ORIGINAL ARTICLE

An alien in an archipelago: *Spathodea campanulata* and the geographic variability of its moth (Lepidoptera) communities in the New Guinea and Bismarck Islands

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ABSTRACT

Aim This analysis of moth (Lepidoptera) communities colonizing an alien tree invading secondary rain forest vegetation in Melanesia examines the predictability of insect herbivorous communities across distances of tens to thousands of km and the effect of dispersal barriers on community composition in the tropics.

Location Six secondary rain forest sites were studied within four equidistant yet distinct geographic areas of the New Guinea mainland and the Bismarck Archipelago, including two watershed areas (Madang and Sepik) on mainland New Guinea and the adjacent large island of New Britain and small island of Unea.

Methods The analysis is based on feeding records obtained by quantitative sampling and rearing of caterpillars from the alien host *Spathodea campanulata* (Bignoniaceae). It examines the variation in Lepidoptera community composition at six study sites distributed on three adjacent islands ranging in size from 30 to 865,000 km^2.

Results *Spathodea campanulata* was colonized by 54 folivorous species of Lepidoptera. Most of them were generalists, feeding on > 1 native plant family. However, the three most abundant species representing 83% of all individuals (*Acherontia lachesis*, *Hyblaea puera* complex and *Psilogramma menephron*) were relatively host specific, feeding predominantly on a single native family that is not the Bignoniaceae. Most of the 23 species analysed in detail had a wide geographic distribution, including 13 species spanning the entire 1000-km study transect. While the Lepidoptera in two New Guinea areas 280 km apart were similar to each other, there was a discontinuity in species composition between New Guinea and the smaller islands. However, no negative effect of small islands on species richness was detected.

Main conclusions *Spathodea campanulata* was rapidly colonized by folivorous Lepidoptera communities with species richness and dominance structure indistinguishable from the assemblages feeding on native hosts, despite its phylogenetic isolation from the native vegetation. Although most species were generalists, the highest population densities were reached by relatively specialized species, similar to the communities on native hosts. The species turnover across distances from 10 to 1000 km was relatively low as most of the species had wide geographic ranges.

Keywords

Beta diversity, caterpillar community, host specificity, insect dispersal, invasive species, islands, Malesia, similarity decay, species turnover.

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INTRODUCTION

Tropical island ecosystems are especially vulnerable to invasive species due to reduced competition for available resources, and many tropical islands already host high numbers of exotic species (Denslow, 2003). Their introductions can be also seen as large-scale, replicated experiments that initiate interesting community processes, including the colonization of alien plants by herbivorous species. The study of community assembly in tropical forests is particularly important, as it can inform us about the processes maintaining diversity in species rich and poorly understood ecosystems.

Aliens introduced across archipelagos represent particularly suitable study systems as they enter multiple island ecosystems with species pools of variable size and composition, determined largely by the island's size and isolation (Gillespie & Roderick, 2002). An archipelago setting is also suitable for the study of distance decay of similarity between communities, caused by a combination of decreasing environmental similarity and increasing dispersal limitation with distance (Nekola & White, 2004). Equidistant sites located within and between islands can be used to study the effect of dispersal limitation caused by an unsuitable intervening matrix, such as the sea, on insect distribution.

Alien plant species tend to be rapidly colonized by native folivorous insects, mostly by generalists (Strong, 1974b; Banerjee, 1981; Andow & Imura, 1994; Memmott et al., 2000; Novotny et al., 2003). Generalist herbivores are less sensitive to changes in the composition of vegetation between islands so that they can also be more widely distributed than the specialists. We can therefore hypothesize that herbivorous communities on alien plants have predictable, uniform composition even on islands of variable size and isolation, unlike the communities feeding on native hosts (Adler & Dudley, 1994; Dennis, 1997; Koh et al., 2002).

Despite the obvious appeal of comparative studies of herbivore communities from a particular plant species, comparisons between herbivore communities colonizing the same alien plant species at different sites within a large geographic area are rare and often concern crops (Strong, 1974b; Strong et al., 1984). Novotny & Weiblen (2005) advocated the comparative approach to the study of herbivore communities, using replicated samples from a particular plant species at different sites and in different environments. This approach proved effective in the study of the response of insects to altitude (Allison et al., 1993; Novotny et al., 2005a), habitat (MacGarvin et al., 1986) or climate (Andrew & Hughes, 2004), but has much wider potential in ecological studies, including those on alien species.

The present study surveys moth (Lepidoptera) communities feeding on alien tree Spathodea campanulata at six sites forming a 1000-km long transect from New Guinea to the Bismarck Archipelago. It tests the predictability of species composition and species richness in the communities assembled from different species pools available on three islands of very different size.

METHODS

Study sites

The six study sites (Wamangu, Baitabag, Mis, Ohu, Nighilani and Samo; Fig. 1) form a transect 1000-km long, including three islands: New Guinea (865,000 km^2), Unea (30 km^2) and New Britain (36,800 km^2). These islands have never been connected by land bridges. Unea is a volcanic island while New Guinea and New Britain are located on different, converging tectonic plates separated by deep waters (Pigram & Davies, 1987). The four sites within New Guinea represent two geographic regions: the floodplains of the Sepik River (Wamangu) and the coastal lowlands near Madang town (Ohu, Mis and Baitabag). The three Madang sites are close (6–17 km) to each other.

The study sites were standardized for altitude, climate and forest type as far as possible. All sites are located in lowland (0–200 m a.s.l.) hilly rain forests. The average annual rainfall is 2000–3500 mm at all sites except Wamangu, which is somewhat drier (1700–1900 mm of rainfall annually; McAlpine et al., 1983).

Study tree

Spathodea campanulata Beauv. (Bignoniaceae) is a large pioneer tree native to tropical Africa, but presently with a pantropical distribution. Although it was a common ornamental plant in the Bismarck Archipelago in the 1940s (Peekel, 1984), on the neighbouring island of New Guinea the tree may have been restricted to the main centres of settlement. For example, the tree was missing from Henty & Pritchard's (1988) list of weeds of New Guinea, as well as Streimann's (1983) checklist of plants of the Wau–Bulolo area. The earliest specimen of S. campanulata from the island of New Guinea in a major herbarium was collected in Manokwari in 1958
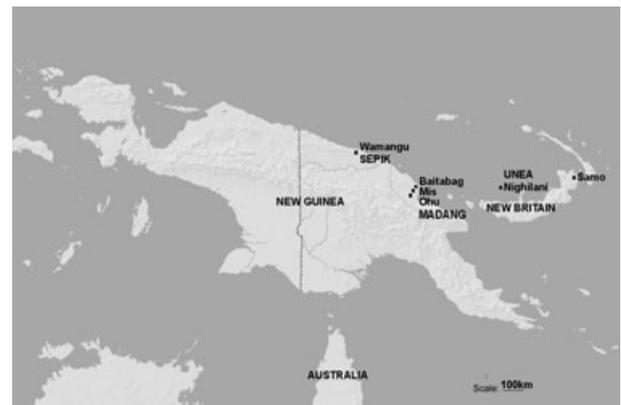
Figure 1 Locations of study sites: Wamangu (143°49′ E, 3°49′ S) in the Sepik area, Baitabag, Mis and Ohu (145°41–8′ E, 5°08–14′ S) in the Madang area, Nighilani (149°07′ E, 04°54′ S) on Unea island, and Samo (152°18′ E, 04°29′ S) on New Britain.

(Leiden Herbarium, P. C. van Welzen, personal communication) while the earliest specimen from the country of Papua New Guinea (PNG) was collected in Lae in 1978 (Lae Herbarium).

Since its introduction, the tree has become, together with *Piper aduncum* L., the most successful woody invader of secondary forests in the northern New Guinea lowlands and adjacent Bismarck Archipelago. It is now common along the northern coast of New Guinea, although it has not penetrated inland, south of the Sepik River (V. Novotny, personal communication). The tree invades early stages of rain forest succession developing in abandoned gardens from swidden (slash-and-burn) agriculture or after natural disturbance, such as large forest gaps and landslides, but it does not penetrate into closed primary forests (Swarbrick & Hart, 2000; Leps *et al.*, 2002). In some secondary forests, including those studied in Madang, *S. campanulata* is among the most abundant plant species. For instance, it represented 14% of the plant basal area in the Ohu secondary forest and ranked there as the second most abundant plant species (Novotny *et al.*, 2004).

Spathodea campanulata has 31 native species of the same family in New Guinea and adjacent islands (Höft, 1992), but none in the same genus. There was no Bignoniaceae tree species other than *S. campanulata* present at any of the study sites.

Insect sampling

All externally feeding caterpillars (Lepidoptera), including leaf rollers and leaf tiers, were collected by hand from the foliage of *S. campanulata*. The sampling took place within approximately 2 × 2 km area of mostly secondary forests at each site. On each sampling occasion, a collector spent 1 day searching the *S. campanulata* foliage throughout the study area for caterpillars. The sampling was irregular, as it included any tree encountered during the sampling. Numerous trees were thus sampled at each sampling occasion, and many of the trees were sampled repeatedly at different sampling occasions. The sampling included accessible branches, which could be climbed or reached from the ground. The approximate area of foliage sampled was estimated visually (Table 1).

In the laboratory, each caterpillar was provided with fresh leaves of *S. campanulata* and reared to an adult whenever possible. Only caterpillars that fed in captivity were considered in the analyses. This amounted to 5593 individuals from 54 species. All feeding caterpillars were assigned to morphospecies that were later verified and refined according to reared adults. The adult morphospecies were identified as far as possible by taxonomic experts. Taxonomic methods, which involved genitalic morphology, DNA barcodes (COI), and comparisons with type specimens, are detailed in Holloway *et al.* (2001) and Miller *et al.* (2003). Insect vouchers are deposited in the Smithsonian Institution (Washington, USA) and the National Agricultural Research Institute (Port Moresby, Papua New Guinea).

The sampling programme was completed between October 2002 and February 2004.

The three Madang sites (Baitabag, Mis and Ohu) were sampled continuously every week for 1 year, with the area of foliage sampled ranging from 7000 to 14,000 m^2 per site (Table 1). This sampling effort represented approximately 100 person-days of sampling per site. The remaining three sites were each sampled daily during a period of 3 weeks, reaching 2000–5000 m^2 of sampled foliage area per site. This was possible because the seasonality in the insect communities on *S. campanulata* (Bito, 2005) as well as other plant species (Novotny & Basset, 1998) was low.

Data analysis

The analysis was performed using complete samples from each site, not standardized for equal sampling effort, as well as on partial samples each including 300 individuals, i.e. the sample size available from the least sampled site (Nighilani; Table 1). The partial samples included 300 individuals obtained by sampling over a continuous period of time, rather than selected randomly from the entire data set. This made the partial samples from the extensively sampled Madang sites comparable to the samples from other sites, obtained during short collecting periods. Seventeen partial samples, one to six per site, were available.

The species richness was assessed from species accumulation curves, combining samples from individual sampling days in

Table 1 Description of the Lepidoptera communities feeding on *Spathodea campanulata* at different study sites. Foliage: the leaf area (in m^2) sampled; N: the number of Lepidoptera individuals; S: the number of Lepidoptera species; S300: the number of Lepidoptera species in a partial sample of 300 individuals (average and range); n: the number of partial samples of 300-individuals; s: the number of singleton species; BP: the dominance (in percentage of individuals) of the most common species; Dominant sp.: the most common species at each site.

Site	Sampling period	Foliage	N	S	S300	n	s	BP	Dominant sp.
Wamangu	12 Sep 03–03 Oct 03	4349	602	38	30.3 (25–35)	2	12	54	*Acherontia lachesis*
Baitabag	16 Oct 02–14 Nov 03	8104	1118	26	15.3 (14–16)	3	5	37	*Hyblaea puera* complex
Mis	16 Oct 02–21 Oct 03	13918	1921	28	14.2 (11–17)	6	7	34	*A. lachesis*
Ohu	08 Oct 02–21 Oct 03	7075	976	23	12.3 (10–16)	3	6	62	*A. lachesis*
Nighilani	15 Dec 03–31 Dec 03	2175	300	12	12	1	6	75	*H. puera* complex
Samo	19 Jan 04–06 Feb 04	4770	676	19	14 (14–14)	2	7	79	*H. puera* complex
All sites	*08 Oct 02–06 Feb 04*	40391	5593	54			17		

randomized sequence. Five thousand random sequences were created for each curve. Further, the number of species was estimated for each partial sample. The dominance was expressed as the Berger-Parker index (BP), i.e. the proportion of the most abundant species in the community.

The similarity between samples was estimated using the Sorensen index, i.e. the average proportion of shared species, and the Percentage Similarity index, which is an extension of the Sorensen index for quantitative data (Magurran, 2004). The Sorensen index was modified to include the effect of unseen shared species, as proposed by Chao *et al.* (2005) and implemented in the EstimateS software (Colwell, 2005). This Chao-Sorensen index removed the sensitivity of the index to sample size.

The similarity relationships among partial samples were also analysed by Correspondence Analysis (CA), using $\log(n + 1)$ transformed data and down weighting of rare species option. The analysis was performed with the Canoco software (Leps & Smilauer, 2003).

Although only *S. campanulata* was sampled in the present study, information on native host plant species at Baitabag, Mis and Ohu sites was available for numerous Lepidoptera species from previous studies that sampled over 90,000 caterpillars from 90 species of native shrub and tree species from 30 families (Novotny *et al.*, 2002a, 2005b).

RESULTS

Species richness, dominance, composition and host specificity

The sampling of species richness at any one site was incomplete as none of the species accumulation curves reached an asymptote (Fig. 2). The combined species accumulation curve for all six sites also exhibited a steady increase throughout the sampling, indicating that species richness of the whole area was not exhaustively sampled. However, the three sites from the Madang area provided an adequate estimate of the local species richness as the combined species accumulation curve for these sites approached an asymptote. The observed species richness of 32 species was identical or approaching the total species richness estimated by various indices implemented in the EstimateS software (ICE = Chao 2 = Jacknife 1 = Bootstrap 1 = 32 species, ACE = 34 species, Chao 1 = 36 species; see Colwell, 2005 for an explanation of the indices).

The species accumulation curve for the Madang sites levelled off at the sample size of approximately 3000 individuals and 20,000 m^2 of sampled foliage (Fig. 2). Despite the statistical evidence of nearly complete sampling, some species using *S. campanulata* rarely as a marginal host were probably still missed. In particular, *Herpetogramma* sp., *Syllepte ochrifusalis*, *Hyblaea constellata* and *Isotenes* sp. near *miserana* were sampled from *S. campanulata* only in Wamangu, but they were also present at the Madang study sites and sampled there from hosts other than *S. campanulata* (Novotny *et al.*, 2004).
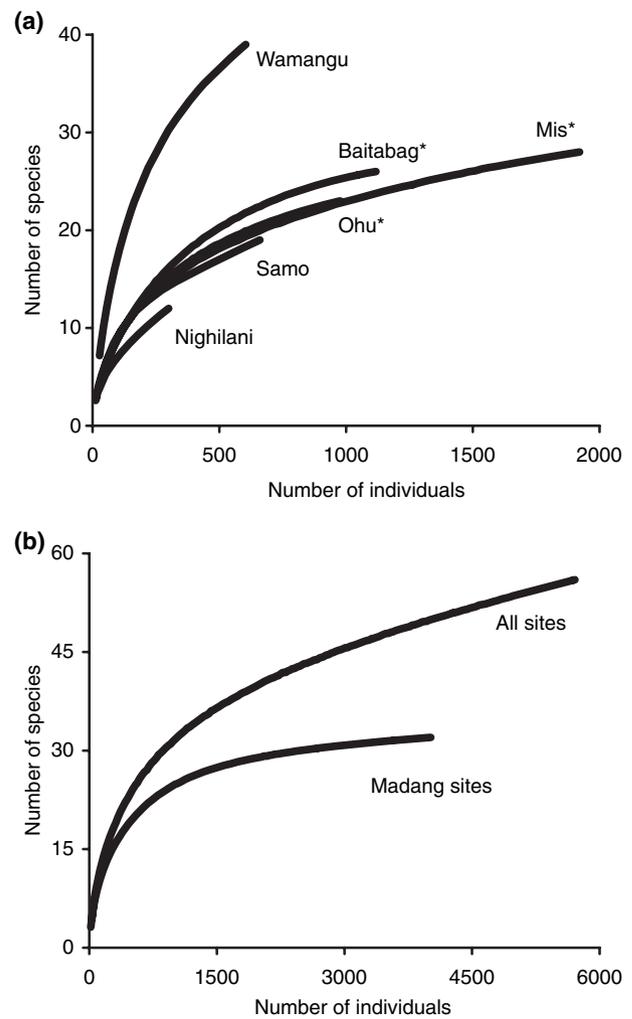
Figure 2 Randomized species accumulation curves for individual sites (a) and for the three Madang sites combined and all six sites combined (b). Note the differing *y*-axis scales (number of species). In part (a) the Madang sites are marked with an asterisk.
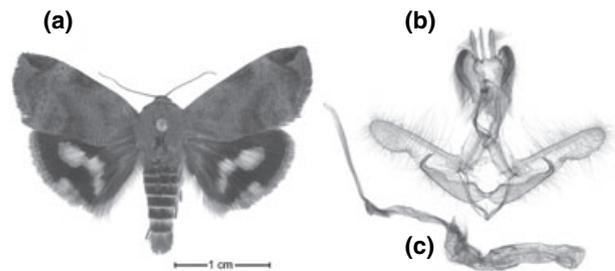
Figure 3 Species of *Hyblaea puera* complex (Lepidoptera: Hyblaeidae) commonly found on the alien *Spathodea campanulata* in New Guinea. (a), adult; (b), male genitalia, ventral view, aedeagus removed; (c), aedeagus, lateral view.

Even the incomplete species accumulation curves demonstrate that the Wamangu site is extraordinarily species rich in comparison to the remaining five sites, which are all similar to one another in species richness (Fig. 2). This conclusion is

corroborated by 25 and 35 species present in the two samples of 300 individuals available from Wamangu, while the remaining 15 equally sized samples from the other five sites included only between 10 and 17 species each (Table 1).

The most abundant species at Baitabag, Nighilani and Samo was a species in the *Hyblaea puera* complex (Hyblaeidae) representing 37–79% of the individuals (Table 1). This species was also the second most abundant in Mis (29%) and the third most abundant in Wamangu (8%). In contrast to its high abundance at the two nearby sites, the species was virtually absent from Ohu and represented there only 0.4% of the caterpillar community.

Until recently, *H. puera* was considered a cosmopolitan pest of teak and other tropical trees (e.g. CABI, 1982). However, genitalic morphology (Fig. 3) and DNA analyses indicate that *Hyblaea puera* is a species complex, and it is not clear what name applies to the species in Papua New Guinea (S. E. Miller, personal communication). Because the species was recorded from New Britain by Pagenstecher (1900), it is assumed to be native.

The most abundant species at Mis, Ohu and Wamangu was *Acherontia lachesis* (Sphingidae), representing 34–62% of the community (Table 1). It was also the second most common species at Baitabag (34%), but was absent from the two smaller islands, i.e. the Nighilani and Samo sites.

The dominance of the most abundant species ranged widely among study sites, from 34% to 78% (Table 1). Even the three Madang sites, which are close to one another and were sampled simultaneously for the entire year, ranged in the dominance values from 37% to 61%. The wide range of dominance values was exhibited by both the dominant species, *H. puera* complex and *A. lachesis*.

The two dominant species were followed in abundance by *Psilogramma menephron*, *Scopula amala* and *Adoxophyes nebrodes*, each present at five to six sites (Table 2). These five most abundant species together represented 90% of all individuals. Rare, singleton species sampled as only one individual represented 19–26% of all species in large samples from the Madang sites and 31–50% of all species in smaller samples from the remaining three sites.

Information on native hosts at the Madang sites was available for 23 of the 32 species collected there from *S. campanulata*, including all common species collected as more than 10 individuals (Novotny *et al.*, 2002a, 2005b). Eighteen species were generalists, feeding on more than one native family, while five species were collected exclusively, or almost exclusively, from a single plant family: *Acherontia lachesis* from Rubiaceae, *Psilogramma menephron* from Loganiaceae, and *Hyblaea puera* complex, *H. amboinae* and *Pycnarmon jaguaralis* from Verbenaceae. *A. lachesis* is reported from 19 plant families in other parts of its geographic range, including prominently Verbenaceae and Solanaceae, but also Leguminosae and Bignoniaceae (Robinson *et al.*, 2005). Likewise, *P. menephron* is reported from 12 families, particularly Verbenaceae, Bignoniaceae and Oleaceae. *Hyblaea puera* complex is reported from 14 families, most often Verbenaceae

and Bignoniaceae, and *P. jaguaralis* from Leguminosae and Verbenaceae (Robinson *et al.*, 2005). These data indicate that although none of these species is limited to a single family in its entire geographic range, Verbenaceae hosts represent an important resource for all of them. These five relatively host-specific species included the three most abundant species in the *S. campanulata* communities and together represented 83% of all individuals feeding on *S. campanulata*.

Community similarity and geographic range of species

Lepidoptera communities from the four New Guinea sites were similar to each other, as indicated by the Chao-Sorensen index values of > 0.95 obtained for all six pairwise comparisons between these sites (Fig. 4). The comparisons between New Guinea and one of the smaller islands produced Chao-Sorensen values of 0.23–0.77. There was no obvious decrease in similarity from 400 to 1000 km distance between the sites included in the present study. The overall negative correlation between the geographic distance of Lepidoptera communities and their Chao-Sorensen similarity was only caused by a decrease in similarity between the short-range comparisons within New Guinea and the long-range inter-island comparisons. The results of the analysis using partial 300-individual samples were similar and are not reported here.

The geographic patterns in community dominance structure, reflected by percentage similarity (PS), were analogous to those obtained for species composition using the Chao-Sorensen index. The PS values were highly variable even between the neighbouring sites. However, the similarity between pairs of sites from the same island was always PS > 0.5, whereas the similarity between pairs of sites from different islands was always PS < 0.5 (Fig. 4).

The ordination analysis of the 300-individual samples clearly separated different islands along the first axis, while the second axis captured the difference between the Sepik and Madang areas of New Guinea (Fig. 5). The samples from Madang formed a distinct cluster but did not separate according to individual sites. The three Madang sites can therefore be considered as harbouring a single type of Lepidoptera community feeding on *S. campanulata*.

Most of the 23 species with the sample size sufficient for analysis (i.e. collected as at least 10 individuals) had a wide geographic distribution, including 13 species spanning the entire length of the study transect from Wamangu to Samo (although not necessarily sampled at all intermediate sites). The second most frequent distribution pattern included both areas of New Guinea (seven species), pointing to the discontinuity between New Guinea and the smaller islands (Fig. 6).

The three Madang sites harboured 32 species feeding on *S. campanulata*, from the total of 54 species found in the entire study. The 22 species apparently absent from Madang however included also 11 species sampled at Baitabag, Mis and/or Ohu sites from other plant species (Novotny *et al.*, 2002a, 2005b). The remaining 11 species not known from Madang included

Table 2 Lepidoptera species feeding on *Spathodea campanulata* at the six study sites. The sample size for each site is given in Table 1.

Species	Family	Wamangu	Baitabag	Mis	Ohu	Nighilani	Samo	Total
Acherontia lachesis (Fabricius)	Sphingidae	327	375	656	600	0	0	1958
Hyblaea puera complex	Hyblaeidae	50	416	549	7	226	536	1784
Psilogramma menephron Cramer	Sphingidae	46	219	451	153	0	20	889
Scopula amala Meyrick	Geometridae	53	12	45	105	44	21	280
Adoxophyes nebrodes Meyrick	Tortricidae	6	10	32	34	0	23	105
Scythropiodes sp. nov. near *perissa* (Diakonoff)	Lecithoceridae	4	9	62	9	1	9	94
Adoxophyes sp. *templana* complex	Tortricidae	1	5	41	26	0	1	74
Homona mermerodes Meyrick	Tortricidae	7	5	11	6	0	8	37
Ectropis bhurmitra (Walker)	Geometridae	9	2	13	2	0	10	36
Spodoptera litura (Fabricius)	Noctuidae	4	19	1	2	0	1	27
Xylinophylla maculata Warren	Geometridae	3	1	2	3	0	17	26
Chrysodeixis eriosoma Doubleday	Noctuidae	3	3	4	1	6	9	26
Oiketicus sp.	Psychidae	13	7	5	1	0	0	26
Adoxophyes thoracica Diakonoff	Tortricidae	4	0	8	4	0	5	21
Cleora repetita Butler	Geometridae	3	1	4	1	2	9	20
Homona trachyptera Diakonoff	Tortricidae	4	2	10	1	0	0	17
Adoxophyes trirhabda Diakonoff	Tortricidae	0	0	0	0	14	0	14
Homona sp. near *salaconis* (Meyrick)	Tortricidae	6	2	4	3	0	0	14
Macrothyma sanguinolenta (Diakonoff)	Tortricidae	10	2	1	0	0	0	13
Adoxophyes faciculana (Walker)	Tortricidae	1	3	3	5	0	0	12
Moca congrualis (Walsingham)	Immidae	2	1	8	1	0	0	12
Diacrisia costata vivida Rothschild	Arctiidae	10	0	0	0	0	0	10
Herpetogramma hipponalis (Walker)	Crambidae	3	9	1	0	0	0	13
Spilosoma niceta Stoll	Arctiidae	1	0	1	7	1	0	10
Omiodes diemenalis Guenée	Crambidae	0	5	2	0	1	0	8
Syllepte polydonta Hampson	Pyralidae	3	1	0	0	2	2	8
Hyblaea amboinae Felder	Hyblaeidae	0	4	2	0	0	0	6
Herpetogramma sp.	Pyralidae	6	0	0	0	0	0	6
Thosea monoloncha (Meyrick)	Limacodidae	0	2	2	1	0	0	5
Syllepte ochrifusalis Hampson	Crambidae	5	0	0	0	0	0	5
Hyblaea constellata Gueneé	Hyblaeidae	5	0	0	0	0	0	5
Homona aestivana (Walker)	Tortricidae	1	0	1	2	0	0	4
Isotenes sp. near *miserana* (Walker)	Tortricidae	3	0	0	0	0	0	3
Diacrisia turbida sordidion Rothschild	Arctiidae	0	0	0	2	0	0	2
Hypolycaena phorbas (Fabricius)	Lycaenidae	0	0	0	0	1	1	2
Xenothictis gnetivora Brown, Miller & Horak	Tortricidae	0	2	0	0	0	0	2
Hipoepa porphyrialis (Pagenstecher)	Noctuidae	2	0	0	0	0	0	2
Haritalodes adjunctalis Leraut	Crambidae	0	0	0	0	0	1	1
Pycnarmon jaguaralis Munroe	Crambidae	0	1	0	0	0	0	1
Hyposidra talaca Walker	Geometridae	0	0	1	0	0	0	1
Oenospila sp. near *flavilinea* Warren	Geometridae	0	0	0	0	1	0	1
Scythropiodes scribaria (Meyrick)	Lecithoceridae	0	0	1	0	0	0	1
Condica illecta (Walker)	Noctuidae	0	0	0	0	0	1	1
Isocentris sp.	Pyralidae	0	0	0	0	1	0	1
Choreutis sp.cf. *anthorma* (Meyrick)	Tortricidae	0	0	0	0	0	1	1
'New genus near *Peritornenta*'	Elachistidae	0	0	0	0	0	1	1
Creatonotos gangis (Linnaeus)	Arctiidae	1	0	0	0	0	0	1
Thalassodes (s. l.) *albifusa* (Warren)	Geometridae	1	0	0	0	0	0	1
Unidentified sp.	Geometridae	1	0	0	0	0	0	1
Eudocima phalonia (Linnaeus)	Noctuidae	1	0	0	0	0	0	1
Omiodes lasiocnemis Hampson	Pyralidae	1	0	0	0	0	0	1
Cydalima laticostalis (Guenee)	Pyralidae	1	0	0	0	0	0	1
Choreutis basalis (Felder & Rogenhofer)	Tortricidae	1	0	0	0	0	0	1

eight rare species found as singletons and only two species sampled as at least 10 individuals. The latter were both limited to a single study sit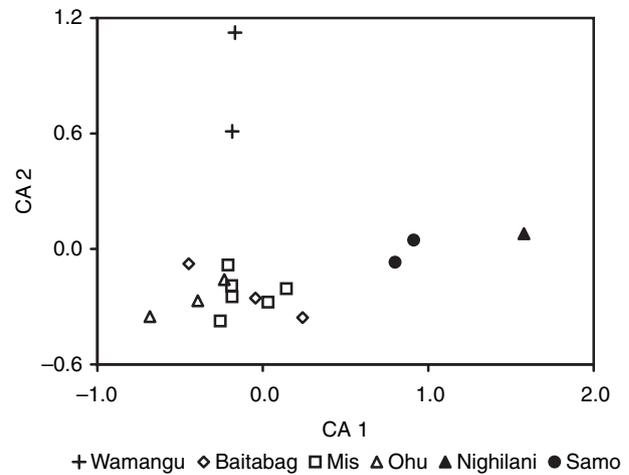e: *Diacrisia costata vivida* to Wamangu and *Adoxophyes* sp. to Nighilani (Fig. 6). There was no obvious difference between geographic range size of relatively specialised species compared to generalists.
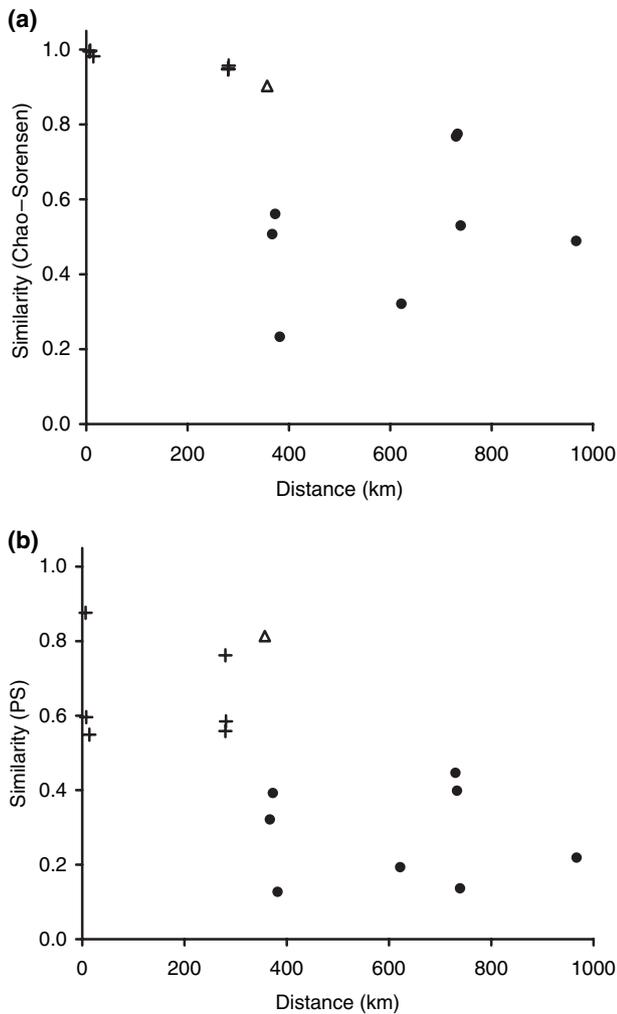
Figure 4 Similarity decay in moth communities on *Spathodea campanulata* with geographic distance. The Chao-Sorensen index (a) and the Percentage Similarity index (b) are shown for all pairwise comparisons between the study sites. Crosses = both sites are from New Guinea; circles = one site is from New Guinea, the other is from one of the smaller islands; triangles = both sites are from the smaller islands. There is a significant negative correlation between community similarity and distance (Chao-Sorensen: $r = -0.589$, $P < 0.05$, Percentage Similarity: $r = -0.654$, $P < 0.05$, Mantel test).

Figure 5 Ordination diagram for the first two axes of a Correspondence Analysis (CA) performed on 17 partial samples from moth communities, each including 300 individuals, from the six study sites. The two axes explain 39% of variability in the data.
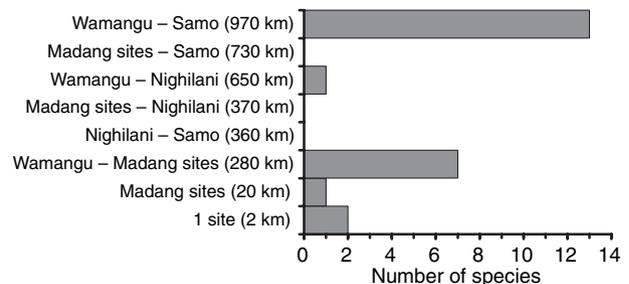
Figure 6 Geographic distribution of moth species feeding on *Spathodea campanulata*. The distribution of species along the Wamangu–Madang–Nighilani–Samo transect. The two most distant sites where the species was recorded along the 970-km transect were used to define its geographic range. Only species collected as at least 10 individuals were included. All possible pairs of sites were included (with their geographic distance in parentheses). The three Madang sites were grouped together.

DISCUSSION

Spathodea campanulata is a striking example of an alien plant species rapidly colonized by exophagous folivores (Strong, 1974a,b; Strong *et al.*, 1977; Kennedy & Southwood, 1984; Andow & Imura, 1994; Novotny *et al.*, 2003; Lewinsohn *et al.*, 2005). The Lepidoptera community on the alien host has attained a species richness and dominance structure indistinguishable from assemblages feeding on native hosts (Basset & Novotny, 1999; Novotny *et al.*, 2002b). The colonization dynamics tend to be slower for more specialized herbivore guilds (Strong *et al.*, 1984; Zwölfer, 1988; Yukawa & Uechi, 1999; Memmott *et al.*, 2000). For instance, there were no leaf

mining species feeding on *S. campanulata* at our study sites (D. Bito, unpublished data). As expected for an alien host species, most of the colonizing Lepidoptera species were generalists, feeding also on more than one native plant family (cf. also Novotny *et al.*, 2003). However, all six *S. campanulata* communities were composed mostly of individuals belonging to three relatively specialized species. These species are known to feed also on Verbenaceae, a member of the Lamiales, which also includes the Bignoniaceae (Angiosperm Phylogeny Group, 1998). The specialized species were thus able to maintain larger populations on *S. campanulata* than any of the numerous generalists. This pattern is widespread in Lepidoptera communities on native plant species (Novotny *et al.*, 2002a,b). The colonization of alien *S. campanulata* greatly increased the population size of some of the native Lepidoptera species. For example, *H. puera* complex colonized *S. campanulata* from a

single native host, *Premna obtusifolia* R. Br., but the alien supported 95% of its local population (Novotny *et al.*, 2004).

Although there is little information on the Lepidoptera feeding on *S. campanulata* in its native range, Robinson *et al.* (2005), reported 12 feeding records for eight Lepidoptera species from other tropical areas, including all three most common species from the present study: *A. lachesis* (India, Taiwan), *H. puera* complex (Cuba, Puerto Rico), and *P. menephron* (Indo-Australian region).

The geographic variability in species richness did not follow the expectation that the number of species should decrease on smaller islands (Adler & Dudley, 1994; Gillespie & Roderick, 2002). The observed pattern was idiosyncratic, with all communities but one having remarkably uniform species richness, despite differences in island size of four orders of magnitude. This pattern is difficult to explain without more detailed knowledge of Lepidoptera species pools available on each island.

The asymptotic species accumulation curve obtained for the Madang area is of interest for methodological reasons. Price *et al.* (1995) demonstrated the difficulty, if not impossibility, of achieving a complete census of Lepidoptera species feeding on a tropical plant species. Other studies (Barone, 1998; Novotny *et al.*, 2002b) were likewise unable to produce complete lists of Lepidoptera on their tropical hosts. This sampling problem is caused by the large number of rare species present in tropical communities (Novotny & Basset, 2000). Extensive sampling is thus needed to investigate the ecological and biological attributes of rare species and their contribution to the structure of insect assemblages.

The present results, although possibly relevant only to alien species, demonstrate that a nearly complete census is possible, but that it requires a large sampling effort. The asymptotic species richness was approached only after surveying 20,000 m^2 of the foliage and sampling 3000 caterpillars. This is significantly more than was required for Lepidoptera communities on another alien species, *Piper umbellatum*, which were completely surveyed by sampling 2500 m^2 of foliage and 500 caterpillars at the same study sites (Novotny *et al.*, 2003). The large difference in the minimum sampling effort may be explained by the smaller size of *P. umbellatum*, which is a large herb or sub-shrub, rarely exceeding 1 m in height. Extensive studies, ideally on native plant species, are urgently needed to establish the minimum sample size needed to census various herbivorous communities on tropical plants (cf. Longino *et al.*, 2002).

The high similarity of Lepidoptera communities between the Sepik and Madang areas, 300 km apart, was not surprising as both areas are connected by a continuous mosaic of secondary forests with *S. campanulata*. The greater discontinuity in Lepidoptera composition between different islands than between equidistant sites within New Guinea was also expected. In contrast, the expectation of a relatively impoverished community on the small island of Unea separated by 50 km from the nearest larger landmass was not corroborated.

The low beta diversity of Lepidoptera along the 1000 km transect is notable. The apparently geographically restricted species were almost always rare, making it difficult to separate sampling bias from genuine endemism. Unfortunately, no comparison with data from native host species is available so it remains unclear whether the predominantly generalist communities on *S. campanulata* exhibit higher or lower beta diversity than those on the native plant species. In theory, the generalists can be either better than specialists at tracing the host plant's distribution range due to the availability of alternative hosts facilitating dispersal, or less efficient than specialists at locating and colonizing any particular host plant species.

Apart from a predictable pattern of geographic variation, exemplified by the easily interpretable results of the CA analysis, some apparently inexplicable patterns in species distribution and abundance were also encountered. In particular, the extremely low population density of *H. puera* complex in Ohu, in contrast to the nearby sites of Baitabag and Mis, is hard to explain in the view of virtually identical Lepidoptera communities hosted by the native plants (Novotny *et al.*, 2002b), and very similar climate, soil and vegetation conditions, as well as the high abundance of *S. campanulata* at all three sites. The factors determining which species will be dominant in a particular community and how strong this dominance will be also remain unknown.

The failure of *A. lachesis* to colonize smaller islands can probably be explained by its apparently recent introduction to New Guinea from Asia. The species was first recorded from the Indonesian part of New Guinea in 1991 (S. E. Miller, personal communication), while Moulds & Lachlan (1998) reported the earliest records from Papua New Guinea from 1993. *Psilogramma menephron*, the other common hawk moth species, is native to New Guinea and was also recorded on New Britain.

The present study provided data on the geographic variability of tropical herbivorous communities feeding on a particular plant species across distances up to 1000 km. This approach was pioneered in a study of herbivore communities feeding on the bracken fern (*Pteridium aquilinum*) at multiple sites from different continents (Lawton *et al.*, 1993). The intercontinental comparisons of herbivorous communities colonizing alien plants in their native and introduced ranges may be useful for understanding the origin of herbivorous communities.

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