

MINOR REVIEW

Beta diversity of plant–insect food webs in tropical forests: a conceptual framework

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Abstract. 1. Beta diversity of plant–herbivore food webs, defined as turnover of trophic interactions between the food webs, represents a potentially useful extension of traditional studies of plant and herbivore beta diversity as it integrates spatial turnover of plant and herbivore species with changes in herbivore host plant preferences.

2. Beta diversity of plant–herbivore food webs can be partitioned into four components, corresponding to the turnover of plant–herbivore interactions due to change in (i) both plant and herbivore species, (ii) plant, but not herbivore, species, (iii) herbivore, but not plant, species, and (iv) herbivore host preferences between food webs. These components can be quantified using a range of existing beta diversity indices.

3. Relative magnitude of plant and herbivore beta diversity of plant–herbivore food webs can be analysed as an outcome of herbivore (i) host specificity, (ii) ability to track host plant populations by dispersal, and (iii) response to environmental conditions, competitors and enemies. The relative importance of these factors in tropical ecosystems remains to be determined.

Key words. Community similarity, diversity, environmental gradients, herbivory, geographical distribution, host specificity, Papua New Guinea, plant–herbivore interactions, rainforests, species turnover, tropic specialisation.

Introduction

Important methodological advances in the analysis of species distribution patterns on large spatial scales include null models of species distribution, based on speciation and dispersal in uniform environments (Hubbell, 2001; Condit *et al.*, 2002; Volkov *et al.*, 2003; Leigh *et al.*, 2004), models of metapopulation dynamics (Hanski, 1999), and increasingly sophisticated extrapolation of species distribution using spatially explicit environmental information (Corsi *et al.*, 2000; Segurado & Araujo, 2004), often obtained by remote sensing (Tuomisto *et al.*, 2003a).

This progress has not been matched by advances in collecting empirical data on tropical beta diversity, which remains the least studied of the alpha, beta and gamma aspects of diversity in tropical forests (Novotny & Weiblen, 2005). This bias is largely due to incomplete taxonomic knowledge of tropical plants and

particularly insects, making comparisons of multiple communities difficult.

The studies of plants and insects on large geographical scales fall into two broad categories: those studying spatial variability in species composition of particular taxa or guilds, including plants (Condit *et al.*, 2002; Tuomisto *et al.*, 2003b) and their insect herbivores (Ødegaard, 2006; Novotny *et al.*, 2007), while ignoring their interactions with the rest of the food web, and those focusing on the structural parameters of plant–insect food webs, including the number of herbivore species per plant species (Lewinsohn *et al.*, 2005), number of host species per herbivore species (Novotny & Basset, 2005), or web connectance (Kitching, 2000; Tylianakis *et al.*, 2007), while ignoring changes in species composition among these food webs.

We suggest that these two approaches can be combined and the study of beta diversity usefully broadened from plant and insect communities to plant–insect food webs, applying analytical tools used in community studies. In particular, Lewinsohn and Roslin (2008) demonstrate the importance of simultaneous study of plant and herbivore alpha and beta diversity in combination with herbivore host specificity for the analysis of tropical

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		H1	H2	H3	H4
P1	x	x	x		
P2	x	x	x		
P3					

(a)

		H1	H2	H3	H4
P1					
P2			x	x	
P3		x	x	x	

(b)

		H1	H2	H3	H4
P1	ph	p	p		
P2	h	0		h	
P3		p	p	ph	

(c)

Fig. 1. Trophic interactions between plant (P1–P3) and herbivore (H1–H4) species in two hypothetical food webs X and Y.

The food web X includes six plant–herbivore interactions between two plant species (P1, P2) and three herbivore species (H1–H3), while the food web Y includes five interactions between two plant species (P2, P3) and three herbivore species (H2–H4) (Fig. 1a,b). Only one interaction, between P2 and H3, occurs in both food webs (shaded field in Fig. 1c). One more interaction can potentially occur in both food webs, as both interacting species (P2 and H2) are present in both webs (0 field in Fig. 1c). The remaining interactions cannot occur in both webs due to absence of the plant species (p fields), herbivore species (h fields) or both plant and herbivore species (ph fields) from one of the webs.

biodiversity. This amounts *de facto* to the study of beta diversity of plant–herbivore food webs.

Ideally, a contiguous area of rainforest vegetation should be censused for plants, herbivores and their trophic interactions in order to document plant–herbivore food webs. A more feasible alternative includes comprehensive sampling of herbivores from a particular taxon or guild, feeding on plant species from a particular taxon, or the entire vegetation, with sample size on each plant species proportional to its biomass or abundance (Novotny *et al.*, 2004). This sampling protocol is markedly different from the one used by a majority of rainforest studies, which focus mostly on the host specificity of herbivores (Novotny & Basset, 2005). These studies typically examine arbitrarily selected sets of plant species, often including a balance of closely and distantly related species and/or single representatives of numerous plant lineages, sampled with constant sampling effort per plant species (Basset, 1996; Barone, 1998; Ødegaard, 2000). This dichotomy in sampling protocols leads to two largely separate lines of research, one on herbivore host specificity, another on food web structure.

Although the present paper is concerned mostly with plant–herbivore food webs, the concepts and methods discussed here can be equally well applied to insect–insect food webs, for instance food webs between herbivorous hosts and their parasitoids (Morris *et al.*, 2005), as well as to tri-trophic plant–herbivore–predator systems (Dyer & Letourneau, 2003).

Beta diversity analysis applied to food webs

Beta diversity estimates

Turnover of species between two communities, X and Y, can be fully described using three variables: the number of species present in both X and Y (*a*), only in X (*b*), and only in Y (*c*). These variables can be integrated into over 20 similarity and beta diversity indices presently in use (Koleff *et al.*, 2003), including the Jaccard similarity index $J = a/(a + b + c)$ and its complementary beta diversity measure, $\beta_{cc} = 1 - \text{Jaccard index} = (b + c)/(a + b + c)$, used here.

These indices, traditionally used to quantify differences in species composition between communities, can be also used to quantify differences in plant–herbivore interactions between food webs. Similarly as for communities, differences between

food webs X and Y can be characterised by the number of plant–herbivore interactions present in both X and Y, only in X, and only in Y. Beta diversity is then defined as the turnover of trophic interactions between food webs.

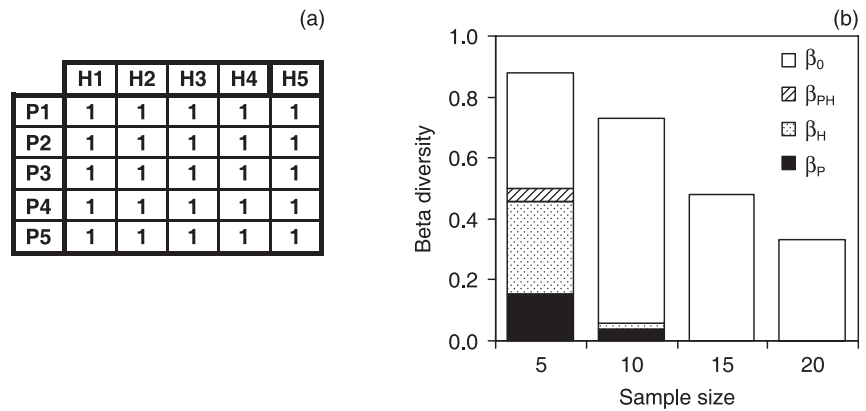
The plant–herbivore interactions present in only one of the two compared webs (*b* and *c*) can be classified into trophic interactions restricted to a single web because (i) neither the plant nor the herbivore species are present in both webs (b_{PH} , c_{PH}), (ii) only the plant species is absent from one of the webs (b_p , c_p), (iii) only the herbivore species is absent (b_H , c_H), and (iv) both the plant and the herbivore species are present in both webs, but the trophic interaction between them is not (b_0 , c_0). Beta diversity can be then partitioned into these four components as follows:

$$\beta_{cc} = (b_{PH} + c_{PH})/(a + b + c) + (b_p + c_p)/(a + b + c) + (b_H + c_H)/(a + b + c) + (b_0 + c_0)/(a + b + c) = \beta_{PH} + \beta_p + \beta_H + \beta_0.$$

The partitioning of beta diversity can be illustrated on hypothetical food webs X and Y (Fig. 1). The food web X includes six plant–herbivore interactions between two plant species (P1, P2) and three herbivore species (H1–H3), while the food web Y includes five interactions between two plant species (P2, P3) and three herbivore species (H2–H4) (Fig. 1a,b). Only one interaction, between P2 and H3, occurs in both food webs (Fig. 1c). One more interaction can potentially occur in both food webs, as both interacting species (P2 and H2) are present in both webs. The remaining interactions cannot occur simultaneously in both webs due to absence of the plant species (four interactions), herbivore species (two interactions) or both plant and herbivore species (two interactions) from one of the webs. The beta diversity of the two food webs $\beta_{cc} = 1 - a/(a + b + c) = 1 - 1/(1 + 5 + 4) = 0.9$ can be thus partitioned into $\beta_{PH} = 0.2$, $\beta_p = 0.4$, $\beta_H = 0.2$, and $\beta_0 = 0.1$ components.

The partitioning of food web beta diversity is not limited to any particular index of beta diversity. Koleff *et al.* (2003) reviewed 24 beta diversity indices, recognising ‘broad sense’ measures incorporating differences in composition attributable to species richness gradients, and ‘narrow sense’ measures that focus on compositional differences independent of such gradients. While β_{cc} is an example of a broad sense index, $\beta_{sim} = \min(b, c)/(\min(b, c) + a)$ is one of the frequently used ‘narrow sense’ indices. The beta diversity of the X and Y food webs (Fig. 1) can be also estimated as $\beta_{sim} = 4/(1 + 4) = 0.8$, where $\beta_{PH} = 0.2$, $\beta_p = 0.4$, $\beta_H = 0.2$, and $\beta_0 = 0.0$.

Fig. 2. Beta diversity generated by incomplete sampling of two identical food webs. Two identical food webs, each comprising five herbivore and five plant species, where each of the 25 possible plant–herbivore interactions was represented by one feeding individual (Fig. 2a), were sampled by randomly drawing 5, 10, 15 and 20 individuals from the total of 25 individuals representing each web and the beta diversity β_{cc} estimated from these samples (Fig. 2b). The beta diversity components β_p , β_H , β_{PH} and β_0 are explained in the text. Mean values from 10 replicated beta diversity estimates for each sample size are presented.



Beta diversity and sampling bias

Sampling of food webs, that is, plants, herbivores and their interactions produces more complete data on species than on their trophic interactions, as most species participate in more than one trophic interaction. Plant–herbivore food webs in tropical rainforests are particularly difficult to sample as they comprise many rare species, participating in numerous, even rarer trophic interactions (Novotny & Basset, 2000).

Incomplete sampling tends to overestimate beta diversity as some trophic interactions shared between two food webs are sampled in only one of them. Chao *et al.* (2005) provided a revised formula for some of the commonly used beta diversity indices correcting for this bias. It should be noted that incomplete sampling can also affect the relative importance of beta diversity components β_{PH} , β_p , β_H and β_0 . In particular, β_{PH} beta diversity can be misrepresented as β_p or β_H beta diversity or, when sampling is particularly poor, as β_0 . This is because the presence of each plant and herbivore species in each particular food web is also subject to sampling error, depending on the abundance of these species and the number of trophic links in which they are involved.

Let us assume that the trophic interaction between P2 and H3, the only shared interaction between our hypothetical food webs X and Y (Fig. 1), was missed by sampling in the web Y, while all remaining interactions in both webs were sampled. The P2–H3 interaction thus erroneously contributed to the β_0 beta diversity component as both P2 and H3 species were documented from both webs from other trophic interactions. However, more limited sampling could miss these species from the food web Y entirely, by failing to document also P2–H4 and/or P3–H3 interaction. In such case, the incompletely sampled shared interaction would erroneously contribute to the β_p or β_H component of beta diversity, or, in case both the plant and the herbivore species were missed from the web Y, to the β_{PH} component.

Poor sampling of food webs thus tends to misrepresent shared trophic links as β_{PH} beta diversity component, intermediate sampling as β_p or β_H components, and relatively good sampling as the β_0 component. This bias is illustrated by sampling two identical food webs, each comprising five plant and five herbivore species (Fig. 2a). All herbivore species feed on all plant species

and each of the 25 possible trophic interactions is represented by a single individual herbivore so that the entire web comprises 25 herbivorous individuals. Random samples of 5, 10, 15 and 20 individuals from each food web produced beta diversity estimates which were entirely due to sampling bias, as the food webs were identical. As expected, the sampling bias manifested itself entirely as β_0 at large sample sizes (> 10 individuals), partly as β_p and β_H at the sample size of 10 individuals and partly also as β_{PH} at the smallest sample size of five individuals (Fig. 2b).

Beta diversity in Macaranga – caterpillar food webs

The analysis of β_{PH} , β_p , β_H , and β_0 components of the food web beta diversity is illustrated using caterpillar communities feeding on *Macaranga* trees at eight sites within a 150 × 500 km area of lowland rainforest in New Guinea. At each site, the three locally most common *Macaranga* species were sampled for their caterpillar communities. The resulting plant × herbivore matrix included 254 distinct *Macaranga*–caterpillar interactions, involving nine species of *Macaranga* and 109 species of Lepidoptera (see Novotny *et al.*, 2007 for details). Mean beta diversity between pairs of food webs from different sites amounted to $\beta_{cc} = 0.85$. It was generated mostly by the turnover of plant species (mean $\beta_p = 0.34$) and simultaneous turnover in plant and herbivore species (mean $\beta_{PH} = 0.23$), while the turnover of herbivore species alone (mean $\beta_H = 0.20$), and particularly the changes in host plant range (mean $\beta_0 = 0.08$) were less important (Fig. 3a).

The overall food web beta diversity increased with geographical distance between the sites (Fig. 3b). Interestingly, individual beta diversity components exhibited contrasting trends with geographical distance. The importance of plant, and simultaneous plant and herbivore turnovers increased with distance, while the importance of herbivore turnover on the same plant species and changes in herbivore host range decreased with distance. Beta diversity in trophic interactions was thus generated mostly by changing herbivore species and their host preferences on identical plant species between nearby sites, and by changes in plant species, which generated also changes in herbivore species, between more distant sites.

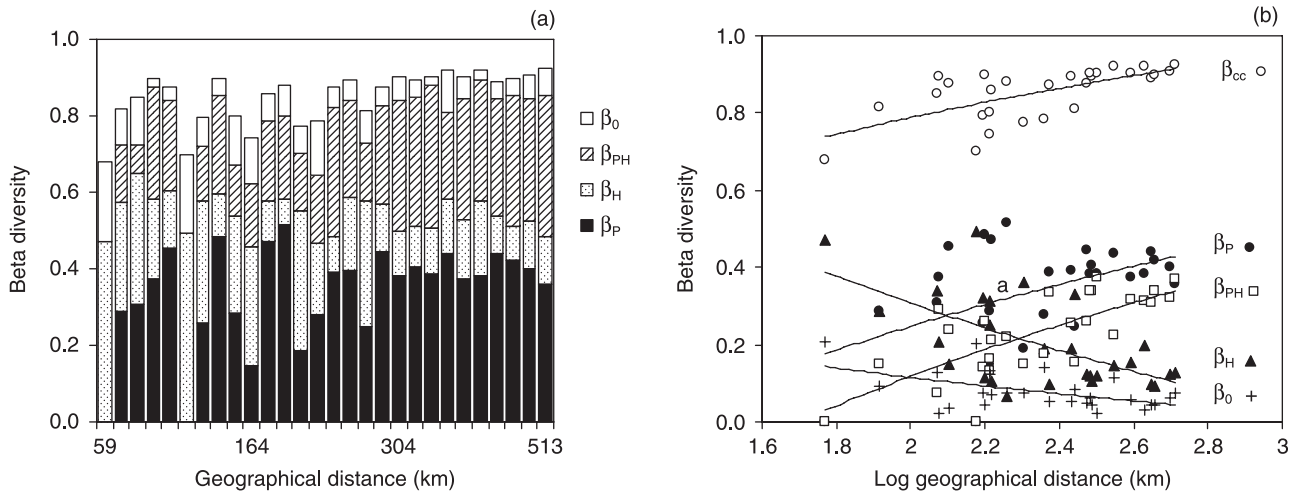


Fig. 3. Beta diversity of *Macaranga*–caterpillar food webs from a lowland rainforest in New Guinea. Beta diversity (β_{cc}) between food webs comprising three locally most common *Macaranga* tree species and their caterpillars (details in Novotny *et al.*, 2007) is shown for all pairs of eight study sites 59–513 km apart (Fig. 2a). Beta diversity is partitioned into the effects of the turnover of plant species (β_p), herbivore species (β_h), both plant and herbivore species (β_{ph}), and host preferences by herbivores (β_0) between sites. Beta diversity and geographical distance of food webs was correlated (Fig. 2b) for the overall beta diversity β_{cc} as well as its individual components ($r_{\beta_{cc}} = 0.627$, $r_{\beta_p} = 0.405$, $r_{\beta_h} = 0.543$, $r_{\beta_{ph}} = 0.713$, $r_{\beta_0} = 0.433$, $P < 0.05$ in all cases, Mantel test). In all cases, beta diversity can be best approximated by a logarithmic function of geographical distance, fitted to the data in Fig. 2b.

<i>Ficus</i> spp.	<i>F. dammaropsis</i>		<i>F. pachyrrhachis</i>	<i>F. dammaropsis</i>		<i>F. iodotricha</i>
	<i>F. dammaropsis</i>	<i>F. wassa</i>		<i>F. dammaropsis</i>	<i>F. wassa</i>	
Lepidoptera spp.						
<i>Euploea leucosticos</i>		x				
<i>Talanga exquisitalis</i>					x	
<i>Philiris moira</i>			x	x		
<i>Asota plana</i>			x			x
	lowland			montane		

Fig. 4. Plant–herbivore trophic interactions between four caterpillar species feeding on four *Ficus* hosts in lowland and montane forests of New Guinea. The insect and plant species shared between the two forests are shaded, the trophic interactions observed are marked by x and shading. Data from Novotny *et al.* (2005).

Determinants of beta diversity in food webs

Plant–herbivore food webs change in space as a result of speciation, extinction and dispersal of their component species (Hubbell, 2001) as well as their response to spatial variability in the environment. Beta diversity patterns of plants are often correlated with environmental variables as well as distance per se, presumably reflecting dispersal limitation (Tuomisto *et al.*, 2003b; Legendre *et al.*, 2005). The beta diversity of herbivores is determined by their host specificity and their ability to follow

host plant species in space and time and across different environments.

This is illustrated by caterpillars (Lepidoptera) feeding on *Ficus* hosts in lowland and montane rainforests in New Guinea (Fig. 4; details in Novotny *et al.*, 2005). The two forests were 120 km apart, a distance not likely to cause dispersal limitation in Lepidoptera communities (Novotny *et al.*, 2007). They represented two very different environments, climatically distinct and sharing only few plant species, mostly *Ficus* species (Novotny *et al.*, 2005).

The Lepidoptera species *Euploea leucosticos* and *Talanga exquisitalis* were limited to a single elevation, unlike their widespread host *Ficus wassa*. The herbivores thus exhibited lower environmental tolerance than their host plant. *Philiris moira* used a widespread host *Ficus dammaropsis* only in the montane forest, while in the lowlands it used another, exclusively lowland host *Ficus pachyrrhachis*. Furthermore, the moth species *Asota plana* had a wider distribution than either of its hosts. Wider distribution of both herbivores compared with their hosts was made possible by their high tolerance to a range of environmental conditions and low host specificity.

Studies relating beta diversity of plants to that of their herbivores are rare so that the relative importance of host specificity, dispersal and environmental factors as determinants of beta diversity in plant–herbivore food webs is poorly known. Beta diversity of leaf-chewing beetles between two climatically different forests in Panama was lower than the beta diversity of their plants (Ødegaard, 2006), suggesting low host specificity, high dispersal and high environmental tolerance of herbivores. In New Guinea, we found low beta diversity of herbivores in uniform rainforest environment, probably due to their low host specificity and high dispersal (Novotny *et al.*, 2007). Heard & Pettit (2005) reported on low beta diversity of herbivores feeding on a Neotropical

shrub *Mimosa pigra* over several thousands of kilometres, suggesting high dispersal ability and environmental tolerance of the herbivores. In contrast, high beta diversity of caterpillar communities feeding on the same host at different altitudes in New Guinea suggests low tolerance of herbivores to environmental factors along the altitudinal gradient (Novotny *et al.*, 2005). These studies suggest that herbivores can be rather efficient in tracking their hosts, even in highly diverse tropical vegetation. However, quantitative studies, including those using quantitative methods of beta diversity partitioning proposed here, are needed to explore fully the patterns and determinants of plant and herbivore distribution and their interaction in tropical food webs.

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