Running Head: Habitat edges create novel food webs

Non-random food-web assembly at habitat edges increases connectivity and functional

redundancy

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Abstract

Habitat fragmentation dramatically alters the spatial configuration of landscapes, with the creation of artificial edges affecting community structure and dynamics. Despite this, it is not known how the different food webs in adjacent habitats assemble at their boundaries. Here we demonstrate that the composition and structure of herbivore-parasitoid food webs across edges between native and plantation forests are not randomly assembled from those of the adjacent communities. Rather, elevated proportions of abundant, interaction-generalist parasitoid species at habitat edges allowed considerable interaction rewiring, which led to higher linkage density and less modular networks, with higher parasitoid functional redundancy. This was in spite of high overlap in host composition between edges and interiors. We also provide testable hypotheses for how food webs may assemble between habitats with lower species overlap. In an increasingly fragmented world, non-random assembly of food webs at edges may increasingly affect community dynamics at the landscape level.

Keywords: edge effects, food-web structure, generalism, host, native forest, network dissimilarity, parasitoid, plantation forest, rewiring of interactions, species composition.

INTRODUCTION

Land-use change is the primary driver of global biodiversity decline (Sala *et al.* 2000). Habitat conversion for human use also dramatically increases the extent of edges between different ecosystems (Ries *et al.* 2004). These habitat edges can influence patterns of species abundance, distribution and diversity (Dyer and Landis 1997; Ewers and Didham 2008; Murphy *et al.* 2016), alter dispersal processes (Duelli *et al.* 1990; Macfadyen and Muller 2013) and even interactions among species (Fagan *et al.* 1999; Ries *et al.* 2004; Ewers *et al.* 2013). Species interactions underpin many important ecosystem functions and services (Klein *et al.* 2003; Macfadyen *et al.* 2011), and they are frequently altered by changes in the

abundance, spatial and temporal distribution, and behaviour of the interacting partners (Tylianakis *et al.* 2008). These interactions can be viewed as a network, the structure of which may determine the persistence of communities following habitat fragmentation (Fortuna and Bascompte 2006), and affect ecosystem functioning via the partitioning of resources among species (Peralta *et al.* 2014).

Although natural and anthropogenic habitats have been shown to differ in their network structure (Tylianakis *et al.* 2007), it is still unknown how species assemble at habitat edges to create interaction networks such as food webs. Understanding this merging of networks at edges will be essential for scaling up our knowledge of community responses to, and ecological dynamics within, fragmented systems and natural ecotones at the landscape level. Ultimately, how interaction networks merge at habitat edges will determine whether habitat patches function as isolated networks, and the extent to which landscape permeability affects metacommunity and coevolutionary dynamics (Hagen *et al.* 2012).

Cross-habitat differences in interaction-network structure (Tylianakis *et al.* 2007), combined with spillover of consumers between adjacent habitats (Rand *et al.* 2006; Macfadyen and Muller 2013; Frost *et al.* 2015), strongly suggest that blending of species interactions at habitat edges may be important for linking food webs in space. Here we propose three hypothetical scenarios for how trophic interaction networks at habitat edges ('edge webs') may be assembled from source populations of potentially-interacting species in the two adjacent habitats (Fig. 1).

The first scenario (we call this a '*non-stick*' edge web) would occur if adjacent habitats do not share any species or interactions, in which case the edge would mark a clear division between the different habitat types in the composition of species and interactions (Fig. 1). The name (which takes an analogy from non-stick cookware) indicates a lack of

interaction among the two communities. The structure of the '*non-stick*' edge web would have clearly defined compartments (i.e. network modules), each of them representing a habitat type, as has been observed in seed-dispersal networks of the Canary islands (Nogales *et al.* 2015).

A second scenario would be that the networks of different habitats are closely connected through spillover (Frost *et al.* 2015) and compositional overlap of species. Under this hypothesis, the species and interaction composition of the edge web would be a simple mixture of those from the adjacent habitats. We call this the '*blended*' edge web hypothesis, and formulate it as the frequency of each pairwise interaction being proportionate to that in the two adjacent habitat types. The structure of the '*blended*' edge web would thus be predictable based on knowledge of the interactions that occur in each adjacent habitat, and easily modelled as a passive diffusion process.

Finally, differing responses of species to edges (Ewers and Didham 2008) may generate edge webs that are not a random subset of those species and interactions in either adjacent habitat, i.e. the alternative hypothesis to the '*blended'* hypothesis. For instance, trophic generalists may benefit from exploiting complementary resources in the two habitats (Wimp *et al.* 2011), and reach higher densities and prey consumption rates at the edge (Duelli *et al.* 1990; Rand *et al.* 2006). A higher proportion of generalists at edges would result in networks being more connected. Furthermore, even with no major change in species composition, network structure could be altered by changes in the abundance of consumers or resources due to spillover (Rand *et al.* 2006), altered abiotic conditions at edges (Didham and Lawton 1999; Ewers and Banks-Leite 2013), altered prey encounter rates due to differences in habitat structural complexity (Laliberte and Tylianakis 2010), and/or the formation of novel interactions (Fagan *et al.* 1999) due to the mixing of a few new species or changes in

conditions that facilitate potential interactions (Summers and Underhill 1996). Therefore, our third hypothesis, a '*hyper*' web, could occur if the mixing of species across the edge interface results in novel interactions or alters the frequency of existing interactions compared with those observed in the adjacent habitats. In this '*hyper*' web scenario, named for its analogy to the 'hyperdynamism' observed for some ecological processes at edges (Laurence 2002; Leidner *et al.* 2010), the resulting network structure within edge webs would differ systematically from that expected based on the adjacent habitat types.

To test these hypotheses, we sampled quantitative host-parasitoid food webs across large-scale edge gradients from remnant native forest into exotic plantation forests in New Zealand. We used community-wide changes in quantitative species interaction networks to demonstrate that habitat edges affect the assembly of interactions within a community, and produce novel food-web structures that could not be predicted simply by combining webs from adjacent habitats.

METHODS

Study region and sampling

We sampled host-parasitoid food webs at eight sites in the Nelson and Marlborough region of New Zealand (172°47'E to 173°53'E and 41°12'S to 41°33'S). Each site was established along a large-scale (ca. 1 km) edge gradient from native southern beech forest (*Nothofagus spp.*, Fagaceae) into exotic *Pinus radiata* plantation forest. All plantation forests were closed-canopy monocultures, between 19-26 years old, such that vegetation structure was similar between forest types. The minimum distance between sites was at least 2.7 km (maximum distance 94.6 km), i.e. nearly three times the distance between sampling plots within an edge gradient. The understory vegetation of both forest types shared a range of native shrubs, ferns and juvenile trees. Some exotic shrub species also made up part of the understory of both forest types, but were more abundant in the plantation forest.

At each site, we established four sampling plots: one in the interior of each forest type (500 m from the mid-point location at the edge, i.e. the last row of pine trees of the plantation forest) and one immediately adjacent to the edge in each forest type (i.e. 10 m from the edge) (Fig. S1). Interior sampling plots were a minimum of 400-500 m from any other edge of the forest patch, to ensure that other edges adjacent to different habitats did not confound our treatments. At each site, we sampled one 50 x 2 m transect (parallel to the edge) in each sampling plot. Sampling was repeated once per month from December 2009 to February 2010, and from October 2010 to February 2011.

Along each transect, all plants up to a height of 2 m were beaten to dislodge insect herbivores. White collecting sheets (1 x 1 m) were placed under the plants prior to beating, and dislodged Lepidoptera larvae (caterpillars) were collected from these. In addition, at 5 m intervals along each transect (i.e., at 10 sampling points) the canopy of the nearest accessible tree was sampled by using a 9 m pole pruner to cut subcanopy branches, which were then beaten over the sheets. More details on the sampling procedure can be found in Peralta *et al.* (2014).

Herbivores were taken to the lab, identified to species or morphospecies (hereafter "species") and reared individually (in separate containers) under ambient conditions (16 °C, relative humidity of 60 % and a light rhythm of 16L:8D), until they either developed into adults or parasitoids emerged. Parasitoids were identified morphologically after their emergence, and males (which in some genera cannot be identified to species level using morphology) were identified using molecular techniques (see Appendix S1: Supplementary methods for details on morphological and molecular identification of specimens). See Table S1 for a list of the host and parasitoid species, and their abundances, sampled in this study.

Edge and interior webs

We pooled monthly samples into a single dataset for each of the 32 sampling plots, because individual sampling dates were not independent replicates of locations (edge vs. interior) or forest types (native vs. plantation), which were our primary treatments of interest, and also because sample sizes on each date were insufficient to allow robust time-series analysis. We also pooled samples from the two adjacent edge sampling plots (native side and plantation side of the edge) and from both interior sampling plots (native interior + plantation interior) per site, to form the edge and pooled-interior webs for each of the eight sites (hereafter 'edge web' and 'interior web' respectively).

'Non-stick' edge web hypothesis

To test whether edge webs might conform to a '*non-stick*' pattern, such that different habitats (native and plantation forests) form distinct compartments in edge webs, we identified modules (subsets of the web whereby species interact primarily with each other and little with species outside the module) formed by hosts and parasitoids of each edge web. Modules were identified using the findModules function (with 1000 iterations) from the lpbrim package (Poisot and Stouffer 2015) in the R environment (R Development Core Team 2014). If species were not interacting across two habitat types, the interactions forming each module would be expected to occur only in one of the habitats (either native or plantation forest), but not in both (Fig. 1 '*non-stick*' hypothesis).

To classify each interaction according to its presence in one or both forest types, we used information from all sampling plots. An interaction was assigned to a specific forest type if it had been sampled in at least one interior location of that forest type. We then counted in each edge web the number of modules containing interactions that were assigned to both forest types. If edge webs conformed perfectly to a '*non-stick*' pattern, we would expect them to contain modules formed by interactions assigned to only one forest type, whether native or plantation. Alternatively, the proportion of single-forest-type modules would be higher than the proportion of modules containing interactions assigned to both forest types and modules formed by the combination of interactions that

are found only in one of the forest types. Because there could be modules formed by interactions that only occur at edges, i.e. which do not occur in any of the interior forests, for testing the non-stick hypothesis we only considered modules that included at least one interaction that was also sampled in either of the forest interiors.

We performed a one-tailed binomial test to determine whether the probability of finding a module formed by interactions found in both forest types and/or formed by the combination of interactions that are found only in one forest type was equal to or greater than 0.5. This probability was calculated from the total number of modules with at least one interaction present in either or both interior forests, across the eight edge webs. Rejection of this null hypothesis would suggest that the majority of modules contained interactions from only one habitat type, conforming to a '*non-stick*' pattern.

'Blended' and 'hyper' edge web hypotheses

In addition to the '*non-stick*' hypothesis, we tested whether the structure of edge webs could be predicted simply by mixing species and interactions from the adjacent habitats (i.e. the interior web, which was generated by pooling interior native and interior plantation forest webs), which we called the '*blended*' web hypothesis (Fig. 1). Alternatively, the edge web could contain interactions or species that were absent from the interior of either habitat or have different interaction frequencies, and thereby exhibit a novel ('*hyper*' web) structure.

To determine whether the structure of the edge webs could be predicted from the interior webs, we compared the structure of empirical edge webs to that of simulated webs (hereafter 'null webs') generated by randomly subsampling from their respective interior webs at each site. This allowed us to determine whether the observed web structures matched what would be expected by random mixing of their constituent habitat webs ('*blended*' hypothesis). To generate the null webs for each site, we selected interactions from the interior webs of each site using the 'mgen' randomization algorithm in the netstat function in R (Vázquez *et al.* 2009), which allows interactions to be selected

according to a probability matrix while keeping the number of species constant (i.e. null webs have the same number of species as the interior web from which they were formed). The probability of an interaction (i.e. a parasitism event) from the interior webs being selected for the null web was proportional to that interaction's frequency of occurrence in the interior webs. This results in null webs having more realistic species degree and interaction frequencies, because these are derived from the distribution of degree and interaction frequencies observed in the interior habitats. This approach also means that interactions that were frequent in the interior habitats had a higher chance of being selected in the null webs, as would be expected by random mixing of the two adjacent webs.

When generating the null model, we constrained the null webs to have the same number of parasitism events as found in the edge webs (for each site), so that differences in food-web structure between empirical and null webs would not be an artefact of differences in the number of parasitism events observed in the interior vs. edge webs. Repeated assignment of parasitism events to the same pair of species generated the frequencies of each interaction in the null webs, such that null webs were quantitative with weighted links between species, as were the empirical edge webs. Only species that were present in the interiors could be selected for the null webs, so species richness of the interior web placed the limit on the richness of the null webs. We did not constrain our model by the number of species, as species richness did not differ significantly between edge and interior webs (Appendix S1). In addition, half of our sites presented webs with more species in the interiors, while the other half had more species in the edge webs, so there was no consistent difference in web size. Nevertheless, we conducted sensitivity tests to confirm that differences in the metrics between empirical edge and null webs were not related to differences in web size (Appendix S1).

To assess the differences in food-web structure between edge and null webs, we calculated quantitative connectance, generality, vulnerability, link density, interaction evenness and modularity food-web metrics (Bersier *et al.* 2002). The first four metrics refer to the extent to which species interact with many other species, with connectance describing the proportion of potential interactions in the web that are realized, generality and vulnerability denoting the mean number of host species interacting with each parasitoid species and vice versa, and link density defining the mean number of

links per species (in all cases weighted by interaction frequencies). Also, to have an idea of the energy flow within the web, we measured interaction evenness (how evenly distributed interactions are within a web), which is also known to vary across habitat types (Tylianakis *et al.* 2007), and modularity (the extent to which different parts of the network interact with each other), which has been shown to stabilize antagonistic food webs (Thebault and Fontaine 2010). We used quantitative versions of the metrics, which take into account species abundances and the strength of each trophic interaction (formulas of these metrics can be found in Bersier *et al.* 2002, Tylianakis *et al.* 2007, Stouffer *et al.* 2012), and have the advantage of being relatively insensitive to sampling effort compared to their qualitative counterparts (Banasek-Richter *et al.* 2004). These metrics were calculated using the 'networklevel' function in the bipartite package (Dormann *et al.* 2008) and the 'netcarto' function from the rnetcarto package (Doulcier and Stouffer 2015) for R.

The model generated a set of 9,999 null webs per sampled web and calculated their quantitative food-web metrics, returning the mean and 95 % confidence interval of each metric. We then compared the edge web metrics with those generated by the null models (for each site) and counted the number of edge webs (replicates) that differed significantly from the null expectations (i.e. that fell outside the 95% confidence interval of the null metric distribution). In order to plot standardised differences between edge web metrics and their null expectations, we calculated Z-scores by subtracting the mean null expectation of each metric from its corresponding empirical metric and dividing it by the standard deviation of the null distribution.

Because testing multiple edge webs (one per site) against their respective null webs creates a cumulative risk of Type I error, we used a Bernoulli process to calculate the probability of each test being significant by chance alone, given the number of webs tested (eight) and the number of tests performed (Moran 2003) (for details on the Bernoulli process see Appendix S1: Supplementary methods). In addition, our use of several metrics of web structure produced the same inflation of Type I error rate (with respect to our hypothesis that 'structure' itself is a random mixture). Therefore, we used the same approach of the Bernoulli process to determine the probability that all the significant results of tests performed over all metrics could have been significant by chance.

Mechanisms driving differences in food-web structure at edges

Differences in food-web structure between edge and interior webs (i.e. departures from the '*blended*' hypothesis) could be driven by differences in species composition between habitats, changes in parasitoid behaviour, such as their generalism in host use, and/or due to different interactions occurring in different habitats despite the same species being present, i.e. rewiring of interactions.

To determine whether the host and parasitoid species composition of edge and interior communities differed, we used permutational multivariate analyses of variance (permanova) (Anderson 2001). The response variables were dissimilarity in community composition of hosts and dissimilarity in community composition of parasitoids, which we compared across edge and interior habitats, using site as a random factor to account for the non-independence of edge and interior communities sampled at the same site. We used two dissimilarity measures because they differ in the emphasis they give to species presence-absence (Jaccard) vs. species relative abundances (Hellinger). These were obtained with the vegdist and distHellinger functions in the vegan (Oksanen *et al.* 2013) and topicmodels (Grün and Hornik 2011) R packages respectively. We used the adonis function of the vegan R package (Oksanen *et al.* 2013) to perform the permanova analyses.

Because generalist species can benefit from exploiting their full spectrum of potential hosts at habitat edges (Wimp *et al.* 2011), it could be possible that parasitoid species behave more like generalists (i.e. use a greater proportion of their host range) in edge webs. We therefore tested whether the normalised degree (number of host species attacked, normalised to account for differences in web size) of parasitoid species that were shared between edge and interior habitats differed between these habitats. We combined all the edge webs into a single regional edge web from which we calculated the parasitoids' normalised degree at edges, and also combined all the interior webs into a regional interior web from which we calculated the parasitoids' normalised degree in interior habitats. We calculated normalised degree by using the specieslevel function (Dormann 2011) of the bipartite R package (Dormann *et al.* 2008). We then used a linear mixed-effects model (lmm) with a gaussian error distribution to test whether the normalised degree of shared parasitoid species responded to

habitat type (edge vs. interior) as the predictor variable, with parasitoid species as a random factor.

An alternative hypothesis to explain any changes in web connectivity is that generalism of a given species does not change between edges and interiors, but rather that generalist species are more likely to occur at edges. We therefore tested whether the presence of parasitoid species in edge webs would be predicted by their normalised degree in the interior webs. To test this, we used a generalized linear mixed-effects model (glmm) with a binomial error distribution and presence/absence of each parasitoid species in the edge web of each site as the response variable. The interior web normalised degree of each parasitoid species was the predictor variable and site was included as a random factor. Because degree could be correlated with abundance (Vázquez *et al.* 2005), we ran the model a second time including each parasitoid species' abundance as a covariate. We also tested the effect of the covariate itself by removing degree as a predictor. Between these three models (with degree-only, degree and abundance, and abundance-only as predictors), the model with the lowest Akaike information criterion (AIC) value was selected as the best fitting model (Burnham and Anderson 2002).

We used the lmer and the glmer functions of the lme4 R package (Bates *et al.* 2015) for the gaussian and binomial models respectively and tested for their corresponding assumptions (normality and homoscedasticity, and overdispersion). All analyses were conducted in the R 3.0.2 environment (R Development Core Team 2014).

Finally, overall food-web structure is a coarse descriptor, as the same structure can be achieved with different species interacting. Therefore, we explored whether differences between edge and interior webs were driven by different species interacting vs. the same species interacting differently (i.e. rewiring). To partition these sources of interaction dissimilarity, we used a measure of web dissimilarity developed by Poisot *et al.* (2012). This index (calculated from binary webs) can be partitioned into dissimilarity explained by differences in community composition and dissimilarity of

interactions between shared species. We used the betalink function (with Whittaker dissimilarity index) from the betalink R package (Poisot 2015) to calculate the different components of dissimilarity between edge and interior webs.

RESULTS

We sampled 99 different plant species, from which we collected and successfully reared 5,743 Lepidoptera individuals from 90 species. From 49 of these herbivore species, 719 parasitoids from 60 species emerged (Table S1, Fig. S3-S4). We constructed eight host-parasitoid edge webs and eight interior webs. The number of species that formed the edge (30 ± 8 [mean ± SD]) and interior webs (32 ± 3), i.e. interaction-network size, did not differ significantly ($Z = 0.800$, $P = 0.421$). Edge webs had on average 12 ± 4 host and 19 ± 4 parasitoid species, while interior webs had 11 ± 2 host and 17 ± 2 parasitoid species.

'Non-stick' edge web hypothesis

Edge webs had 8 ± 2 [mean ± SD] modules, with 36 % ± 22 % formed by interactions that only occurred at edges, while the remaining 64 % ± 22 % of them contained interactions that were present either in native interior forests, plantation interior forests or both (Fig. 2, S2). From this majority of modules, 49 % ± 14 % of them were formed by interactions that were found both in native and plantation forests (Figs 2-3, S3). In contrast, 51 % ± 14 % of these edge web modules were formed either by interactions only present in native or by interactions only present in plantation forests. The probability of finding modules that violated the non-stick hypothesis (i.e. those formed by interactions present in both habitats and/or a combination of interactions present in only one forest type) was not lower than 0.5 (binomial one-tailed test: $p = 0.500$), hence rejecting the *"non-stick"* hypothesis.

'Blended' and 'hyper' edge web hypotheses

Despite the high proportion of interactions shared by the two forest types (Fig. 3), which would tend to suggest a certain degree of blending of community compositions at edges, the quantitative web metrics for empirical edge webs could often not be predicted by simply mixing interactions from the interior habitats (Fig. 4). Empirical values of vulnerability, linkage density, interaction evenness and modularity frequently differed significantly from null expectations, thus rejecting the *'blended'* web hypothesis in favor of the *'hyper'* web hypothesis. These differences between edge and null webs were not related to differences in the number of species forming the webs (Appendix S1, Fig. S2, Table S2). For instance, edge webs tended to have more links per species (linkage density), potentially because hosts were attacked by more parasitoid species (higher vulnerability), and this elevated connectivity occurred across modules, which could lead to less modular edge webs (Fig. 4). In spite of multiple tests, there was a very low probability that these significant results would have all arisen by chance (the probability calculated using a Bernoulli process was lower than 0.05; Table S3). In contrast, only one or two out of eight edge webs differed from null expectation in their connectance and generality (Fig. 4), which could plausibly have arisen by chance (Bernoulli probability > 0.05).

Mechanisms driving differences in food-web structure at edges

The rejection of the '*blended*' hypothesis could be explained by several factors such as changes in species composition between edge and interior habitats, different behaviour of the species (e.g. changes in realised generalism), and/or new interactions occurring at habitat edges.

We found that host composition did not change significantly between edge and interior webs, either when taking into account just the presence-absence of species (Fig. 5a, Table S4) or when incorporating species abundance (Fig. S5, Table S4). Conversely, there were significant differences in parasitoid composition, both when considering species relative abundances (Fig.S5) and not (Fig. 5b, Table S4). Despite the significant differences in parasitoid composition between edge and interior habitats, 67% (33 out of 49) of the parasitoid species found in edge webs were also present in interior

habitats. Among these shared parasitoid species, we found no differences in their normalised degree between edge and interior habitats ($t = 0.584$, $P = 0.563$), suggesting that species do not change the number of host species they attack at the edge. This suggests that changes in parasitoid composition, rather than behavioural increases in parasitoid generalism, were likely responsible for driving the different web structure at edges. This conclusion was further supported by evidence that the more generalist parasitoids from the interior habitats were significantly more likely to be present at the edge (i.e. the normalised degree of parasitoid species in the interior habitats significantly predicted their occurrence at edges: $Z = 3.007$, $P = 0.003$; Fig. 6, Table S5). However, the influence of parasitoid generalism could not be disentangled from the collinearity between normalised degree and parasitoid abundance (more abundant parasitoids were observed to engage in more interactions), so when parasitoid abundance was included as a covariate in the model (best fitting model), it became the only explanatory variable that significantly affected the presence of parasitoid species at the edge ($Z = 1.992$, $P = 0.046$; Table S5). Nevertheless, when normalised degree was removed from the model, parasitoid abundance no longer determined the presence of parasitoid species at the edge ($Z = -0.269$, $P = 0.787$; Table S5), and this was also the worst fitting model, suggesting that degree might have some influence on determining parasitoid species presence in the edge.

In cases where interactions differed between edges and interiors, the contribution of species dissimilarity to this web dissimilarity (i.e. dissimilarity of interactions due to species turnover) was 44.2 % ± 19.6 (Fig. 6), whereas over half of the difference between edge and interior webs (55.8 % ± 19.6 %) was due to rewiring, such that species shared between edges and interiors interacted differently.

DISCUSSION

Although there is widespread evidence for the spillover of prey and consumers between adjacent ecosystems (Rand *et al.* 2006; Vacher *et al.* 2008; Johnson *et al.* 2011; Macfadyen and Muller 2013), the implications of this for species interactions have not previously been addressed beyond simple

changes observed in pair-wise interactions (McGeoch and Gaston 2000; Ewers *et al.* 2013). Here, we show in the first direct test of edge effects on food-web structure, that the structure of the food webs at habitat edges could not be predicted from a simple random draw of interactions from the adjacent interior habitats. Instead, edges exhibited a novel web structure (our '*hyper*' web hypothesis, Fig. 1), with frequently higher than expected complexity (density of links per species and number of parasitoid species that attack each host species) at the interface of two habitats.

Even though we found that there were modules formed by interactions that were present only in one forest type (either native or plantation), a higher proportion (65 %) of modules was formed by a mixture of interactions present in both forest types. Hence, the edge did not represent a clear division among adjacent habitats, allowing for the rejection of the *'non-stick'* hypothesis. However, species and interactions can differ in their susceptibility to habitat edge characteristics (Laurence 2002; Ries *et al.* 2004; Ewers and Didham 2008), such that adjacent habitats with greater contrast in their vegetation structure, reduced permeability of the edge to species dispersal (Stamps *et al.* 1987), or little to no overlap in species composition, could still generate a '*non-stick*' edge web. Thus, our example of two habitats with high species overlap and structural similarity provided the greatest likelihood of blending in edge webs.

Despite finding considerable blending of species composition in the lower trophic level, which was congruent with previous findings that interior habitat species can be prevalent at edges (Ewers and Didham 2008), the interaction structure of edge webs could not be predicted by simply combining the interactions of adjacent interior habitats. Measures of the extent to which species interact with others, such as linkage density and vulnerability, tended to be consistently higher than expected at edges, and this increased connectivity linked food-web modules together and unified the food webs of the two adjacent habitats. Consequently, we observed that modularity was lower in habitat edges, compared with the null expectation based on the interior habitats.

Food-web structure can affect the persistence and resilience of communities (Thébault and Fontaine 2010), and have strong impacts on the rate and variability of ecosystem functions, such as

biological control (Peralta *et al.* 2014; Tylianakis and Binzer 2014). In our study, the increased number of parasitoid species attacking the same host species at edges provides functional redundancy, which has been shown using the same dataset here to reduce the spatial variability of parasitoid-host interactions (Peralta *et al.* 2014) and elsewhere to increase parasitism rates (Tylianakis *et al.* 2006). Because variability in the risk of being parasitized creates refuges for hosts (Hochberg and Hawkins 1992), increasing availability of edges with spatially-stable attack rates could remove these refuges, which are necessary for supporting parasitoid diversity (Hochberg and Hawkins 1992).

Furthermore, lower than expected modularity of edge webs under the ´*blended*´ model, could be related to lower species persistence in these communities (Thébault and Fontaine 2010). This could be an extreme disadvantage for species in edge communities, in particular due to the frequent disturbances associated with managed habitats. Modularity in food webs has been shown to buffer the propagation of extinctions and increase species persistence (Thebault and Fontaine 2010; Stouffer and Bascompte 2011), suggesting that the reduced modularity in our edge webs could allow faster propagation of disturbances in the community as well as decreasing species survival in the edge.

Differences in parasitoid species composition and rewiring of interactions seem to explain the non-random structure of food webs at habitat edges. In particular, the most generalist parasitoid species from forest interiors were more likely to be found at edges, potentially benefiting from exploitation of complementary resources in the adjacent habitats (Wimp *et al.* 2011). In addition, over half of the differences in edge vs. interior webs were due to shared species interacting differently, which implies that conditions at edges lead generalist parasitoids to more frequently encounter or use a different subset of their potential host niche. Rewiring of interactions in food webs has also been observed in aquatic systems under pressures such as climate change (Blanchard 2015) and drought (Lu *et al.* 2016), reinforcing the idea that various environmental changes can strongly modify species interactions (Tylianakis *et al.* 2008).

Land-use change is increasing the prevalence of habitat edges (Ries *et al.* 2004; Haddad *et al.* 2015), and juxtaposing natural communities against anthropogenic assemblages with which they may

share little recent evolutionary history (Hagen *et al.* 2012). The non-random mixing of interactions we observed at edges suggests that this habitat exerts strong pressures over communities, making them more susceptible to cascading effects and potentially diminishing species persistence. Greater focus placed on fully understanding the rules that govern food-web structure at edges could help in the prediction of food web assembly at the landscape level.

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Appendix S1. Supplementary methods, tables and figures.

FIGURE LEGENDS

Figure 1: Schematic representation of the hypothetical webs formed at the interface of two habitats (in this example, one native and one managed). White represents species and interactions occurring in the native habitat, black those that occur in the managed habitat. Grey species co-occur in both habitat types and striped interactions (in the *'hyper'* web) represent new interactions that do not occur in either habitat. The dashed line between habitats delimits the centre of the edge. Below are three hypotheses for the merging of food webs at edges: the '*non-stick'* edge web represents the scenario whereby adjacent habitats do not share species; '*blended'* webs occur when edge webs are formed by a mixture of species and interactions from the two habitats, whereby interaction frequencies are proportional to those in the adjacent habitats; '*hyper'* webs occur when species interact differently at habitat edges, changing the food-web structure.

Figure 2: Example of an edge web (site 3) showing parasitoid and host species, upper and lower bars respectively, color-coded according to the module to which they belong. Links between host (below) and parasitoid species (above) represent interactions, color-coded according to whether the interaction is also present in native forest interiors (white), in plantation forest interiors (black), in both forest interiors (grey) or if only occur at edges (striped).

Figure 3: Proportion of modules of each edge web formed by interactions that are only present in 'One habitat' (native or plantation forests) or 'Both habitats'. Numbers at the top of each bar indicate number of modules in each web that have at least one interaction that is also present in the interior habitats.

Figure 4: Standardized difference (Z score) between the empirical values of quantitative food-web metrics (a-f) for edge food webs vs. the mean value of the null distribution for '*blended'* models across the 8 sites. * = empirical value significantly different from the null expectation ($\alpha = 0.05$).

Figure 5: Species community composition across edge and interior habitats. Principal Coordinate analyses (PCO) showing (a) host and (b) parasitoid community compositions (based on the Jaccard distance metric) across edge (black) vs. interior (white) habitats. Sites close together in multivariate space have similar species composition. Percentages between brackets in PCO1 and PCO2 axes indicate the percent total variation explained.

Figure 6: Dissimilarity of interactions between edge and interior webs due to species turnover (grey) and dissimilarity of interactions established between species present in both edge and interior food webs (black).
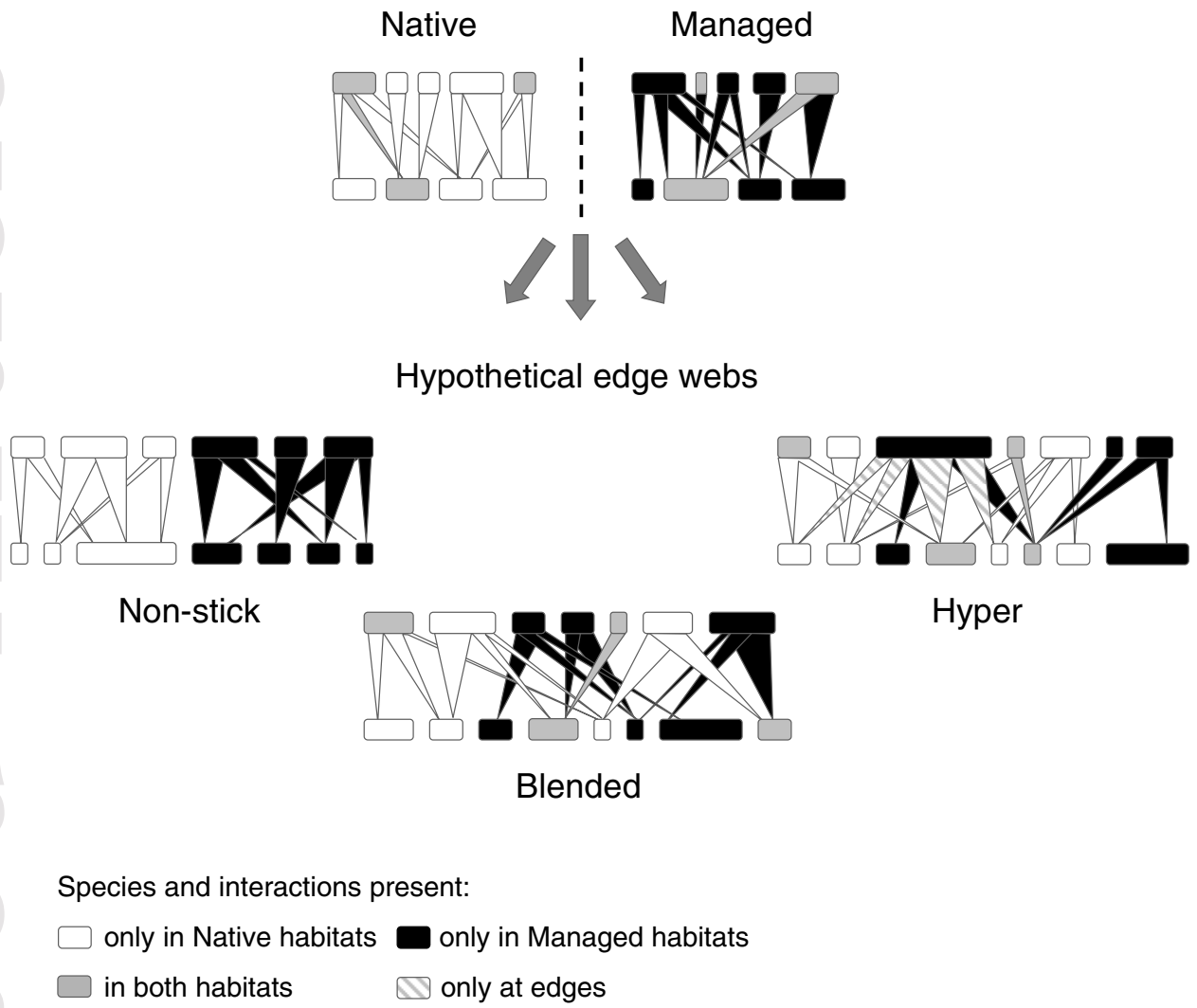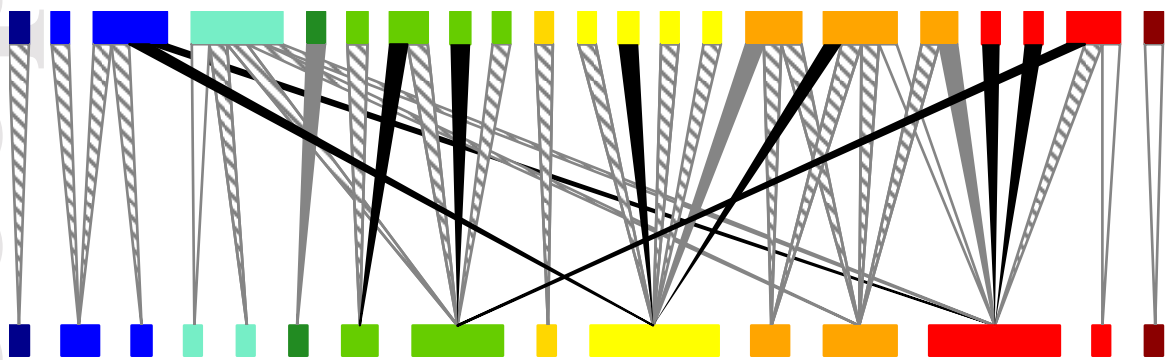
Figure 1

Native

Managed
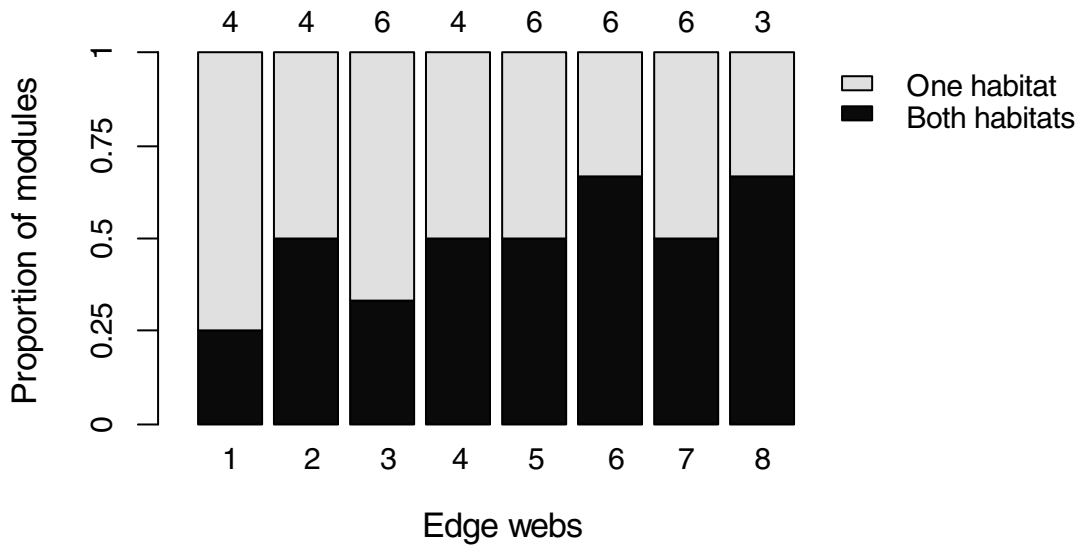
Hypothetical edge webs

Non-stick

Hyper

Blended

Species and interactions present:

☐ only in Native habitats   ■ only in Managed habitats

▨ in both habitats   ▧ only at edges

Figure 2

Figure 3

Figure 4

Figure 5

a) Host

b) Parasitoid

Figure 6

□ Due to species turnover
■ Due to rewiring of interactions