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Deforestation homogenizes tropical parasitoid–host networks

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Abstract. Human activities drive biotic homogenization (loss of regional diversity) of many taxa. However, whether species interaction networks (e.g., food webs) can also become homogenized remains largely unexplored. Using 48 quantitative parasitoid–host networks replicated through space and time across five tropical habitats, we show that deforestation greatly homogenized network structure at a regional level, such that interaction composition became more similar across rice and pasture sites compared with forested habitats. This was not simply caused by altered consumer and resource community composition, but was associated with altered consumer foraging success, such that parasitoids were more likely to locate their hosts in deforested habitats. Furthermore, deforestation indirectly homogenized networks in time through altered mean consumer and prey body size, which decreased in deforested habitats. Similar patterns were obtained with binary networks, suggesting that interaction (link) presence–absence data may be sufficient to detect network homogenization effects. Our results show that tropical agroforestry systems can support regionally diverse parasitoid–host networks, but that removal of canopy cover greatly homogenizes the structure of these networks in space, and to a lesser degree in time. Spatiotemporal homogenization of interaction networks may alter coevolutionary outcomes and reduce ecological resilience at regional scales, but may not necessarily be predictable from community changes observed within individual trophic levels.

Key words: biodiversity; body size; Ecuador; food web; insect; interaction network; parasitoid; predator; prey.

Introduction

Land use change is the main driver of global biodiversity loss (Sala et al. 2000), with important consequences for ecosystem functioning, services, and resilience (Foley et al. 2005). Paradoxically, human activities often increase local (alpha) diversity (Sax and Gaines 2003), while reducing regional (beta) diversity. This phenomenon, termed "biotic homogenization" (Olden et al. 2004), reduces variability and uniqueness of flora and fauna, thereby reducing the regional "insurance" of ecosystem services under changing environmental conditions (Loreau et al. 2003). However, calls to expand our current focus on taxonomic homogenization to include higher order ecological effects, such as homogenization of interaction network (e.g. food web) structure (Olden et al. 2004), have not yet been answered. Here, we explicitly address this important yet neglected aspect of food web ecology (de Ruiter et al. 2005, McCann and Rooney 2009) by comparing the spatial and temporal structural variability of 48 parasitoid–host food webs across five habitat types in coastal Ecuador. Parasitoids are not only among the most diverse organisms on the planet, but their ability to regulate host populations under certain circumstances makes them important biological control agents (Godfray 1994).

In its fundamental form, the structure of an interaction network is characterized by the identity of its constituent interactions, but more recent empirical research has also started to consider their relative frequencies (Memmott 1999, Vázquez and Simberloff 2003). In that view, network homogenization is the process through which networks within a given region become increasingly similar to each other in their interaction composition (i.e., the identity and frequency of the pairwise interactions or links constituting the web). Recent work has shown that habitat modification can alter different network structural properties such as vulnerability or interaction evenness, even in the absence of biodiversity loss (Tylianakis et al. 2007). Yet, such studies constructed networks by pooling long-term samples, and only with quantitative networks replicated in space and time can we explore how human activities affect network spatial and temporal structural variability, and whether network homogenization occurs.

To date, biotic homogenization has been discussed strictly in terms of biotic effects such as species invasions and extinctions (Olden and Poff 2003). In general, homogenization is greatest following the invasion of functionally similar species that cause the extinction of resident native species (Olden and Poff 2003). This

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process is often catalyzed by human alteration of habitats. For example, bee communities in Europe become more homogeneous in regions with fewer remaining seminatural habitats and receiving greater pesticide inputs (Dormann et al. 2007). It follows that homogenization of species interaction networks may result from communities of interacting species becoming homogenized (in our case, parasitoid and/or host communities), such that the regional pool of potential interactions becomes increasingly limited. However, other mechanisms may drive the homogenization of species interaction networks. In particular, reduced hunting efficiency of predators in structurally complex habitats (Brose et al. 2005) could partially decouple network structure from predator or prey community structure, thereby increasing regional interaction diversity. This could also occur because of greater temporal turnover of parasitoid and host communities in forested habitats (Tylianakis et al. 2005), thereby preventing some species from interacting with each other at any given point in space and time.

Previous research has treated biotic homogenization as a spatial process (Olden et al. 2004), whereas its temporal analogue has until now been overlooked, particularly in the context of ecological networks. Temporal resolution also represents a new frontier in quantitative food web research (de Ruiter et al. 2005). Our repeated sampling through time for each site allowed us to quantify temporal variability in network structure. As with spatial network variability, temporal network variability may decrease following loss of structural complexity (again, because of increased hunting efficiency) or be altered indirectly through changes in parasitoid and host community structure and their functional attributes. In particular, predator and prey body size are known to affect the structure (Woodward et al. 2005, Petchey et al. 2008), interaction strength (Emmerson and Raffaelli 2004) and stability (Otto et al. 2007) of ecological networks. Besides providing physical and metabolic constraints on which species can interact, body size generally correlates negatively with abundance (Cohen et al. 2003) and positively with prey diversity (Otto et al. 2007), home range size, and dispersal ability (Woodward et al. 2005).

In this paper, we test whether parasitoid–host networks from five distinct habitat types (forests, abandoned agroforests, managed agroforests, pastures, and rice fields; Tylianakis et al. 2007) become more homogenized across space under habitat simplification, and suggest potential mechanisms. We also explore how land use intensity, temporal variability in parasitoid and host communities, and parasitoid and host mean body size directly and indirectly affect temporal variability in the structure of parasitoid–host interaction networks.

Methods

Study region and sampling.—The study was conducted within the province of Manabi, in southwest Ecuador (see map in Appendix A). We constructed standardized nesting resources for communities of cavity-nesting bees, wasps and their parasitoids in 48 spatially separated sites from five habitat types spread across a gradient of land use intensity: forests ($n = 6$), abandoned coffee agroforests ($n = 6$), managed coffee agroforests ($n = 12$), pastures ($n = 12$), and rice fields ($n = 12$; Tylianakis et al. 2007). These trap nests were constructed by inserting reed internodes into PVC tubes to provide nesting sites. In any month (sampling period), no more than one-third of reeds were occupied for a given trap, therefore, nesting sites within traps were never limiting. Land use intensity can be broadly defined as the frequency and/or intensity of disturbance (i.e., biomass removal), as well as the use of external inputs (e.g., fertilizer). Nine trap nests per plot were used, but data from these traps were pooled for each plot. Trapped host larvae were reared to maturity for identification of emerging hosts and parasitoids (Tylianakis et al. 2007). This allowed us to identify three distinct biotic components at each site: host community structure (abundance of each host species present, regardless of whether parasitoids emerged from them), parasitoid community structure (abundance of each parasitoid species present, regardless of the host species they emerged from), and parasitoid–host food web structure (which parasitoid species emerged from which host species, and in what frequencies).

Our 48 quantitative food webs comprised 4315 parasitism events (emerging parasitoids) distributed among 51 different parasitoid–host interactions (links) involving nine parasitoid and 33 host species (bees and wasps; Tylianakis et al. 2007). A matrix showing parasitoid–host combinations and body sizes (see below) is provided in Appendix B. We defined the strength or number of a given parasitoid–host interaction (link) as the number of parasitoids emerging, except for *Melittobia acasta* (Hymenoptera: Eulophidae, which produced hundreds of individuals per host) which was defined as the number of hosts killed. Each trap was evaluated monthly for 17 months (June 2003–October 2004), allowing us to measure network spatial variability across sites within a given land use and network temporal variability within each individual site (rather than pooling this temporal variability as in previous studies; Tylianakis et al. 2007). Host and parasitoid species lists can be found in previous work (Tylianakis et al. 2006, 2007).

Spatial variability.—Anderson (2006) described a permutational distance-based test for homogeneity of multivariate dispersions to test for differences in beta diversity between groups of sites (Anderson et al. 2006), from which species abundance data are collected. The test is essentially a multivariate extension of Levene's (1960) test for homogeneity of variances, and is robust and powerful with relative abundance or presence–absence data (Anderson 2006). First, a distance matrix between sites is computed, and principal coordinate analysis (PCoA) is used. Individual distances of each site to its

group centroid in PCoA space are computed, and these distances are used in a one-way permutational ANOVA to test for differences in multivariate dispersions between groups of sites (Anderson 2006). We used Anderson's (2006) procedure to test for differences in spatial variability in (1) interaction network structure, (2) host community structure, and (3) parasitoid community structure between habitat types. For spatial analyses, data were pooled across all months, because individual times could not be used as independent replicates. Analyses were repeated for binary networks. More details on these spatial analyses can be found in Appendix C. We also tested for homogeneity of geographical dispersions of sampling sites among land uses. To do so, we generated a Euclidean distance matrix between all sampling sites, using latitude and longitude coordinates, and used Anderson's (2006) test as described above for interaction and community structure data.

Realization of interactions.—To be conservative, we defined a "potential interaction" as the presence in a site of two species that are known (from our samples) to interact, as opposed to the potential number of parasitoid–host species combinations, which is used as the denominator for calculating connectance (Schoenly and Cohen 1991, Closs and Lake 1994, Tylianakis et al. 2007) may include links that never actually occur. We compared the proportion of these potential interactions that were actually realized (observed) in each site across habitat types using a generalized linear model (glm command) with a binomial error and logit link function, conducted in R version 2.8.1 (R Development Core Team 2006). The proportion of potential interactions that were realized was the response variable and habitat type was the predictor. The maximal model containing all five habitat types separated was simplified by collapsing levels of the habitat factor until no significant reduction in residual deviance occurred (Crawley 2007; changes in residual deviance are measured using AIC).

Determinants of temporal variability.—To determine the direct and indirect pathways through which habitat modification may affect temporal within-site variability in the structure of quantitative networks, we used a structural equation model conducted in Amos version 16.0.1 (Amos Development Corporation 2007). Times during which no interaction was observed were excluded because no pairwise distances between them can be computed from asymmetric distance measures. For completeness, we re-ran the analysis using Jaccard dissimilarity to assess temporal variability in the presence-absence of each parasitoid–host interaction (link). The maximal (initial) model contained a path from management intensity (ordinal variable) to temporal variability in the network, as well as indirect pathways mediated via temporal variability in host and parasitoid community structure, and mean body size. A detailed description of how mean body sizes were calculated is given in Appendix D. A figure showing the maximal (initial) model with justifications for each path is available in Appendix E. All pathways in the initial model (Appendix E) were treated as optional. We conducted an all subsets specification search to reduce the initial model to the best fitting final model, determined by the lowest ratio of the chi-square to the degrees of freedom (a ratio of less than two indicates good fit; Grace 2006). A chi-square test assesses whether the sample covariance matrix differs significantly from the model-implied covariance matrix, or in other words, whether the model fits the data (a nonsignificant P value is an indicator of good fit).

Results

Spatial variability.—We found striking differences in the spatial (site to site) variability of quantitative interactions between networks of different habitat types, such that deforestation greatly homogenized networks at the regional level (Fig. 1a, b). Tighter clustering in ordination space of networks from deforested habitats (rice fields or pastures) illustrated that they were much more similar to each other in the identity and relative frequency of their constituent interactions than were less modified, forested habitats (Fig. 1a). This pattern was confirmed by significant differences ($P \leq 0.005$, after Bonferroni correction) in multivariate dispersions between forested and deforested habitats (Fig. 1b). Importantly, this was not an artefact of the sampling design, as the spatial dispersion of sampling sites within the study region (i.e. their spread in geographical space) did not differ significantly between habitats ($P = 0.116$, Appendix A). Moreover, these results were not simply due to a few frequent interactions, because square-root transformed interaction frequencies yielded similar results (Appendix F).

We found that host communities in coffee sites were significantly more variable than abandoned coffee plantations, pastures, or rice fields when relative abundances were considered (Fig. 1c–f), but we did not detect any homogenization effect (reduced variability) with presence–absence data (Appendix G). Similarly, we found some evidence for spatial homogenization of parasitoid communities when relative abundances (Fig. 1c–f), but not presence–absence data (Appendix G), were considered. However, habitat simplification had effects on network homogenization beyond what could be explained by homogenization of the host or parasitoid communities alone. Indeed, even after controlling for host and parasitoid variability there remained highly significant ($P \leq 0.0001$) differences in network spatial variability between habitat types (Table 1 and Appendix H). Importantly, post hoc pairwise comparisons revealed that the significant differences in network spatial variability between habitat types were identical to those previously shown in Fig. 1b ($P \leq 0.005$, after Bonferroni correction).

Realization of interactions.—Land use intensification significantly affected the proportion of potential interactions (species A can attack species B) that were

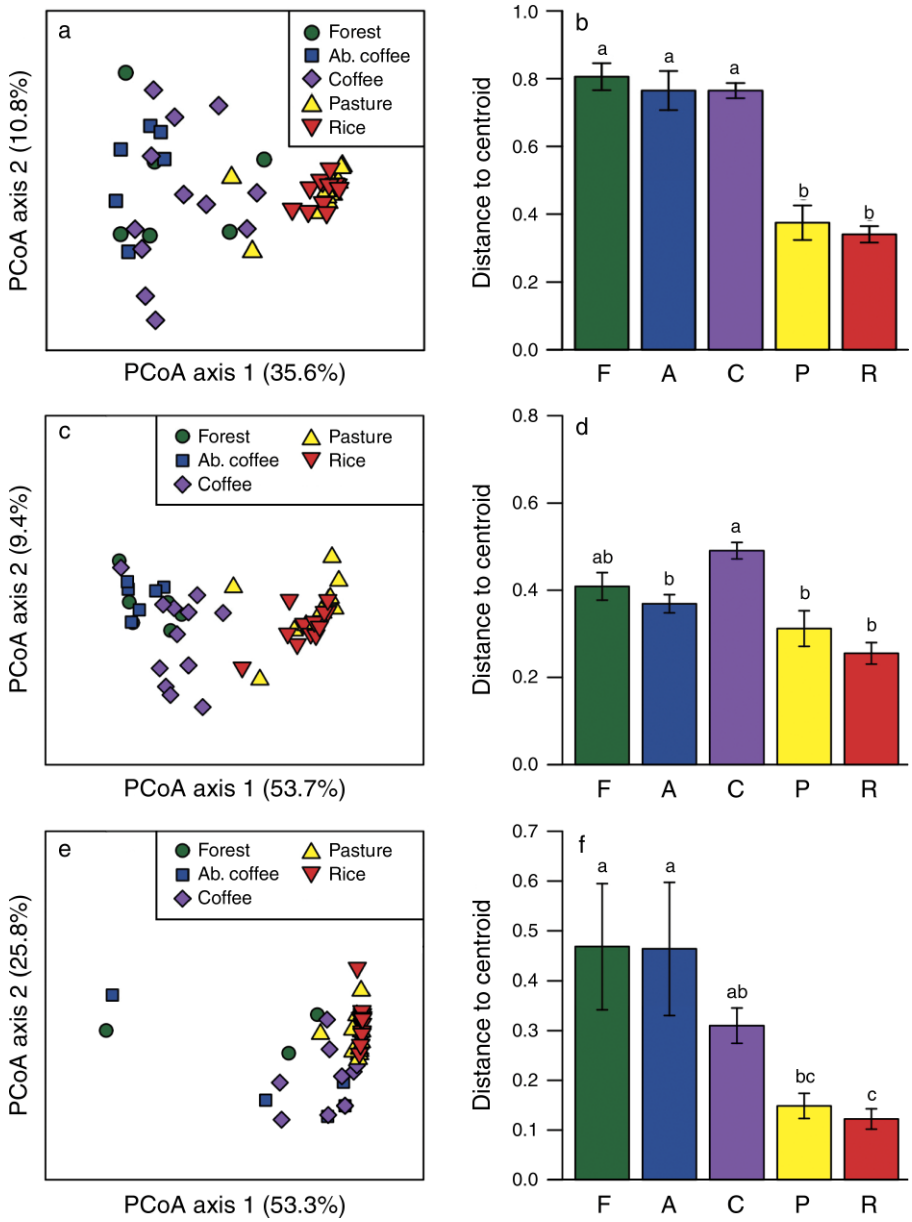

FIG. 1. Spatial variability in network structure across different habitat types. (a) Principal coordinate analysis (PCoA) of the 48 quantitative parasitoid–host networks based on the Hellinger distance. Sites depicted as close together in multivariate space have similar compositions and relative frequencies of interactions. The first two PCoA axes represent 35.6% and 10.8% of the total variation, respectively. The deforested habitats (pasture and rice) show the least variability in network structure across sites (they are clustered together in multivariate space). (b) Average distance (±SE) of individual networks to their group centroid (mean network) for each of the five habitat types. (c, e) Spatial variability in (c) host relative abundances and (e) parasitoid relative abundances across different habitat types, as shown by principal coordinate analyses (PCoA) of the 48 sites based on the Hellinger distance. (d, f) Mean distance (±SE) of individual (d) host communities or (f) parasitoid communities to their group centroid for each of the five land use types. Letters indicate significant differences in multivariate dispersion at a Bonferroni-corrected α of 0.005: F, forest; A, abandoned (Ab.) coffee; C, coffee; P, pasture; R, rice.

realized (A actually attacked B in that site). The maximal model had the poorest fit (AIC = 189.66), and the best fit (AIC = 184.57) was obtained by collapsing together the three forested habitats and the two deforested habitats into one level each of the habitat factor, and these levels differed significantly ($Z = 2.27$, $P = 0.022$, residual deviance = 18.72, df = 46). A higher proportion of potential interactions (links) were realized in deforested habitats (45%) compared to forested habitats (33%).

Determinants of temporal variability.—In the best fitting model, land use intensity did not directly

TABLE 1. Effects of parasitoid and host spatial variability in community structure (distance to centroid) and habitat type on network spatial variability (distance to centroid).

Source	df	SS	MS	*F*	*P*	VCE
Parasitoid variability	1	1.3465	1.3465	201.64	0.0001	0.16707
Host variability	1	0.7031	0.7031	105.29	0.0001	0.13686
Habitat type	4	0.4196	0.1049	15.709	0.0001	0.11547
Residual	41	0.2738	0.0067			0.08172
Total	47	2.7430				

Notes: VCE stands for variance component estimates. Type-I SS were used, with habitat type entered last in the model to test its effects after controlling for host and parasitoid variability. *P* values were computed using 9999 permutations of the residuals under a reduced model.

homogenize webs through time (Fig. 2). Rather, its net negative effect on temporal network variability (Appendix I) was the result of interplay between different indirect pathways involving altered variability in community structure, and shifts in mean body size of parasitoids and hosts (Fig. 2). Land use intensification was associated with reduced body size (Fig. 2, paths a and d), though this path was only significant for hosts (Fig. 2; hosts: $P < 0.001$, parasitoids $P = 0.242$). These smaller hosts directly decreased temporal variability in network (Fig. 2, path i) and host community (Fig. 2, path f) structure, as did the direct effect of land use intensification (Fig. 2, path c). In contrast, smaller parasitoids directly increased temporal interaction variability (Fig. 2, path g), but this was partially offset by an indirect effect due to communities composed of smaller parasitoids being more homogeneous in time (Fig. 2, path e), which in turn strongly homogenized networks (Fig. 2, path h). These results were qualitatively similar when variability in only the presence/absence (rather than frequency) of interactions was used (Appendix J).

DISCUSSION

We found that in deforested habitats (pastures and rice fields), parasitoid–host networks in coastal Ecuador were strikingly similar to each other compared to networks from forested habitats (forests, abandoned agroforests, and managed agroforests). Interestingly, such network homogenization was only apparent when comparing forested with non-forested habitats, despite all habitat types being ordered along a gradient of land use intensity. Thus, increasing management intensity had little effect on the regional variability of parasitoid–host networks as long as canopy cover was maintained, but once it disappeared, a strong threshold effect was observed by which networks became greatly homogenized. These results are consistent with earlier findings that several architectural properties of pooled interaction networks became altered in deforested habitats (Tylianakis et al. 2007). On the other hand, while these architectural changes went largely unnoticed with binary (presence-absence) networks (Tylianakis et al. 2007), network homogenization was detectable even with binary networks (Appendix G). Together, these findings

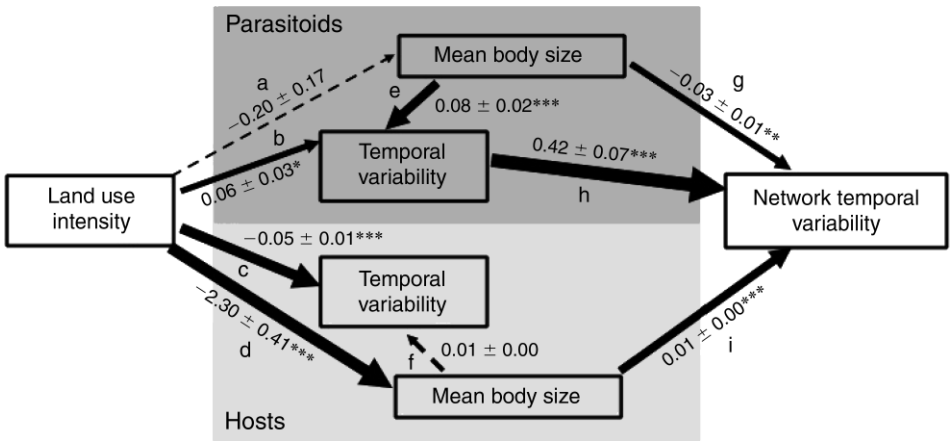

FIG. 2. Final (best-fitting) structural equation model examining the indirect effects of land use intensity on temporal variability (distance from each sampling date to the multivariate centroid for a site) in quantitative networks. Nonsignificant paths retained in the best-fitting model are presented as dashed lines. Unstandardized estimates are shown with standard error. Width of each path is proportional to its standardized direct effect. The final model gave a good fit to the data (chi-square = 4.17, df = 6, $P = 0.654$).
* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

suggest that shade-grown tropical agroforestry systems can maintain the structure and regional diversity of parasitoid–host networks, which brings us a step closer towards the emerging goal of conserving interaction biodiversity in natural and managed systems (Thompson 1994, Ings et al. 2009; Tylianakis et al., *in press*).

The finding that the homogenizing effects of land use persisted after controlling for homogenization of parasitoid and host species composition provides strong evidence that while variability of host or parasitoid communities influences web variability (the inverse of homogenization), other causal processes associated with deforestation drove network homogenization. One possibility is that a reduced hunting efficiency of predators in structurally complex habitats (Brose et al. 2005) could partially decouple network structure from predator or prey community structure, thereby increasing regional interaction diversity. Evidence in support of this hypothesis was the large number of potential interactions that were not realized in forested habitats compared with pasture and rice fields, where parasitoids have a greater likelihood of finding all available hosts. This could have important consequences for network adaptability, as the ability of mobile consumers to behaviorally adapt to resource density and spatially couple isolated resource patches (McCann and Rooney 2009) may be hindered when habitat complexity moderates their ability to forage in different habitats. The recent incorporation of foraging behavior into food web research has already yielded numerous insights, particularly regarding the mechanisms responsible for structuring networks (Ings et al. 2009).

That network temporal variability was directly negatively affected by parasitoid body size (Fig. 2) was surprising given the recent finding that body size is a poorer predictor of the structure of parasitoid–host interactions than of predacious or herbivorous feeding interactions (Petchey et al. 2008). Although our results are observational, previous evidence suggests potential mechanisms for the effects of parasitoid body size. First, body size correlates negatively with species turnover in time (Soininen et al. 2007), potentially reducing interaction turnover (i.e., causing homogenization). Second, larger parasitoids live longer (Bezemer et al. 2005) and disperse further (Woodward et al. 2005), thus allowing them to search a greater total area and to locate a greater proportion of available host species. Large top predators are known to stabilize aggregate food web properties by coupling alternative energy channels and reducing fluctuations in single channels (McCann et al. 2005, McCann and Rooney 2009). We have now shown that large consumer species also reduce temporal variability of two fundamental components of food webs: the composition and frequency of their constituent interactions. If this pattern is found to be general across systems, the disproportionate loss of large predators following human activities such as overharvesting (De Roos and Persson 2002) may increase network temporal variability.

In contrast to their mobile foraging parasitoids, hosts are sedentary larvae or pupae at the time a parasitoid–host interaction is realized. Because body size scales negatively with abundance and positively with territory and home range size (Woodward et al. 2005), larger hosts are likely to be rarer and more patchily distributed at local scales, and are thus less likely to be found by a parasitoid within a given time. This may explain the increase in network variability with increasing host body size, and suggests that small prey species, by virtue of their ubiquity, could stabilize network structure through time. Future experimental and theoretical exploration of this mechanism is required.

Seminal work in aquatic systems showed that temporal turnover in species composition may result in species being depicted together in pooled networks when they do not actually co-occur in the system (Thompson and Townsend 2005). If this effect were constant across habitats, it would not affect the use of networks as an ecological tool for cross-site comparisons. However, we have shown that networks from structurally complex habitats are likely to be a poorer representation of the spatiotemporally variable community in these habitats than are networks from structurally simple (i.e., deforested) habitats, thus hindering comparisons of quantitative networks across habitats.

Empirical food web ecology has made enormous progress in evaluating the consequences of global environmental changes (reviewed in Tylianakis et al. 2008, Ings et al. 2009), but our results show that following the loss of forest canopy, particular interactions between species are favored at the expense of others, thus homogenizing parasitoid–host interaction networks in space and time. Our work on complex multispecies networks reveals an important yet previously unexplored facet of humanity's march into the "Homogecene" era (the global erosion of regional diversity due to unprecedented current rates of species exchange; Rosenzweig 2001). On the other hand, our results also reinforce the view that tropical agroforestry systems can be compatible with biodiversity objectives if canopy cover is maintained (e.g., Perfecto et al. 1996). Reduced regional interaction diversity under deforestation could reduce the resilience of parasitoid–host webs to environmental changes or extreme events, analogous to the effect of reduced genetic (Hughes and Stachowicz 2004) or species (Loreau et al. 2003) diversity. Further, if host survival depends on refuge from predation, the loss of enemy free space or time (Holt and Lawton 1994) in modified habitats (where more potential interactions are realized) may increase coupling of parasitoid–host population dynamics, potentially reducing their population persistence (Holt 2002). Network homogenization could also alter coevolution between interacting species, one the main forces shaping the Earth's biodiversity (Thompson 1994, Olden et al. 2004). Thus, spatiotem-

poral network homogenization may have important consequences, yet it may not necessarily be predictable from community changes observed within individual trophic levels.

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APPENDIX A

Map of study area showing the location of the 48 sites (*Ecological Archives* E091-118-A1).

APPENDIX B

Binary parasitoid–host interaction matrix for all sites pooled, with body size data used for analyses (*Ecological Archives* E091-118-A2).

APPENDIX C

Details of spatial analyses (*Ecological Archives* E091-118-A3).

APPENDIX D

Details on how parasitoid and host body sizes were defined (*Ecological Archives* E091-118-A4).

APPENDIX E

Maximal (initial) SEM model (*Ecological Archives* E091-118-A5).

APPENDIX F

Spatial variability in network structure after square-root transformation of interaction frequencies (*Ecological Archives* E091-118-A6).

APPENDIX G

Spatial variability in binary networks, host community composition, and parasitoid community composition (*Ecological Archives* E091-118-A7).

APPENDIX H

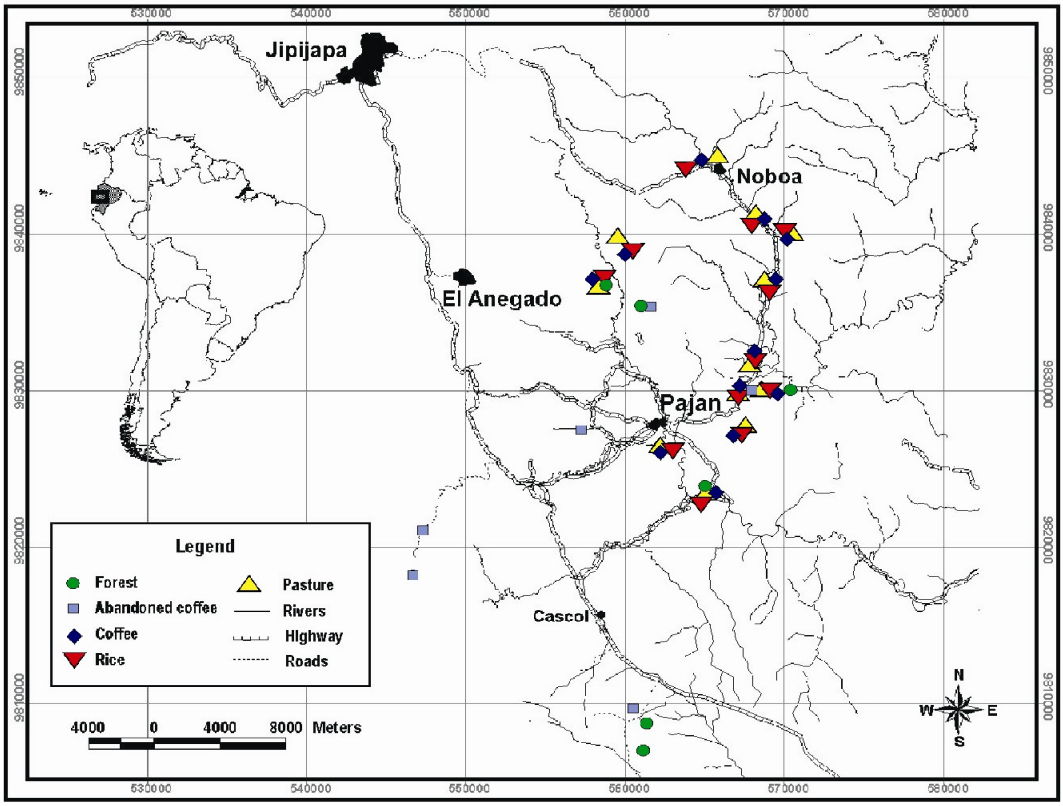
Network spatial variability after controlling for variation in host community structure and parasitoid community structure (*Ecological Archives* E091-118-A8).

APPENDIX I

Table showing the standardized total effects for the SEM model (*Ecological Archives* E091-118-A9).

APPENDIX J

SEM results for binary networks (*Ecological Archives* E091-118-A10).



APPENDIX A. Map of the study area showing the 48 sampling sites (Tylianakis et al. 2006). There were no significant differences in spatial dispersion of sampling sites between the five land use types (P = 0.116, 9999 permutations).

Appendix B. Binary parasitoid–host interaction matrix for all sites pooled, with body size d

Species/"Morphospecies"	Parasitoids	Chalcidi	*Coelioxys* s	Phygadeuontinae (	*Melittobia a*
Hosts	Average length (mm)	8	9.6	10	1.2
Anthidiini Gen. sp.	11.67	0	0	0	0
Anthidium sp.	22.44	0	0	0	1
Apidae Gen. sp.1	47.14 (N.B.	0	0	0	0
Apidae Gen. sp.2	15.34	0	0	0	0
Centris sp.	11.31	0	0	0	0
Eumeninae Gen sp. 6	15.2	0	0	0	0
Euglossa variabilis	13.83	0	0	0	1
Monobia angulosa	21.98	0	0	0	1
Eumeninae Gen sp. 2	12.5	0	0	0	0
Eumeninae Gen. sp. 3	20.17	0	0	0	1
Eumeninae Gen. sp. 4	18.75	0	0	0	1
Apidae Gen. sp.3	40 (N.B. on	0	0	0	0
Megachile sp.1	25.96	0	1	0	1
Megachile sp.2	9.2	0	1	0	0
Megachilidae Gen. sp.1	6.3	0	0	0	0
Megachilidae Gen. sp.2	9.35	0	0	0	0
Megachilidae Gen. sp.3	8.1	0	0	0	0
Megachilidae Gen. sp.4	100 (N.B. o	0	0	0	0
Megachilidae Gen. sp.5	27.5	0	1	0	0
Neofidelia sp.	16.97	0	1	1	1
Priochilus nigrocyaneus	26.72	0	0	0	1
Pseudodynerus sp.	17.06	1	1	0	1
Sceliphrinae Gen. sp.	16.5	0	0	0	0
Sphaeropthalminae Gen. sp.	8.24	0	0	0	0
Sphecidae Gen. sp.1	8.95	0	0	0	0
Sphecidae Gen. sp.2	25.15	0	0	1	1
Sphecidae Gen. sp.3	20.89	0	0	0	1
Tetrapedia sp.	12.86	0	1	0	1
Unidentified host sp. 1	35 (N.B. on	0	0	0	0
Trypoxylon sp.1	19.74	0	0	0	1
Trypoxylon sp.2	18.97	0	0	0	1
Trypoxylon sp.3	17.35	0	0	0	1
Zeta sp.	19.77	0	0	0	1

lata used for analyses

Unidentified par	Bombyliida	*Leucospis* s	*Chrysis* s	Leucospid
11	7.2	9	6.48	9.27
0	0	0	0	0
0	1	0	1	1
0	0	0	0	0
0	0	0	0	0
0	0	0	0	0
0	0	0	0	0
0	0	0	0	0
0	0	0	1	0
0	0	0	0	0
0	0	0	0	0
0	0	0	0	1
0	0	0	0	0
0	0	0	0	0
0	0	0	0	0
0	0	0	0	0
0	0	0	0	0
0	0	0	0	0
0	0	0	0	0
0	0	0	0	1
0	0	1	1	0
0	0	0	0	0
0	1	1	1	0
0	0	0	0	0
0	0	0	0	0
0	0	0	0	0
0	1	1	1	0
1	0	0	1	0
0	0	1	1	0
0	0	0	1	0
0	0	0	1	0
0	0	0	1	0
0	0	0	1	1
1	1	0	1	0

Appendix c. Details of the spatial variability analyses.

Because it is recommended to test for differences in multivariate dispersions using distance measures that emphasise either presence/absence changes or changes in relative abundances (Anderson et al. 2006), we conducted two sets of analyses. The first incorporated interaction frequencies and host or parasitoid abundance, using the Hellinger distance (Legendre and Legendre 1998). Hellinger distance was selected because it is asymmetric (excludes joint absences), emphasizes relative and not absolute differences in abundance, does not give high weight to rare species or interactions, and can slightly better represent an artificial ecological gradient than the widely used Bray-Curtis distance (Legendre and Legendre 1998, Legendre and Gallagher 2001). The second set of analyses was based on binary networks (presence-absence of interactions) or presence-absence of hosts or parasitoid species, using the Jaccard dissimilarity (Legendre and Legendre 1998). We chose the Jaccard dissimilarity because it is the most widely used dissimilarity measure in ecology, including studies of biotic homogenization (Olden and Rooney 2006).

In order to quantify how much of the observed network homogenization could have been driven by the homogenization of host or parasitoid communities, we used two different statistical approaches. In the first approach, we used a linear model with distances of individual networks to their group centroid (i.e. habitat type) as the response variable, habitat type as the predictor of interest, and distances of individual host and parasitoid communities to their group centroids as covariables. Type-I SS were used, with habitat type entered last in the model to test its effects on network spatial variability after controlling for host and parasitoid variability. The second approach, involved a canonical redundancy analysis (RDA) using the Hellinger-transformed (Legendre and Gallagher 2001) interaction frequency matrix as a response variable and the first 10 (host) and 3 (parasitoid) PCA axes of the Hellinger-transformed abundance matrices (representing >90% variation in host and parasitoid composition, respectively) as predictors. We then used the residuals of this RDA as the input data for a

test for homogeneity of multivariate dispersions. This approach essentially removes the variation in interaction composition that can be attributed to variation in host and parasitoid community composition prior to conducting the distance-based test for homogeneity of multivariate dispersions. Distance-based tests for homogeneity of multivariate dispersions were conducted in the PRIMER v6 / PERMANOVA+ environment (Anderson et al. 2008), and RDA was conducted using the "vegan" R package (Oksanen et al. 2009). All tests were performed using 9999 permutations.

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Appendix D. Details on parasitoid and host body sizes

Body size of host species was defined by larval nest cell length (the stage at which the parasitism interaction takes place). This overcomes the common problem that average resource body sizes can describe the individuals that are not consumed, rather than those actually involved in the interaction (Brose et al. 2006). However, because nest cells are not always a perfect approximation of actual larval size (particularly in nests with only one cell) and the actual size of the parasitized host larva will depend on its age at parasitism, we averaged the cell length across all individuals of a species to determine the average size of that host species in that site. Only host species that were parasitized (i.e. that appeared in the interaction webs) were included in these analyses. Nest cell length has no bearing on parasitoid body size, so we estimated parasitoid body size for each species by averaging the body length measurements of pinned specimens of emerging parasitoids. Consequently, our estimate of mean body size is more accurate for more abundant parasitoid species. A consequence of these limitations is that our estimates of average body sizes lose information on the body sizes of the consumers (parasitoids) and resources (hosts) involved in each trophic interactions (Cohen et al. 2005). Thus, we avoid discussion of consumer-resource body-size ratios and fitness consequences of host body size for parasitoids, which may be biased by our use of mean values (Cohen et al. 2005). To get a plot-scale estimate of host and parasitoid body size, body size data were then weighted by the relative abundance of each species that occurred at each site (over all sampling dates combined). This has been termed the "community-weighted trait mean" (CWM) and is an index of functional composition (Díaz et al. 2007).

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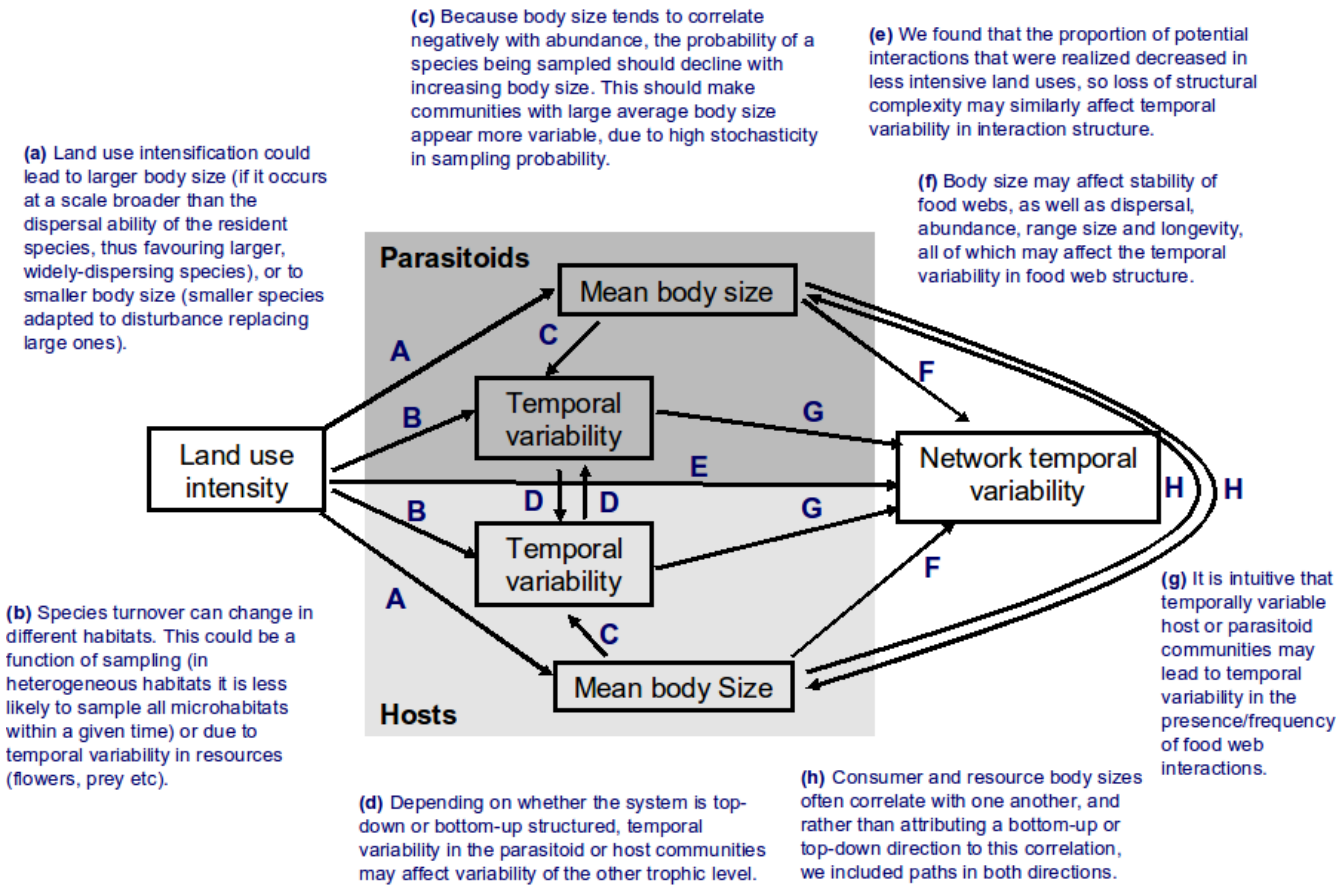
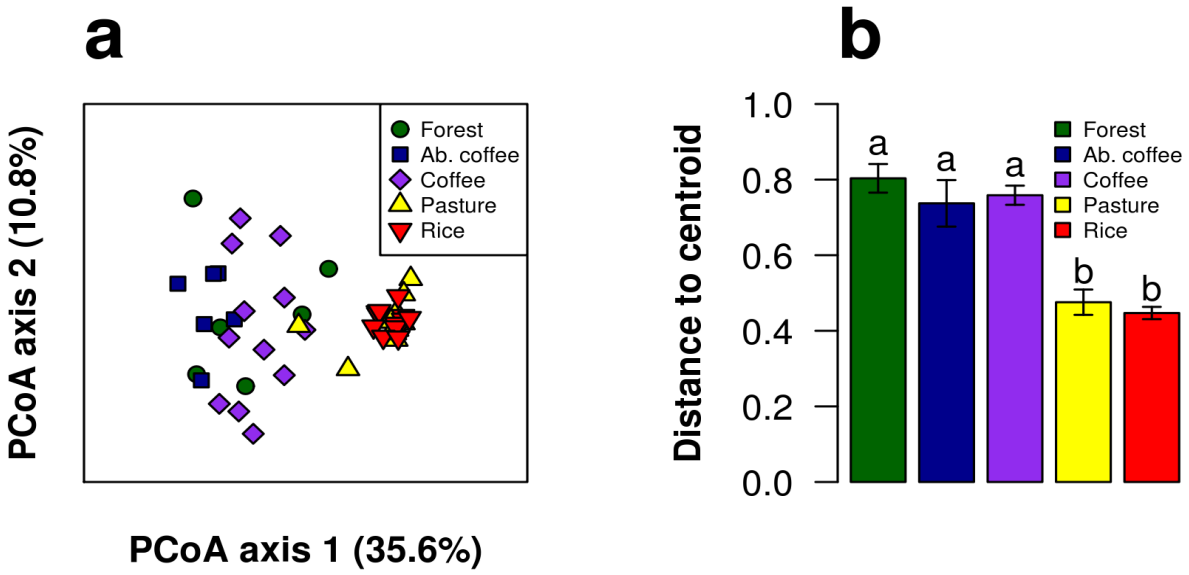
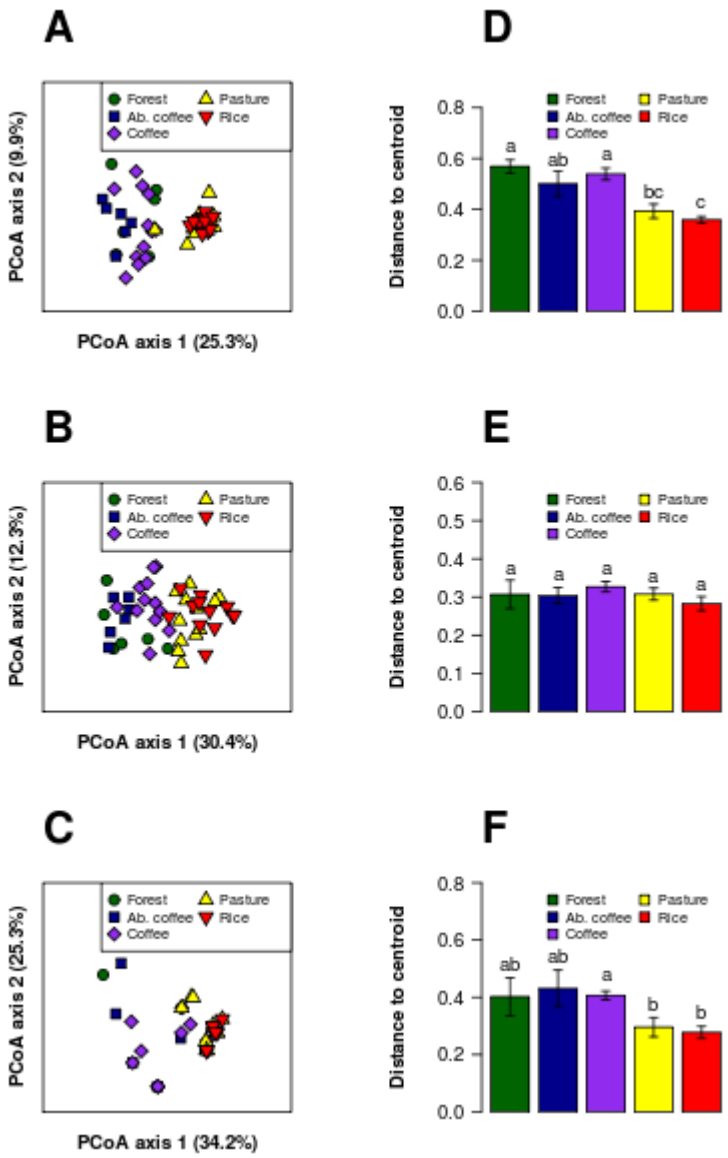


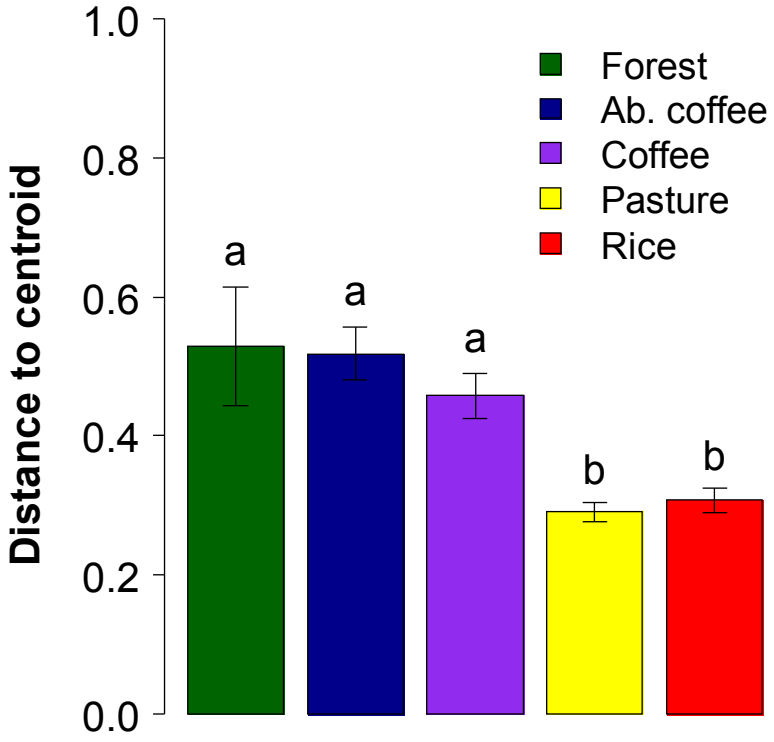
Appendix E. Maximal (initial) structural equation model, with justifications for each direct pathway. Variables related to parasitoids are given in the top part of the diagram, and hosts are given below. Temporal variability in parasitoid and host community structure ("Temporal variability") was measured as the mean distance of individual host or parasitoid communities from individual sampling months to their centroid across all sampled dates, using Hellinger distance for relative abundances (Fig. 3) or Jaccard dissimilarity for presence-absence data (Appendix I).



Appendix F. Spatial variability in network structure (square-root transformed interaction frequencies) between habitat types. This analysis controls for the possibility that a few highly frequent interactions may be driving the patterns we present. (a) Principal coordinate analysis (PCoA) of the 48 quantitative networks based on the Hellinger distance. Sites are arranged in multivariate space according to the occurrence and (square-root transformed) relative frequency of individual parasitoid-host interactions. The first two PCoA axes represent 28.9% and 10.3% of the total variation in interaction structure, respectively. The most heavily modified habitats (pasture and rice) show the least variability in network structure across sites (they are clustered together in multivariate space). (b) Mean distance (±SE) of individual networks to their group centroid for each of the five habitat types. Letters indicate significant differences in multivariate dispersion at a Bonferroni-corrected α of 0.005. Ab. coffee = Abandoned coffee.



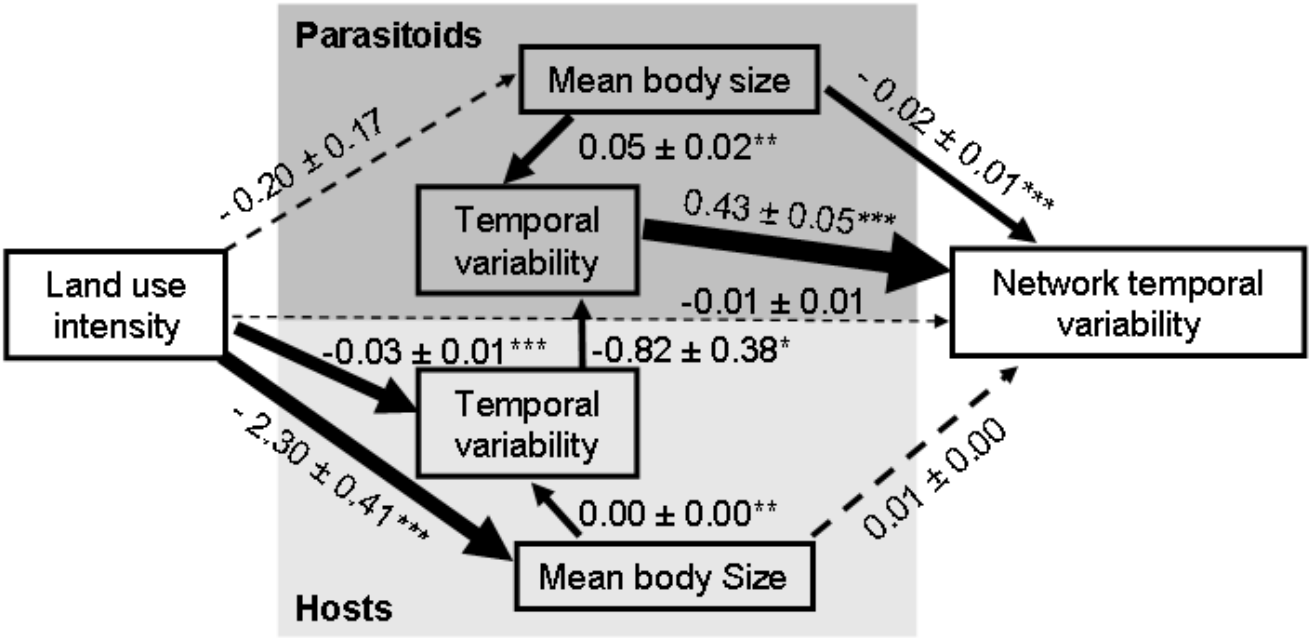
APPENDIX G. Spatial variability in (a) binary networks, (b) host community composition (species presence/absence), and (c) parasitoid community composition (species presence/absence) between habitat types, as shown by principal coordinate analyses (PCoA) of the 48 sites based on the Jaccard dissimilarity (presence-absence data). Mean distance (±SE) of individual (d) binary networks, (e) host communities, or (f) parasitoid communities to their group centroid for each of the five habitat types. Letters indicate significant differences in multivariate dispersion at a Bonferroni-corrected α of 0.005.



Appendix H. Mean distance (±SE) of individual networks to their group centroid for each of the five habitat types, once variation in host community structure and parasitoid community structure were controlled for. To do so, we first ran a canonical redundancy analysis (RDA) involving the Hellinger-transformed (Legendre and Gallagher 2001) interaction frequency matrix as response variables and the first 10 and 3 PCA axes of the Hellinger-transformed host and parasitoid abundance matrices (representing >90% variation in host and parasitoid composition, respectively) as predictors. We then used the residuals of this RDA as the input data for the test for homogeneity of multivariate dispersions. Letters indicate significant differences in multivariate dispersion at a Bonferroni-corrected α of 0.005.

APPENDIX I. Standardized total (direct plus indirect) effects of column variables on row variables for best fitting SEM model (Fig. 3).

	Land use intensity	Mean host body size	Mean parasitoid body size	Host temporal variability	Parasitoid temporal variability
Mean host body size	-0.633	0.000	0.000	0.000	0.000
Mean parasitoid body size	-0.168	0.000	0.000	0.000	0.000
Host temporal variability	-0.692	0.226	0.000	0.000	0.000
Parasitoid temporal variability	0.218	0.000	0.472	0.000	0.000
Network temporal variability	-0.061	0.434	0.018	0.000	0.730



Appendix J. Final (best fitting) structural equation model examining the indirect effects of land use intensity on temporal variability (mean distance to centroid) of binary networks (presence/absence of interactions). Non-significant paths retained in the best-fitting model are presented as dashed lines. Unstandardized estimates shown with standard error. $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$. Width of each path is proportional to its standardized direct effect. The overall final model gave an excellent fit to the data (Chi-square = 2.14, D.F. = 5, $P = 0.829$). Results were qualitatively identical to those obtained using quantitative food webs (incorporating frequency of interactions: Fig. 3)