LETTERS

Habitat modification alters the structure of tropical host–parasitoid food webs

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Global conversion of natural habitats to agriculture has led to marked changes in species diversity and composition[1]. However, it is less clear how habitat modification affects interactions among species[2]. Networks of feeding interactions (food webs) describe the underlying structure of ecological communities, and might be crucially linked to their stability and function[3–7]. Here, we analyse 48 quantitative food webs[8,9] for cavity-nesting bees, wasps and their parasitoids across five tropical habitat types. We found marked changes in food-web structure[10,11] across the modification gradient, despite little variation in species richness. The evenness of interaction frequencies declined with habitat modification, with most energy flowing along one or a few pathways in intensively managed agricultural habitats. In modified habitats there was a higher ratio of parasitoid to host species and increased parasitism rates, with implications for the important ecosystem services, such as pollination and biological control, that are performed by host bees and wasps[12]. The most abundant parasitoid species was more specialized in modified habitats, with reduced attack rates on alternative hosts. Conventional community descriptors failed to discriminate adequately among habitats, indicating that perturbation of the structure and function of ecological communities might be overlooked in studies that do not document and quantify species interactions. Altered interaction structure therefore represents an insidious and functionally important hidden effect of habitat modification by humans.

Habitat modification is the leading global cause of species extinctions and alterations in abundance of persisting species, and is a particular threat to biodiversity in extremely diverse tropical ecosystems[13]. All species are linked in networks of mutualistic and antagonistic interactions[14]. The importance of conserving these interactions and associated processes, as well as the component species, has been stressed repeatedly[2,15,16], particularly as humans rely on ecosystem services associated with species interactions, such as pollination and biological control[17]. Research on 'interaction extinctions' and altered patterns of interactions in ecological communities has been impeded by the lack of appropriate analytical tools, and by a failure to quantify the frequency or even to detect the presence of interspecific interactions[18]. Early food-web studies treated all interactions as equal, irrespective of their magnitude or frequency, and qualitative properties used to describe food webs were found to be highly sensitive to variation in sampling effort[19,20].

Recently, methods have been developed to allow the quantification of interactions at the community scale[9], thereby giving a more robust description of community structure, and providing insights into the dynamic processes that structure ecological communities[21]. Although this approach is most commonly applied to networks of trophic interactions (quantitative food webs[9,22]), it is equally applicable to other interspecific interactions such as pollination[23]. Existing studies have used quantitative food webs to describe the structures of relatively intact species assemblages, but differences in quantitative food-web structure across habitats remain unknown. Nevertheless, these methods have considerable potential for quantifying the effect of human activities on networks of interacting species[24].

The information contained in food webs can be summarized in various ways. Quantitative, weighted equivalents of the food-web statistics that were developed to describe binary webs have now been derived[10]. Here, we use four of these quantitative metrics, with well known qualitative counterparts (connectance, linkage density (LD_q), generality (G_q) and vulnerability (V_q)), and quantitative measures of interaction evenness and compartmentalization (see Supplementary Methods 1), to assess the effect of a habitat modification gradient on food-web structure in the tropical biodiversity hotspot of coastal Ecuador. Our food webs document 4,090 trophic interactions involving 33 species of bees and wasps (Hymenoptera: Apidae, Megachilidae, Mutilidae, Pompilidae, Sphecidae and Vespidae) and nine parasitoid and kleptoparasite (collectively referred to hereafter as parasitoid) species (Hymenoptera: Eulophidae, Ichneumonidae, Leucospidae, Megachilidae and Chrysididae; Diptera: Bombyliidae).

The bees and wasps in our focal food webs perform important ecosystem services[12]. Bees are key pollinators of both crops and wild plants, and even small variations in the number of species can have severe effects on pollination rates[25]. Functional differences between species allow complementarity in pollination, such that extinction or altered abundance of key species can have disproportionate effects[25]. Similarly, predatory wasps can be important predators of herbivorous insects, such as pest caterpillars[12]. The effects of changes in land use on the diversity of bees and wasps have been well documented[25–27]. However, little is known about the structure of interactions between these species and their natural enemies, and how this might affect associated ecosystem services.

We found striking (Fig. 1) and highly significant differences in quantitative food-web structure among habitats (multivariate general linear model (GLM): Wilks' lambda = 0.128, $F_{20,124}$ = 5.30, $P < 0.0001$). Food-web quantitative vulnerability (a measure of the ratio of host to parasitoid species) and interaction evenness (a measure of the uniformity of energy flows along different pathways; see Supplementary Methods 1 for methods of calculation for these and other metrics) showed significant differences among habitats (Table 1). Importantly, differences in food web metrics did not result simply from differences in species richness across habitats: habitat explained a statistically significant portion of variation in the metrics even after controlling for the effects of host and parasitoid richness (multivariate GLM: Wilks' lambda for effect of habitat = 0.34, $F_{20,124}$ = 2.399, $P = 0.002$, Table 1); and host and parasitoid species richness per site did not vary significantly across habitats (ANOVA: $F_{4,43} < 2.5$, $P > 0.05$ in both cases). Rather, habitat modification led

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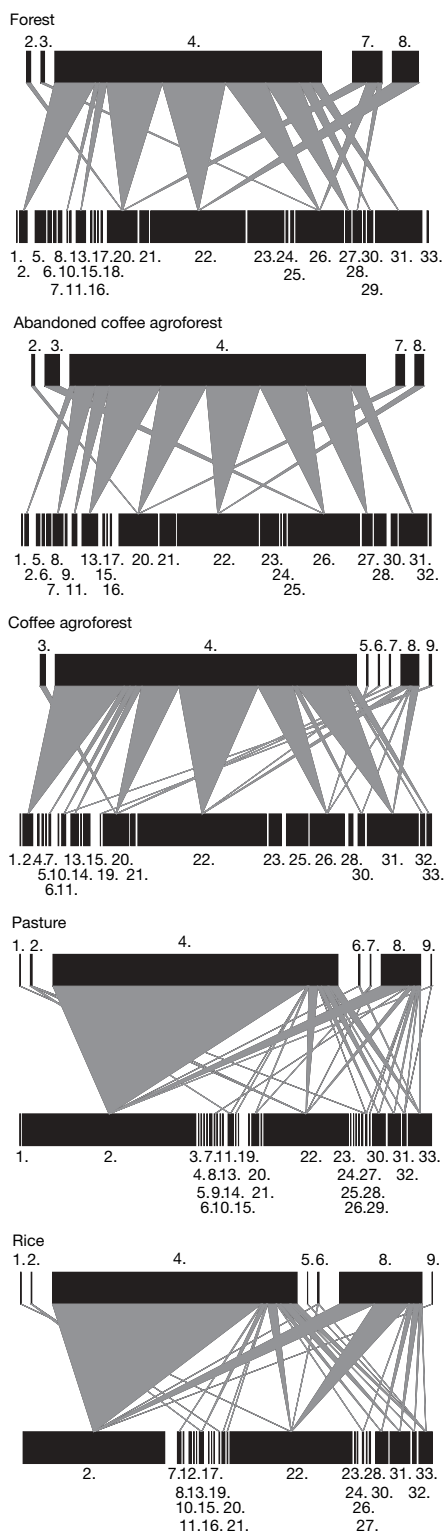
Forest

Abandoned coffee agroforest

Coffee agroforest

Pasture

Rice

Figure 1 | Quantitative host–parasitoid food webs along a gradient of increasing habitat modification (top to bottom). For each web, lower bars represent host (bee and wasp) abundance and upper bars represent parasitoid abundance, drawn at different scales. Linkage width indicates frequency of each trophic interaction. As a summary, the webs show interaction data pooled across all replicates for each habitat type, although analyses were conducted on a per-site basis. Species codes are given in Supplementary Table 3. Host and parasitoid order is consistent across webs, and the webs are drawn at different scales (for total host abundances, see Supplementary Fig. 1). *Melittobia acasta* is parasitoid species 4; *Anthidium* sp. is host species 2.

Table 1 | Effects of habitat type on parasitism rate and individual food web metrics

	Model 1			Model 2		
Variable	$F_{4,41}$	P	r^2	$F_{4,41}$	P	r^2
Parasitism rate*†	15.54	<0.00001	0.579	13.24	<0.00001	0.329
Linkage density	1.32	0.278	0.103	1.24	0.308	0.107
Generality	2.11	0.096	0.158	2.01	0.110	0.131
Vulnerability†	10.08	<0.00001	0.478	9.85	0.00001	0.326
Evenness†	5.85	<0.0001	0.357	5.97	<0.001	0.223
Connectance	2.04	0.106	0.129	1.59	0.195	0.084
Compartment diversity‡	0.48	0.749	0.045	0.49	0.741	0.046

Results derived from independent GLMs. Model 1 has habitat type entering the model first, before parasitoid and host diversity. Model 2 has habitat type entering last, after removal of variation explained by parasitoid and host diversity.
* Arcsine square root transformed.
† Significant at a Bonferroni-corrected α of 0.0071.
‡ Log$_{10}$ transformed.

to large differences in the evenness of interactions (Table 1, Fig. 2). Quantitative weighted vulnerability increased greatly in more modified systems (Table 1, Fig. 2) as did the proportion of individual host bees and wasps that were parasitized (Table 1, Fig. 2). We found no significant difference in linkage density or compartment diversity across habitats (Table 1).

For completeness, we repeated these analyses with qualitative metrics based on binary presence/absence interaction data (see Supplementary Table 1, Supplementary Fig. 1). These metrics showed significant variation among habitats, but failed to reveal the differences observed in the quantitative webs. Rather, they were strongly biased by sample size[11,19], and showed significantly higher linkage density, generality, vulnerability, interaction richness and connectance in rice and pasture, because the abundances of both hosts and parasitoids was two to five times higher in these habitats than in the less modified systems. This contrasts sharply with the higher vulnerability and interaction evenness in less modified systems, using quantitative, weighted measures that are not affected by sample size differences.

Inspection of the quantitative food webs (Fig. 1) indicates the specific changes that are responsible for differences in food-web structure among habitats. Food webs in intensive agricultural systems (rice and pasture) were dominated by a single trophic interaction (a gregarious pupal parasitoid *Melittobia acasta* Walk. (Chalcidoidea: Eulophidae) parasitising a bee *Anthidium* sp. (Hymenoptera: Anthidiinae); parasitoid species 4 and host species 2 in Fig. 1). This shift towards reduced interaction evenness would be
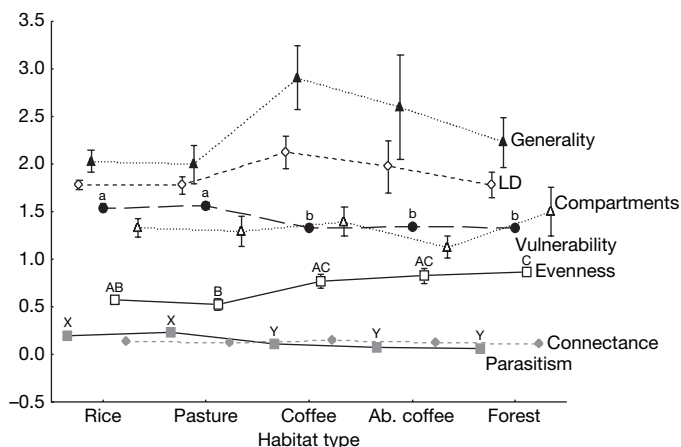

Figure 2 | The effects of habitat modification on rates of parasitism (mean ± s.e.m.) and six quantitative food web metrics (see Supplementary Methods 1): linkage density (LD), generality, vulnerability, evenness, connectance and compartment diversity. Letters above individual means indicate significant differences among habitat types for that particular metric. Letters in common or no letters indicates no significant difference.

impossible to detect with qualitative metrics (see Supplementary Table 1, Supplementary Fig. 1), despite its conspicuousness in the quantitative webs (Fig. 1). *Anthidium* sp. is characteristic of intensive agricultural systems, with 98% of the 7,839 observed individuals found in rice or pasture. *Melittobia acasta* attacked 16 host species across the different habitats, but *Anthidium* sp. was the host for 78% of *M. acasta* individuals, and following removal of *Anthidium* sp. from the data set, vulnerability and evenness showed no significant variation across habitats (see Supplementary Table 2).

However, the high abundance of *Anthidium* sp. in modified habitats was not the only factor driving the changes in food-web structure. Rather, *M. acasta*, the most abundant parasitoid in all habitats, was more specialized in modified habitats, with the evenness (see Supplementary Methods 2) of host species used being significantly lower in rice and pasture (ANOVA: $F_{4,41} = 7.54$, $P = 0.0001$, $r^2 = 0.424$). This specialization on *Anthidium* sp. means that alternative hosts might benefit. Indeed, *Megachile* sp. 1, the host species with the second highest frequency of parasitism from *M. acasta* (11.6% of individuals, compared to 32.6% in *Anthidium* sp.), experiences proportionately reduced parasitism in plots where parasitism of *Anthidium* sp. is high, even after controlling for differences in parasitism among habitats (see Supplementary Methods 3, multivariate GLM, effect of *Anthidium* sp. parasitism rates: $F_{1,9} = 16.19$, $P = 0.003$, $r^2 = 0.484$). *Anthidium* sp. in disturbed habitats might act as an abundant source of the highly generalist *M. acasta*, with possible consequences for other host species in agricultural or adjacent natural habitats through spillover of parasitoids[28]. The low specificity of *M. acasta* could allow parasitoid-mediated apparent competition to occur between host species, as has been documented in another tropical host–parasitoid food web[21].

Both quantitative vulnerability (the weighted ratio of parasitoid to host species) and levels of parasitism were significantly higher in rice and pasture habitats. High parasitoid diversity can promote high rates of parasitism[29], so high vulnerability can be expected to correlate with increased parasitism rates. Furthermore, parasitism was highest in the habitats with lower interaction evenness, consistent with data from the biological control literature showing the strongest top–down control in modified habitats, where food webs were dominated by a single link[30]. As solitary bees are known to be important pollinators of both wild and crop plants, and wasps provide biological control by consuming pest species such as caterpillars[12,25], increased mortality of these guilds in heavily modified systems might be detrimental to the maintenance of the ecosystem services they provide.

No significant differences in either quantitative linkage density or food web compartmentalization were detected among habitats. Linkage density is strongly affected by species richness[19], and the absence of significant differences in richness among habitats might have led to the consistency of this metric. Compartmentalization was consistently low across habitats, largely because there was little tendency for individual parasitoid species to specialize on individual host species and because hosts were typically vulnerable to multiple parasitoid species in each habitat.

Although the most severely modified habitats, pasture and rice, showed characteristic differences in food-web structure relative to other habitats (Fig. 1), both managed and abandoned coffee agroforests had similar food-web structures to forest, with no significant differences observed for any of the food-web metrics (Fig. 2). This is consistent with previous studies that have shown the biodiversity of agroforests to be comparable with that of natural forests[26,27], and indicates that a threshold level of habitat modification or openness, caused by removal of tree cover, might cause a significant step-change in species diversity[26,27] and composition (see Supplementary Fig. 2), with an associated shift in food-web structure. Coffee provides an intermediate habitat, harbouring interactions that are typical of both heavily modified and unmodified systems. Thus, appropriately managed agroecosytems can retain ecological

assemblages that are structurally and functionally similar to unmodified habitats. By contrast, highly modified pasture and rice habitats show marked changes in quantitative food-web structure, even where there has been little overall effect on the diversity of component species. Our results indicate that studies of human influences such as habitat change, fragmentation and climate change that focus solely on diversity and richness metrics might overlook important alterations to community structure, species interactions and ecosystem functions.

METHODS

Study region. The 48 study plots were spread across three cantons in the region of Jipijapa, Manabi province, Southwest Ecuador. Individual plot location, age and area details are given in ref. 26. A map of the region is given in ref. 27. This area falls within the Choco-Manabi region (a biodiversity hotspot), but large-scale agricultural conversion threatens the local biodiversity and the ecosystem services it provides[26,29].

We compared the five predominant land use types in the region. In order of decreasing modification, these were (with percentage of study zone occupied): rice (1.9% including other arable crops), pasture (16.2%), coffee agroforest (54.8%), abandoned coffee agroforests and forests (17.2% combined; not distinguishable using satellite imagery)[27]. Coffee agroforests can vary greatly with individual management and for consistency we selected plots that had been in cultivation for more than 8 years, where no chemical fertilizers had been used, and which had similar shade tree cover (60–80%) comprising a mixture of remnant forest species, legumes (for example, *Inga* spp.) planted for nitrogen enrichment, and various trees planted for fruit or timber. The understorey herb layer in these habitats is cleared twice per year. Sampling was carried out in twelve replicate sites of each of the managed systems, six forest and six abandoned coffee agroforest sites. Each site had experienced the current management regime for at least five years, and on average, there was no significant difference in the area of sites from each land use type (exact age and area of the sites can be found in the electronic supplement to ref. 26).

Trap nests. Nine trap nests, each comprising a 22-cm long, 15-cm diameter plastic tube with reed internodes inserted, were positioned in each of the 48 plots, to provide standardized nesting sites for naturally occurring bee, wasp and natural enemy assemblages[26]. Trap nests were evaluated every month from June 2003 to October 2004. Data from each of the nine traps per plot were pooled across all months for analyses. Species lists of primary trap-nesting species (hosts) and parasitoids are presented in Supplementary Table 2. As both solitary (one parasitoid individual per host individual) and gregarious (multiple parasitoid individuals per host individual) parasitoids were reared, we defined interaction frequency as the number of host larvae that were parasitized. As the dominant parasitoid is gregarious, an alternative food-web representation based on the number of parasitoid individuals recorded leads to a more markedly uneven distribution of interaction frequencies in modified habitats.

Analyses. Analyses were conducted in Statistica 6.1 (Statsoft). Several of the food-web metrics were intercorrelated (see Supplementary Table 4), so, to reduce the probability of a type I error, we tested the effect of habitat on food-web metrics (LD_q, G_q, V_q, connectance, compartment diversity and interaction evenness) per site using a general linear model (GLM) with multivariate responses, then made subsequent individual analyses of each response variable and rates of parasitism. To account for any effects on food web structure of among-habitat variation in species richness of hosts and parasitoids, we fitted GLMs with habitat type as a fixed factor and parasitoid and host richness as covariates. We used a Bonferroni corrected α of 0.0071. By introducing habitat type into the model before or after host and parasitoid diversity, using type I sums of squares, it was possible to quantify the overall variance in food web metrics across habitat types, as well as the variance after controlling for differences in host and parasitoid diversity among habitats. Results after controlling for parasitoid and host abundance were qualitatively the same, but for completeness we present results from both models for each metric (Table 1). We made *post hoc* comparisons using a Tukey Honestly Significant Difference test for unequal sample sizes. Error degrees of freedom for multivariate tests were calculated using denominator synthesis, and values presented are rounded to the nearest integer. Model residuals were tested for adherence to a normal distribution and homogeneity of variances. Compartment diversity was $\log_{10}$ transformed, and proportion parasitism was arcsine square root transformed to meet assumptions of the tests. Residuals from all models were also tested for spatial autocorrelation using a Mantel test conducted in R (R Development Core Team; http://www.R-project.org), with a distance matrix constructed from x and y global positioning system coordinates. The tests used Pearson correlations and a Bonferroni corrected α of 0.0071. No

significant autocorrelation was found (Mantel statistic $r < 0.023$, $P > 0.01$ in all cases).

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Author Contributions J.M.T. was responsible for writing, field data collection, research planning and analysis; T.T. for research planning, site selection and funding application; and O.T.L. for writing, analysis and preparation of food webs (Fig. 1). All authors discussed the results and edited the manuscript.

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