in altitudinal beta diversity, but the β_{AB}, β_{CD}, β_{EF} values can be also calculated for pairs of communities from the same environment, such as altitude.

Beta diversity and dispersal

In neutral community models that assume ecological equivalence of all species in a uniform environment and predict beta diversity patterns generated solely by speciation and dispersal (Bell 2001, Hubbell 2001), dispersal limitation generates relatively species-poor, strongly dominated and non-overlapping communities that together comprise a species-rich metacommunity characterised by low dominance. Conversely, high dispersal leads to relatively species-rich communities with low dominance and overlapping composition that together comprise a strongly dominated metacommunity that is species-poor.

Models recognising that species are not ecologically equivalent regard species habitat as a network of resource patches with patch size and isolation being the principal parameters that define the colonization and extinction probabilities of species (Hanski 2005). Depending on resource distribution, species can reach alternative stable equilibria, occupying either most, or very little, of the suitable habitat patches (Hanski *et al.* 1995). The dispersal ability of species and the configuration of their resource patches determine the magnitude of beta diversity in the metacommunity (Hanski 1999).

The role of dispersal limitation in the distribution of herbivorous insects is due for a reassessment. Most insect herbivores can travel at least hundreds of meters per generation (e.g., Hanski 1999: p. 144). Insect distribution patterns on islands and air screening over oceans indicate that long distance dispersal by wind is common in many insect taxa (Miller 1997). Our appreciation for insect migration is probably biased towards sedentary populations that are easy to study while widely dispersing species are mostly ignored (Dlabola & Taimr 1965, Compton *et al.* 1988, Riley *et al.* 1997). On the other hand, models of metapopulation dynamics predict that insect populations are highly spatially aggregated, even in widespread taxa with the potential for long distance dispersal.

Examples of long distance dispersal are known from geographically isolated volcanic islands such as Krakatau (fig wasps: Thornton *et al.* 1996, Compton *et al.* 1988; butterflies: New *et al.* 1988) and Long Island in New Guinea (fig wasps: Shanahan *et al.* 2001; other insects: Edwards & Thornton 2001). Likewise, many upper montane species have distributions spanning wide geographic areas, as from the Himalayas to New Guinea (Holloway 1986). In Britain, the impact of dispersal limitation on insect diversity across shorter distances was relatively minor when compared to the effect of habitat heterogeneity (Harrison *et al.* 1992).

In contrast, more restricted distribution patterns have been documented for cicadas (de Boer 1995) and water bugs (Polhemus & Polhemus 1998) in New Guinea, suggesting relict distributions limited by historical barriers that may no longer exist. In continuous lowland tropical forests lacking physical migration barriers, both dispersal limitation and environmental variability contribute to the spatially auto-correlated distribution of plants (Condit *et al.* 2002, Tuomisto *et al.* 2003).

Many vegetation types including boreal forests, savannas and mangroves, are dominated by plant species distributed across large geographic areas. Such plants represent a continuous and locally abundant resource for their herbivores. Recent studies by Pitman *et al.* (1999, 2001) suggest that common, widespread species are also numerically important in the tropics. Even when there exists strong regional variation in host plant abundance, this can be compensated by low host specificity of herbivores. Most herbivores are specialised on plant genera and families rather than species (Novotny *et al.* 2002a), and many species-rich plant genera are continuously distributed across large areas of tropical forest (Gentry 1990).

Herbivorous insects should be able to follow changes in the spatial distributions of widespread hosts in both tropical and temperate forests, particularly as insect generation times are usually shorter than for host plants (e.g. 1–3 orders of magnitude shorter for the herbivores of canopy trees). These considerations lead us to predict low beta diversity of herbivore communities on widespread, dominant plant taxa in temperate and tropical forests, bearing in mind that the distribution of herbivore species is also limited by factors other than dispersal barriers and host plant availability. Other factors, such as high levels of intraspecific aggregation due to oviposition behaviour or gregariousness, lead to the opposite prediction of high beta diversity (Summerville *et al.* 2003). Many suitable host plant patches can be repeatedly colonised and abandoned as a result of metapopulation dynamics (Hanski 2005). Herbivores also respond to host-plant quality (Weisser *et al.* 2005, but *see* Gripenberg & Roslin 2005), predation (Denno *et al.* 2005) and parasitism (Harrison *et al.* 2005, Tscharntke 2005, van Nouhuys 2005). They may therefore fail to colonise the entire range of a entire range of a host species, suffering widely different mortality rates across the host's geographic range (Scriber 1988, Quinn *et al*. 1997, Wagner 1999, Brewer & Gaston 2002, 2003).

Beta diversity and host plants

Host specificity of insect herbivores is a key parameter influencing diversity estimates. We may expect, for example, that polyphagous herbivores exhibit lower beta diversity than specialists.

Beta diversity is minimally a combination of between-site turnover of herbivore species on particular host plants, changes in host use by herbivores (Singer & Wee 2005), and turnover of plant species. Another potentially important factor influencing herbivore beta diversity is variation in the distribution of natural enemies (Lill *et al*. 2002). The relative importance of these factors in tritrophic interactions is poorly known as many studies have analysed only overall patterns of insect beta diversity on diverse vegetation along environmental gradients. The effect of plant beta diversity can be controlled by comparing insect herbivores feeding on a particular plant species at different sites and in different environments, including altitude (Allison *et al*. 1993), habitat (MacGarvin *et al*. 1986), climate (Andrew & Hughes 2004) or disturbance regime (Denno 1977). Regrettably, the pioneering study on the cosmopolitan bracken fern (Lawton *et al*. 1993) has not been followed by analogous studies of other widely distributed plant species or genera.

Alpha and gamma diversity of insect herbivores is correlated with life history traits of host-plant species (Southwood 1960, Claridge & Wilson 1981, Lewinsohn 1991, Basset 1996, Basset & Novotny 1999, Kelly & Southwood 1999, Brändle & Brandl 2001). Studies have predicted the local and regional diversity of herbivores from host geographic and altitudinal range, phylogenetic isolation, abundance, leaf phenology and palatability, and other plant traits. Analogous studies relating these plant traits to herbivore beta diversity are unavailable. We can therefore only hypothesise a negative correlation between beta diversity of herbivores and host-plant traits that influence the ability of herbivores to find and colonise hosts, such as abundance, growth form, generation time and taxonomic isolation.

Contrasting alpha and gamma diversity

The extraordinarily high alpha diversity of insects in tropical forests was extrapolated by Erwin (1982) to a global arthropod diversity estimate of 30 million species. This extrapolation was based in part on the untested assumption that herbivores are host specific and therefore exhibit high beta diversity among tree species (Miller *et al*. 2002). Further studies have not corroborated this assumption and revised estimates of arthropod diversity are approximately 5–7 million species (Thomas 1990, Basset *et al*. 1996, Ødegaard 2000, Novotny *et al*. 2002b).

There is now growing evidence that insect alpha diversity exceeds beta diversity in tropical forests. Locally co-existing species represent a large proportion of the regional species pool for the few insect taxa for which regional data are available in the tropics (Gaston & Gauld 1993, de Vries 1994, Gaston *et al*. 1996, Orr & Haeuser 1996, Haeuser *et al*. 1997, Robbins & Opler 1997, Bartlett *et al*. 1999, Novotny *et al*. 2005a). A similar pattern of high alpha and low beta diversity exists for tropical trees (Foster & Hubbell 1990, Kochummen *et al*. 1992).

Erwin (1983) published the first, and therefore influential, beta diversity estimates for tropical rainforest beetles. He reported high beta diversity, but his estimates were inflated by small sample size (Gaston 1991). The low beta diversity values reported later by other authors could conceivably be biased in the opposite direction if sampling failed to include rare species with limited geographic distribution and low population density (Erwin 1991). The existence of such herbivores is difficult to verify, but Hodkinson and Hodkinson (1993) proposed a method, based on the comparison of local species censuses with museum collections, that at least estimated the number of unknown species. The inclusion of these hypothetical species in local-to-regional species diversity comparisons increased estimates of beta diversity (Novotny & Missa 2000), but the accuracy of such estimates is unknown.

The relationship between local and regional diversity studied across multiple sites and regions can elucidate the process of community assembly from regional species pools (Ricklefs 2004). Most studies have found a linear increase in local diversity with regional diversity, suggesting that local communities are founded as proportional samples of regional species pools (Compton & Hawkins 1992, Dawah *et al.* 1995, Arita & Rodriguez 2002, but *see* Soares *et al.* 2001).

One of the exciting developments in the study of local and regional diversity patterns is the recent proliferation of high-resolution atlases of insect distribution, particularly for butterflies (e.g., Asher *et al.* 2001, Marttila *et al.* 2001, Benes *et al.* 2002). Atlases synthesise hundreds of thousands or millions of faunistic records and represent a rich source of information for macroecological analyses, similar to that of more advanced bird atlases (Gaston & Blackburn 2000). They can provide information on changes in geographic distribution of species, including responses to global climate change and anthropogenic disturbance (Warren *et al.* 2001), on latitudinal and longitudinal gradients in species richness (Storch *et al.* 2003), as well as regional species lists for comparison with local communities. The atlases record alpha and gamma diversities, but can also be used to generate beta diversity maps (for an example *see* Koleff & Gaston 2002).

Beta diversity along latitudinal gradients

Alpha and gamma diversities of almost all groups of insects are highest in the tropics (Rosenzweig 1995, Willig *et al.* 2003). The few notable exceptions include aphids (Dixon *et al.* 1987) and ichneumonids (Owen & Owen 1974, Gauld *et al.* 1992). The rate of increase in species richness often accelerates towards the equator (Rosenzweig 1995) and the average size of species' geographic range decreases towards the equator, a pattern established for vertebrate taxa and known as Rapoport's effect (Stevens 1989). These trends combined should result in an increasing rate of species turnover from high to low latitudes, a pattern indeed confirmed for vertebrates and plants, but no information is available on insects (Koleff *et al.* 2003b, Rodriguez & Arita 2004).

The alpha diversity of herbivores feeding on particular plant species appears to be similar in tropical and temperate forests (Futuyma & Gould 1979, Janzen 1988, Basset & Novotny 1999, Morris & Godfray 2005). The ratio of butterfly to plant species also shows no trend with latitude (Gaston 1992). The large increase in alpha and gamma diversities of insect herbivores from temperate to tropical areas is therefore likely to be due to increasing plant diversity.

In his classical study MacArthur (1969) found that while the alpha diversity of birds slightly increased from temperate to tropical areas, the main explanation for much higher gamma diversity in the tropics was higher beta diversity between tropical sites than between temperate ones. Willig *et al.* (2003) reviewed other studies that addressed this problem but sadly the analysis has not been replicated for insects during the 35 years since MacArthur's study. Interestingly, Sepkoski (1988) found a similar prominence of beta diversity when he examined the relative contribution of alpha and beta diversities to global diversity during the Paleozoic.

Beta diversity along altitudinal gradients

Gradients in environmental variation can explain substantial changes in diversity with altitude and are thus among the most pervasive factors explaining species diversity on larger geographic scales. For instance, global maxima of plant diversity, measured as the number of plant species per 10 000 km^2, are associated with altitudinal gradients in the tropics (Barthlott *et al.* 1996). Not surprisingly, insect herbivores exhibit rapid change in species composition with altitude, although there are many more studies available on altitudinal trends in alpha diversity than beta diversity (Hebert 1980, Holloway 1987, McCoy 1990, Allison *et al.* 1993, Fernandes & Lara 1993, Olson 1994, Davis *et al.* 1999, Sanders 2002, Brehm & Fiedler 2004 *vs.* Kremen 1994, Brehm *et al.* 2003).

Rapid turnover in the composition of vegetation with altitude (Givnish 1999) suggests that distribution of many herbivore species could be limited by host-plant availability. Brehm *et al.* (2003) found a close correlation between the change in moth and plant communities along an altitudinal gradient, but both data sets were also closely correlated with temperature. The effect of vegetation change on insect communities can be directly studied using comparative data from herbivorous communities feeding on the same host species at different altitudes (Allison *et al.* 1993). Novotny *et al.* (2005b) found high species turnover with altitude in caterpillars (Lepidoptera) feeding on the same host-plant species, demonstrating the key importance of factors other than host-plant availability. Temperature is an obvious candidate for a limiting factor, particularly in the tropics (Janzen 1967). Possibly the most important biotic factor along tropical elevation gradients is a significant decrease in the abundance of ants with elevation (McCoy 1990, Samson 1997), affecting prey and mutualists (Olmstead & Wood 1990).

Herbivore communities along altitudinal gradients are also determined by spatial constraints, namely that such gradients are bounded by sea level and summit, and that the area of intervening habitat decreases with elevation. These constraints can generate either a monotonous decrease in species richness with elevation due to diminishing area or a peak in species richness at mid-elevations where the ranges of lowland, mid-elevation and high-elevation species overlap (Holloway 1987, McCoy 1990, Lees *et al.* 1999, Sanders 2002). Rapoport's effect of increasing species range with altitude was documented in some insect communities (Sanders 2002). This effect could generate a decreasing rate of change in species composition with altitude, but such a trend has not been well documented. For instance, Brehm *et al.* (2003) showed that in geometrid moths, the altitudinal change in species composition was better explained by models using a constant rate of species turnover with altitude.

Beta diversity in time

Beta diversity measures can also be used to quantify species turnover in time. Temporal variability in herbivore communities is studied less often than their spatial variability. This is illustrated by the limited attention paid to the species–time relationship, describing the accumulation of species in time, compared to the well-known species–area relationship (Adler & Lauenroth 2003). The temporal dimension of species variability is however as equally important as the spatial one. Insect communities tend to accumulate new species with time, partly as a result of a steady inflow of transient species (Basset 1997). For instance, Wolda (1983) reported new species of leafhoppers being regularly found even after seven years of nightly light trapping at a single tropical forest site. Further, garden areas < 0.3 ha accumulated 24%–38% of the entire England fauna in several insect taxa over 8–46 years of collecting (Southwood 1996).

Successional series represent an ecologically important case of change in diversity through time. Most of the information on the successional dynamics of insect communities refers to old-field succession in temperate areas. These studies reveal important changes along successional series in community structure and insect life histories, such as host specificity, migration ability, body size and generation time (Brown 1982, 1985, Brown & Southwood 1983, Brown & Hyman 1986, Hendrix *et al.* 1988, Novotny 1994, 1995). The change in diversity of insect communities was particularly rapid during the first few years of pioneer succession when the vegetation change was also the fastest. Many tropical successions however start with pioneer trees, rather than annual herbs (Ewel 1980, Richards 1996). They may present a more permanent and predictable habitat for insects even at early stages, characterised by slower turnover of herbivore species than is the case for early succession in temperate communities (Leps *et al.* 2001).

The within-habitat beta diversity in early successional communities is probably smaller than in primary forest communities as early successional species of herbivorous insects tend to have wider geographic distribution than species from primary forests (Spitzer *et al.* 1993, Ghazoul 2002). The globally increasing extent of early successional, disturbed and agricultural ecosystems coupled with human-mediated long range dispersal of species lead to global homogenisation of biota, manifested by decreasing beta diversity (Lövei 1997).

Concluding remarks

The rather unsatisfactory state of the art in beta diversity studies of insects, particularly when contrasted with the study of alpha and gamma diversities is demonstrated by the lack of even basic generalisations on beta diversity patterns. It is the result of limited empirical data as broad patterns of insect distribution are difficult to infer in taxonomically understudied insect groups. Many large-scale studies of insect communities, particularly, but not exclusively those from the tropics, result in collections of species that cannot be fully identified. These unnamed species are difficult if not impossible to reference geographically. The integration of local studies into regional databases is thus slow (Holloway & Barlow 1983, Janzen 1992, Kitching 1993). The combination of classical taxonomy based on morphology with DNA sequences that assist species-level identifications could help to alleviate this taxonomic impediment (Hebert *et al*. 2003). Further, on-line databases of specimen data from ecological studies (e.g. Janzen & Hallwachs 2004) and museum collections (Graham *et al*. 2004) can facilitate the integration of insect distribution data on regional scales. Progress in this area is important for conservation biology in helping to identify biodiversity hotspots (Myers *et al*. 2000) and to develop strategies for the optimal selection of protected areas (Howard *et al*. 1998) based on beta diversity patterns.

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