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Habitat loss alters the architecture of plant–pollinator interaction networks

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Abstract. Habitat loss can have a negative effect on the number, abundance, and composition of species in plant–pollinator communities. Although we have a general understanding of the negative consequences of habitat loss for biodiversity, much less is known about the resulting effects on the pattern of interactions in mutualistic networks. Ecological networks formed by mutualistic interactions often exhibit a highly nested architecture with low modularity, especially in comparison with antagonistic networks. These patterns of interaction are thought to confer stability on mutualistic communities. With the growing threat of environmental change, it is important to expand our understanding of the factors that affect biodiversity and the stability of the communities that provide critical ecosystem functions and services. We studied the effects of habitat loss on plant–pollinator network architecture and found that regional habitat loss contributes directly to species loss and indirectly to the reorganization of interspecific interactions in a local community. Networks became more highly connected and more modular with habitat loss. Species richness and abundance were the primary drivers of variation in network architecture, though species composition affected modularity. Theory suggests that an increase in modularity with habitat loss will threaten community stability, which may contribute to an extinction debt in communities already affected by habitat loss.

Key words: community; generalist; landscape; modularity; mutualism; nestedness; specialist; stability.

INTRODUCTION

Habitat loss remains a significant threat to biodiversity. The loss of habitat in a landscape can isolate patches of suitable habitat, thereby reducing dispersal rates and altering the spatial distribution of resources (Kareiva 1987, Andren 1994, Holyoak et al. 2005). A decline in biodiversity often follows. Communities of plants and their pollinators, along with the services they provide, can be highly dependent on the amount of natural habitat in the surrounding landscape (Steffan-Dewenter et al. 2002, Bommarco et al. 2010). Reduced visitation frequency and seed set can accompany pollinator loss when there is little nearby natural habitat (Steffan-Dewenter and Tscharntke 1999, Kremen et al. 2002, 2004). Through changes in the number or abundance of species, habitat loss may also affect the network of interspecific interactions in a community. The topology, or architecture, of these ecological networks may be crucial for community stability (May 1973, Dunne et al. 2002, Bastolla et al. 2009). Although we have a general understanding of the negative effects of habitat loss for biodiversity (reviewed by Harrison and Bruna 1999, Fahrig 2003), little is known about how habitat loss can affect ecological interaction networks and plant–pollinator networks in particular (Fortuna and Bascompte 2006).

The architecture of plant–pollinator interaction networks can be described by the density and pattern of interactions using metrics such as connectance, nestedness, and modularity. Connectance is the density of interactions in a network, or the proportion of all possible interactions in a network that are actually realized. Nestedness describes a pattern of interaction where specialists (species with few interaction partners) interact with a subset of the species with which more generalized species interact. Modularity, or compartmentalization, describes the degree to which interactions occur more frequently within modules than between modules (Newman and Girvan 2004).

There is a longstanding association between the architecture of ecological networks and community stability (e.g., May 1972). Syntheses of published networks have found that mutualistic networks, like plant–pollinator networks, exhibit a relatively high degree of nestedness and connectance, but low modularity, especially in comparison with networks of antagonistic interactions, such as food webs (Bascompte et al. 2003, Thébault and Fontaine 2010). Theory suggests that these general characteristics of mutualistic networks can impart stability and allow more species to persist in a community (Okuyama and Holland 2008, Bastolla et al. 2009, Thébault and Fontaine 2010).

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Greater nestedness and connectance may enhance stability by allowing competitors to facilitate one another by sharing mutualistic partners, thereby reducing the negative effects interspecific competition (Bastolla et al. 2009). Greater modularity in a network, on the other hand, reduces the opportunity for facilitation and may therefore have a destabilizing effect (Thébault and Fontaine 2010).

Though some network research has been conducted on the effect of local variation in habitat quality (e.g., Tylianakis et al. 2007, Weiner et al. 2011), and how habitat loss can result in the non-random loss of interactions from networks (Aizen et al. 2012), we know very little about how variation in species richness, abundance, and composition driven by habitat loss will affect network architecture. Research on the process of network assembly and disassembly may inform predictions. Network assembly is thought to follow a process called preferential attachment (Barabasi and Albert 1999), in which relative specialists entering a network will preferentially establish interactions with more generalized species (Olesen et al. 2008). The resulting interaction asymmetry (specialists tending to interact with generalists) helps generate network nestedness (Bascompte et al. 2003, Vazquez and Aizen 2004). On the other hand, mutualistic networks may disassemble through a process where specialists, being more vulnerable to extinction, are lost from a network before more generalized species (Fortuna and Bascompte 2006, Weiner et al. 2011). If network disassembly (e.g., as a result of habitat loss) follows a strict process whereby specialists are preferentially lost from a network, only the most generalized species will remain in low-diversity networks. Given these assumptions, species loss should alter network architecture by reducing nestedness and modularity because the few remaining species in a low-diversity network will form a well-connected network of generalists.

In this study, we sampled 15 plant–pollinator communities occurring in the same type of local habitat but spanning a gradient in the extent of habitat loss in the surrounding landscape. We hypothesize that the amount of habitat in the surrounding landscape will affect local community structure (the number, abundance, and composition of species), and that community structure will determine how species interact (i.e., network architecture: connectance, nestedness, and modularity). The amount of focal habitat in the landscape will therefore have only an indirect effect on network architecture, mediated by its direct effect on local community structure. We combine structural-equation modeling and null model analyses to examine the direct and indirect effects of habitat loss on community structure and network architecture. Specifically, we ask (1) how does habitat loss affect local community structure, (2) how does community structure effect network architecture, and (3) what are the consequences of habitat loss for network architecture? We then discuss potential implications of habitat loss for community stability.

METHODS

Study area and sampling

We focused our study on plant–pollinator networks within sandhill habitat in north Florida, USA. Sandhill is a fire-maintained upland pine savannah, characterized by an open canopy of longleaf pine (*Pinus palustris*) and an understory of turkey oak (*Quercus laevis*), wire grass (*Aristida stricta*), and a highly diverse mix of herbaceous plants (photo in Appendix A). Sandhill is a xeric subtype of the imperiled longleaf pine forest ecosystem that was once the dominant forest type of the southeastern coastal plain (Myers and Ewel 1990). Timber harvesting has reduced longleaf pine forests to an estimated 5% of its former distribution (Outcault and Scheffield 1996). Sandhill habitat in the Apalachicola National Forest, the location of our study, has also been reduced and fragmented by timber harvesting, making the region ideal for studying the effects of forest habitat loss on local plant–pollinator interaction networks.

Fifteen 60 × 60 m sites, all within sandhill habitat, were selected to span a gradient in sandhill habitat loss in the surrounding landscape (Fig. A2). We used a Landsat-derived land cover classification (Stys et al. 2004) within a GIS to guide the site selection process. The final selection was made after ground truthing to standardize local habitats within a small range of variation (e.g., time since last fire and the density of understory growth) and ensuring that sites were separated by at least 1 km. Though other types of natural habitat are present in some of the landscapes, the non-sandhill habitat surrounding sites is mainly comprised of anthropogenically modified habitats such as clearcut, shrubby secondary growth, or commercial pine plantations, and is almost all former sandhill habitat (Fig. A2). Within the study area these anthropogenically modified habitats harbor few floral resources, especially in comparison with sandhill habitat. Thus, we interpret the effects of a reduction in the area of sandhill habitat in the surrounding landscape as the effects of habitat loss.

Fifteen plant–pollinator interaction networks, one network per site, were analyzed based on standardized observations of flower-visiting insects. Observations were conducted at each site monthly, June through September 2010, capturing pollinator activity and plant flowering periods across most of the growing season. During each of the four observation periods, which excluded rainy days, three to four individuals of all plant species in flower at each site were observed for approximately 25 minutes each. These 879 hours of observations were recorded on video using five high-definition (HD) camcorders (Canon Vixia HF M31; Canon, Melville, New York, USA). From the HD video, we identified flower visitors to morphospecies and to the lowest taxonomic resolution possible with the help of a reference collection made during a pilot study the prior year. The use of HD video was very effective in that it allowed for observation without the potentially disturbing presence of a person. Moreover, the permanent record of each visit could be error checked so that identifications could be revised long after returning from the field. Our HD video provided for the reliable identification to morphospecies of more than 99% of visitors. The very few visitors that could not be identified with confidence, as well as those that did not appear to be foraging for pollen or nectar resources, were removed from the analysis. We are confident that the vast majority of morphospecies represent individual taxonomic species and that lumping of morphologically similar species and splitting of polymorphic species was rare. Although visitors may vary in pollination efficiency, we hereafter refer to all flower visitors as pollinators.

We estimated the relative abundance of all plant species in flower during each observation period by identifying and counting individuals within six 3 × 60 m belt transects at each site. The sum of the abundances of each monthly round of sampling was used as a local estimate of relative plant abundance. Percent canopy cover was quantified using a spherical densitometer.

Deriving explanatory variables

The effect of habitat loss on local plant–pollinator communities was examined using the proportion of sandhill habitat within a 600 m radius of each site center. To determine the spatial extent of our landscape analysis, we examined the effect of the total area of sandhill habitat on local species richness within radii of 300–1000 m in 100-m increments. This range of spatial extents, or landscape sizes, is biologically relevant since it encompasses the upper limit of the foraging range of many pollinators (e.g., Gathmann and Tscharntke 2002, Greenleaf et al. 2007). A 600 m radius explained the highest proportion of variation in total species richness, suggesting that plants and pollinators in our study system perceive and interact with features in the landscape on this scale (Thies et al. 2003).

Species richness for each network was estimated as the count of all species, plants and pollinators, across all sampling periods. Abundance is represented by our estimate of plant abundance. Plant abundance is correlated with the number of pollinator visits ($r = 0.65$, $P = 0.012$), which has been used as a surrogate for pollinator abundance (e.g., Vazquez et al. 2007). The combined composition of the plant and pollinator species comprising each network was quantified using non-metric multidimensional scaling (NMDS; Bray-Curtis distance) of presence–absence data. Because a single-axis solution was highly correlated with species richness and abundance, we specified a two-axis solution, then rotated the first axis to maximize the correlation with species richness, and used the second axis to represent species composition independent of total species richness and abundance. This measure of species composition is positively correlated with the number of Coleoptera and Apoidea species and negatively correlated with the number of Papilionoidea species. All community and network metrics were calculated in R 2.15.2 (R Development Core Team 2012).

Each of the 15 interaction networks was analyzed as an incidence matrix, with plants in P rows and flower visitors in V columns. Elements of a $P \times V$ incidence matrix **A** indicate the presence of a link, or interaction, between a plant and pollinator if element $a_{ij} = 1$ and the absence of an interaction if $a_{ij} = 0$. For each matrix, we quantified three indices of network architecture: connectance, nestedness, and modularity.

Connectance was calculated as $C = \sum a_{ij}/(P \times V)$. Nestedness was quantified using the NODF metric (Almeida-Neto et al. 2008), which calculates nestedness based on the degree of overlap of interactions and decreasing marginal totals of rows and columns of **A**. We calculated NODF using the R package vegan (Oksanen et al. 2012). The modularity M of a network is defined as the proportion of interactions that occur within modules minus the expected proportion of such interactions (Newman and Girvan 2004). Modularity is calculated as

$$M = \frac{1}{2L}\sum_{i,j} a_{ij} - \frac{k_i k_j}{2L}\delta_{m_i m_j}$$

where L is the number of links, or interactions, in the network, a_{ij} is an element of **A**, k is the species' degree, and δ is Kronecker's delta. The parameter $\delta_{m_i m_j} = 0$ if species i and j belong to the same module m, otherwise $\delta_{m_i m_j} = 1$. However, in order to calculate a network's modularity, one must first classify and determine membership within modules. Methods for module detection use search strategies in order to find the classification that optimizes M. We employed three different module detection algorithms: the edge betweenness, walktrap, and fastgreedy algorithms in the R package igraph (Csardi and Nepusz 2006). For each network, we used the classification that maximized M. Both nestedness and modularity were scaled to vary from 0 to 100, with 100 being maximally nested and modular.

Structural-equation modeling

We used structural-equation modeling (SEM) to analyze the direct and indirect pathways linking the amount of focal habitat in the landscape, community structure (species richness, abundance, and composition), and network architecture (connectance, nestedness, and modularity). Because community and network metrics are often correlated and indirect effects may follow multiple pathways, SEM is ideal for examining alternative hypotheses for the factors that govern network architecture (Grace 2006). We hypothesized that the amount of focal habitat in the landscape directly affects the total species richness, composition, and plant abundance, and these in turn affect the pattern and density of interactions within the network (Fig. 1A). The amount of focal habitat in the landscape therefore has only an indirect effect on connectance, nestedness, and modularity, mediated by direct effects on species richness, abundance, and composition. Canopy cover was included as a covariate to help explain local (i.e., within-site) environmental variation. Correlations, as opposed to direct causal pathways, were specified between richness and abundance, and between nestedness and modularity. SEM requires linear pathways between variables, and although species richness generally has a non-linear relationship with connectance (Laurienti et al. 2011) and nestedness, the relationships are approximately linear for the range of values in our study. We used an Akaike information criterion (AIC)-based stepwise model selection process to remove nonsignificant paths and compare alternative models of pathway structure.

Our sample size is considered small for SEM. To assess the final model we used a bootstrapping procedure with 10 000 samples as described in Ievers-Landis et al. (2011). Bias in path coefficients due to low sample size (or multivariate non-normality) can be detected if an observed estimate differs substantially from the mean of the bootstrapped samples. The bias, or the difference between the estimates of the original and bootstrap samples, is considered sufficiently small if the standard error of the bias is less than that of the bootstrap means for each estimate (Ievers-Landis et al. 2011). To further assess the validity of the models as a whole, we used the Bollen-Stine bootstrapped χ^2 test to determine whether our observed models were significantly different from 10 000 bootstrap samples. SEM analyses, including the bootstrapping procedures, was performed using AMOS v5.0.1 (Arbuckle 2003).

Null model analysis

Nestedness and modularity can depend on the species richness and connectance of a network. In order to directly compare networks that differ in these values, we standardized nestedness and modularity relative to a null expectation. This null model analysis also allows us to determine whether a network is significantly more or less nested or modular than expected by chance. We used a null model that maintains the number of species in each trophic level and network connectance but randomizes the interactions between species in a probabilistic fashion based on each species' degree, or number of interaction partners (Bascompte et al. 2003, Thébault and Fontaine 2010). Relative nestedness was calculated for each network as $(N - \bar{N}_r)/\sigma_{N_r}$, where N is the observed value of nestedness, and $\bar{N}_r$ and σ_{N_r} are the mean and standard deviation, respectively, of the nestedness values for the 1000 replicate randomized networks. Relative modularity was calculated in the same way.

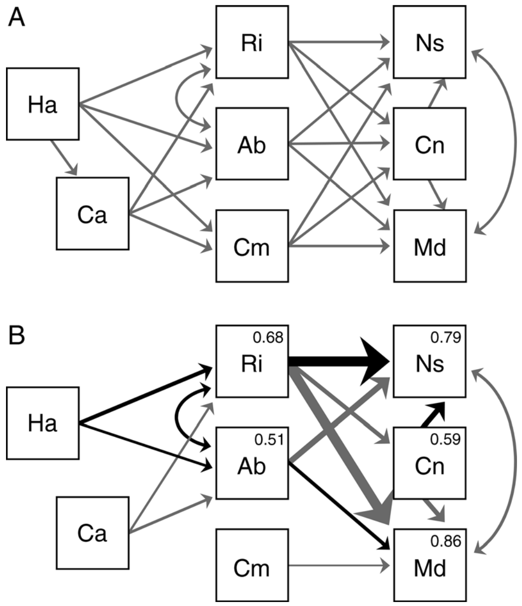

FIG. 1. (A) Initial pathway structure and (B) final structural-equation model (SEM). Ha is the proportion of sandhill habitat in the surrounding landscape. Ca is the percent canopy cover within sites. Ri and Cm are the combined species richness and composition, respectively, of plants and pollinators. Ab is the relative abundance of plants. Cn, Ns, and Md are connectance, nestedness, and modularity as described in *Methods*. Straight single-headed arrows indicate direct causal pathways, whereas curved double-headed arrows indicate unresolved correlations. In the final model (B), arrow widths are scaled to standardized path coefficients/correlations (see Appendix C: Table C1 for values). Black arrows are positive effects, and gray are negative. Single-headed arrows indicate a direct effect, whereas curved double-headed arrows indicate correlations. R^2 values are indicated in the upper right corner of variable names where appropriate. Note that because composition is derived from a nonmetric multidimensional scaling (NMDS) analysis, the sign of its effect on modularity is arbitrary.

RESULTS

Across all sites, we observed 76 plant species belonging to 59 genera in 22 families, with a range of 10–38 plant species per site. Plants were visited by 151 species of pollinator, identified to morphospecies, belonging to at least 35 families in 4 orders, and ranging from 23 to 94 morphospecies (hereafter referred to as species) per site. Lists of the plant and pollinator species are in Appendix B: Tables B1 and B2.

Analyses of land cover data combined with video and field observations revealed that the number and composition of non-sandhill habitat types in the surrounding landscape had no significant effect on combined species richness, composition, or abundance (results not shown). Instead, and as intended by our study design, the amount of sandhill habitat in the landscape had the strongest effect on local communities, indicating that habitat loss and not surrounding habitat heterogeneity is an important driver of local community change in the region.

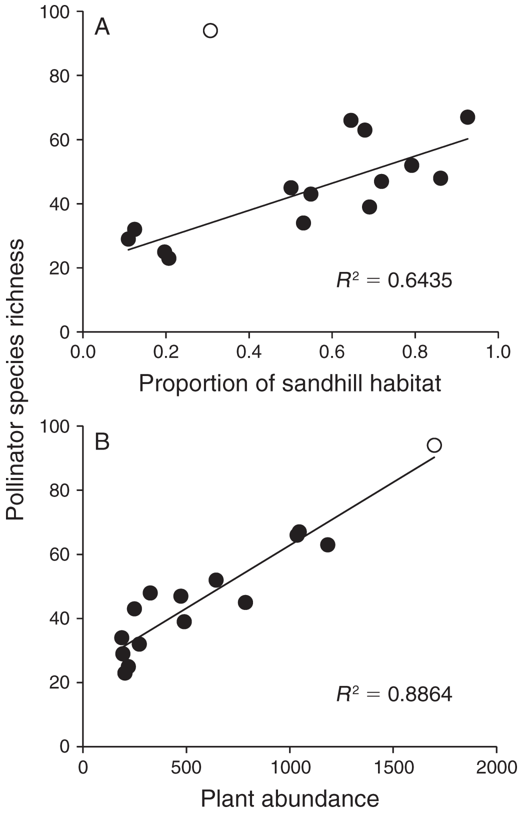

FIG. 2. Relationship between pollinator species richness and (A) the proportion of sandhill habitat in the landscape or (B) the abundance of plants in flower. The fit (solid line) in panel A is shown after removing the outlier (open circle) from the analysis. (B) Pollinator species richness is highly correlated with plant abundance. Therefore, the artificially high plant abundance at this site may explain the high pollinator species richness.

We found that, after excluding one outlier site, combined species richness decreased with habitat loss in the surrounding landscape (Fig. 2A). The outlier site had extremely high pollinator species richness despite being positioned within a relatively degraded landscape (only 30.7% sandhill habitat; Fig. 2A); it had the highest pollinator species richness of all sites, which appears to be driven by the strong relationship between the abundance of flowering plants and pollinator species richness (Fig. 2B). The high abundance of plants in flower at that site was later determined to be a result of native ground cover seeding as part of a previous habitat restoration program. This site was therefore removed from the following analyses. However, the high pollinator richness at this site points to a possible mechanism for the effect of habitat loss on local networks, to which we will return in *Discussion*.

Though habitat loss has a generally negative effect on combined plant and pollinator species richness, a closer look reveals that the effect of habitat loss varied among taxonomic groups. Species richness in the two most speciose plant families in our study, Asteraceae and particularly Fabaceae, decreased with habitat loss (Fig. 3A). However, there was no relationship between richness and habitat loss for the remaining plant families combined, all represented by relatively few species. Similarly, species richness within the two most speciose orders of pollinator in our study, Hymenoptera and Lepidoptera, was more strongly affected by habitat loss than in Coleoptera and Diptera (Fig. 3B).

SEM analysis

The model selection process using absolute nestedness and modularity resulted in a path diagram (Fig. 1B) that

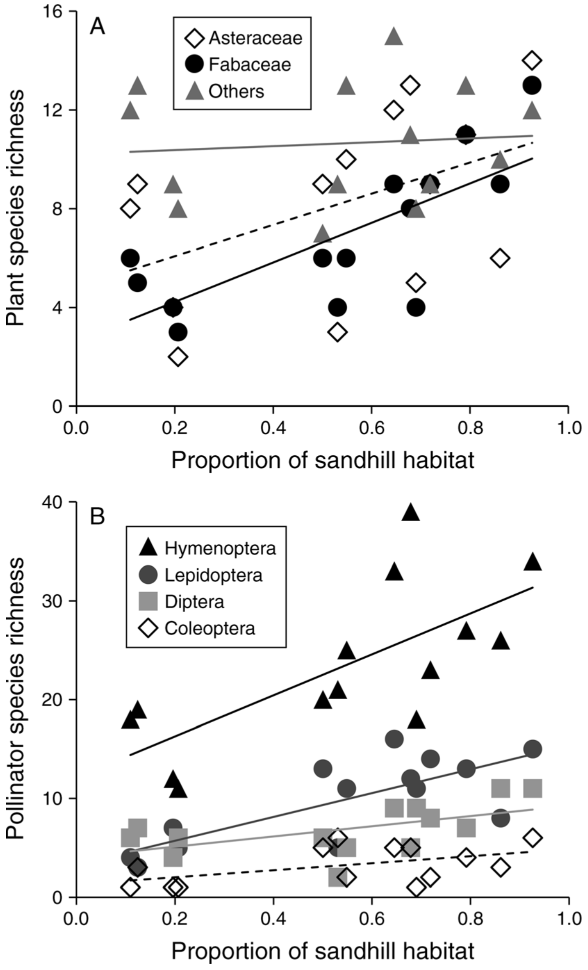

FIG. 3. The effect of habitat loss (i.e., a lower proportion of sandhill habitat) varies among taxonomic groups. (A) For plants, habitat loss had the strongest effect on the species richness of the most speciose families: Asteraceae ($P = 0.093$, $R^2 = 0.217$; dashed line) and Fabaceae ($P = 0.002$, $R^2 = 0.549$; black line), but had no effect on the combined richness of the remaining families ($P = 0.757$; gray line). (B) For pollinators, habitat loss had the strongest effects on the richness of the more speciose Hymenoptera ($P = 0.005$, $R^2 = 0.500$; black line) and Lepidoptera ($P = 0.002$, $R^2 = 0.580$; dark gray line), with weaker effects on species richness within the orders Diptera ($P = 0.040$, $R^2 = 0.307$; light gray line) and Coleoptera ($P = 0.063$, $R^2 = 0.260$; dashed line).

fits the data very well ($\chi^2 = 8.2977$, df = 14, $P = 0.8732$) and is substantially improved relative to the initial model depicted in Fig. 1A (ΔAIC = 8.39). Moreover, results of the bootstrapping procedure show that the model fit is unbiased. For both the unstandardized and standardized path coefficients, each of the observed estimates are very similar to the mean bootstrapped estimates, and the standard error of the bias was always much lower than that of the mean bootstrapped estimate (Appendix C: Table C1). Bollen-Stine bootstrapped χ^2 test results demonstrated that our model was not significantly different from the bootstrap samples ($P = 0.8997$), indicating that the model as a whole was highly stable. This method is effective for assessing the stability of models, such as ours, for which samples capture the full range of variation in the variable of interest (i.e., habitat loss; Ievers-Landis et al. 2011).

The final SEM, using absolute network metrics (Fig. 1B), indicates that the total area of sandhill habitat in the landscape affects local community structure and indirectly affects network architecture. Estimates of path coefficients/correlations and associated significance levels are presented in Table C1. Estimates of standardized total and indirect effects along with bootstrapped P values are presented in Table C2. More sandhill habitat in the landscape was associated with greater species richness and abundance, but had no effect on species composition. The effects of habitat loss on species richness and abundance translated to significant indirect effects on connectance ($P = 0.001$) and modularity ($P = 0.011$), but not nestedness ($P = 0.265$). Variation in species richness, followed by abundance, had the strongest effects on network architecture; simple univariate analysis suggests that species richness and abundance are both negatively related to connectance and modularity, but uncorrelated with nestedness. However, after accounting for the correlation between richness and abundance, species richness had a positive effect on nestedness, and negative effects on connectance and modularity. Abundance, on the other hand, had a negative effect on nestedness, a positive effect on modularity, and no effect on connectance. Species composition did not affect nestedness or connectance but had a significant effect on modularity. Connectance had a positive effect on nestedness, but a negative effect on modularity.

Sandhill canopies displayed a characteristically open structure, ranging from 30.6% to 57.4% cover. Although local canopy cover had significant direct effects on species richness and abundance, it had no indirect effect on nestedness and modularity ($P = 0.602$ and 0.376, respectively), though it did have a positive indirect effect on connectance ($P = 0.019$). Local canopy cover was not related to the amount of sandhill habitat in the surrounding landscape ($P = 0.462$), suggesting that local and landscape habitat variation can have independent effects on community structure and network architecture.

The null model analysis, which preserved network size and connectance and probabilistically maintained degree distributions, showed that seven out of the 15 networks were significantly more nested and two networks were more modular than expected by chance ($P < 0.05$). Two networks were marginally less modular than expected by chance ($P < 0.10$). There was no effect of habitat loss on relative nestedness or relative modularity, suggesting that though habitat loss alters local community structure in ways that affect network architecture, the indirect effects on nestedness and modularity are not different from the null expectation (Fig. 4).

Discussion

We investigated the effects of habitat loss on species richness, abundance, and composition, and the resulting effects on the network of interactions between plants and pollinators. Our results demonstrate that habitat loss in the surrounding landscape can not only reduce species richness and abundance but can indirectly alter the way species interact in a local community. We found that species loss, associated with a reduction of suitable forest habitat in the surrounding landscape, is correlated with reduced nestedness and increased modularity in plant–pollinator interaction networks.

Of the community descriptor variables we examined (richness, abundance, and composition), species richness had the strongest influence on network architecture. We expected nestedness to decrease with species richness based on the idea that specialists are more vulnerable to extinction than generalists (Fortuna and Bascompte 2006, Weiner et al. 2011) and their extinction would reduce network interaction asymmetry, a key property of nestedness (Bascompte et al. 2003, Vazquez and Aizen 2004). Accordingly, low-diversity networks should be comprised mainly of well-connected generalists, and therefore also exhibit low modularity. The positive relationship we found between species richness and network nestedness followed our expectation (Fig. 1B). However, modularity increased with species loss (Fig. 1B) even though connectance, which has a negative effect on modularity, was greatest in the smallest networks. This does not appear to be a result of there being a very small number of well-connected modules at species-poor sites. Though the number of modules in a network does decrease with species loss ($r = 0.793$, $P < 0.001$), networks with the fewest species were still comprised of at least 6 modules. It is possible that shifts in interaction partners, which can follow changes in the local number and abundance of species (Inouye 1978), are important for modularity. Theory suggests that shuffling of interaction partners is important for network architecture (Zhang et al. 2011), though it is rarely examined.

Structural-equation modeling is useful for analyzing systems where covariation among model variables can mask underlying patterns, because it allows one to

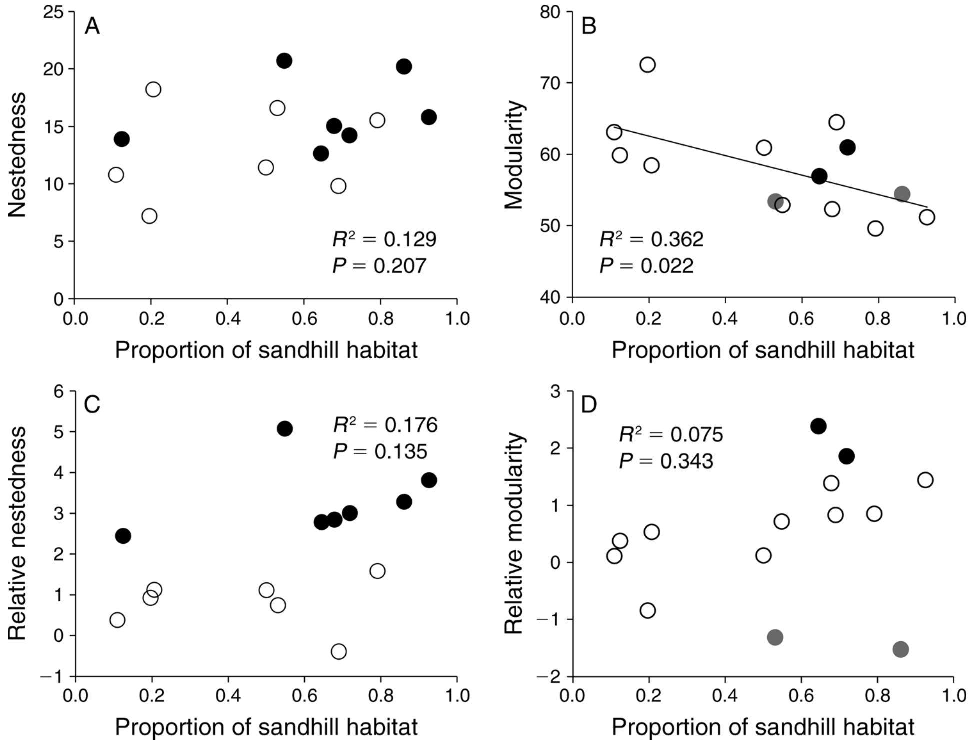

FIG. 4. Relationship between habitat loss and (A) nestedness and (B) modularity. (C) Relative nestedness and (D) relative modularity do not vary with habitat loss. Open circles are not significantly different from the null expectation. Solid circles are either significantly more ($P < 0.05$; black) or less ($P < 0.10$; gray) nested/modular than the null expectation.

consider multiple network metrics and partition effects among multiple pathways (Thébault and Fontaine 2010). A look at some of the individual paths in our SEM reveals relationships not evident in simple univariate analysis. The strong effects of richness and abundance on network architecture, for instance, are not revealed unless correlations among variables are taken into account. Our SEM also illustrates why habitat loss does not have a significant indirect effect on nestedness, even though it has significant direct effects on richness and abundance. A strong positive indirect effect on nestedness through species richness is canceled out by negative indirect effects through the abundance and connectance pathways.

Species composition was not related to connectance or nestedness, suggesting that these metrics are much more dependent on the number and abundance (in the case of nestedness) of species than on the identity of species in a network. Composition did, however, affect modularity. Modules are thought to form in ecological networks as a result of niche organization and resource contiguity (Guimera et al. 2010). Therefore, if competitive interactions vary with the particular combination of species present in a local network (the number of Apoidea, Coleoptera, and Papilionoidea species in this case) realized niche structure may be affected. For example, the presence of a competitor may provoke a pollinator to forage on less-preferred floral resources that occur in different modules than more-preferred flowers, thereby affecting modularity.

The one outlier site (Fig. 2) sheds light on possible mechanisms by which habitat loss affects local species richness and thereby network architecture. For example, two possible mechanisms are that (1) pollinators may not be able to reach isolated patches (i.e., sites with little focal habitat in the landscape) or (2) pollinators may be able to reach isolated patches but choose not to visit patches with few floral resources. Even though the excluded site was relatively isolated, the high pollinator species richness observed in the presence of artificially high plant abundance suggests that pollinators can reach isolated habitats if rewards are abundant (Fig. 2). Moreover, the network at the outlier site was highly nested, suggesting that seeding with native plants as part of habitat restoration programs in fragmented landscapes may not only attract pollinators from surrounding areas, but that the plant and pollinator communities will form functional and robust networks.

In this study, habitat loss was not only associated with reduced species richness and abundance but also increased modularity. Theory suggests that network architecture can be critical for the stability of networks (Okuyama and Holland 2008, Bastolla et al. 2009, Thébault and Fontaine 2010). For example, Thébault and Fontaine (2010) found that species persistence, or the number of species remaining at equilibrium, was strongly and negatively affected by network modularity. A loss of network stability may contribute to a form of extinction debt (Tilman et al. 1994) by placing communities in degraded landscapes at even greater risk of further species loss.

Conclusions and future directions

Habitat loss in the greater landscape may contribute not only to local species loss, but indirectly to the reorganization of interspecific interactions in a local community. We found that interaction networks become more modular and connected with habitat loss in communities of plants and their pollinators. Variation in the number and abundance of species was the primary driver of variation in connectance, nestedness, and modularity, though species composition was also important for modularity. These changes in network architecture may have consequences for community stability; a reduction in stability associated with high modularity (Bastolla et al. 2009, Thébault and Fontaine 2010) may contribute to an extinction debt at sites that have already suffered biodiversity loss.

Habitat loss affected the taxonomic groups in our study in different ways (Fig. 3). It is also likely that the unique characteristics of these groups influence their contribution to network architecture. For example, the most diverse group of pollinators in this study, Hymenoptera, was the most susceptible to habitat loss (Fig. 3B). This has important conservation implications, given the global importance of Hymenoptera for pollination services (Klein et al. 2007). The importance of species richness for network nestedness, suggests that exploring the interactions between individual taxonomic groups' responses to habitat loss and their contributions to network architecture will be useful for making predictions about effects of land use changes on community structure in different types of habitats.

To our knowledge, this is the first study to examine empirically the effects of habitat loss on plant–pollinator network architecture (but see Aizen et al. 2012). General properties of networks have been discovered through syntheses of published networks (reviewed by Bascompte and Jordano 2007), but to complement and expand on these syntheses, additional empirical studies are needed. It will be particularly important to examine multiple networks within the same regional species pool to determine how ecologically driven variation in local richness and composition affects network architecture (e.g., Albrecht et al. 2010, Fründ et al. 2010, Weiner et al. 2011). A deeper understanding of the effects of spatially dependent processes on network architecture will help clarify mechanisms of network assembly and disassembly as well as improve our understanding of the processes that allow for stable networks capable of providing reliable ecosystem services.

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LITERATURE CITED

Aizen, M. A., M. Sabatino, and J. M. Tylianakis. 2012. Specialization and rarity predict nonrandom loss of interactions from mutualist networks. Science 335:1486–1489.

Albrecht, M., M. Riesen, and B. Schmid. 2010. Plant–pollinator network assembly along the chronosequence of a glacier foreland. Oikos 119:1610–1624.

Almeida-Neto, M., P. Guimaraes, P. R. Guimaraes, R. D. Loyola, and W. Ulrich. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117:1227–1239.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366.

Arbuckle, J. L. 2003. AMOS 5.0.1. AMOS Development Corporation, Spring House, Pennsylvania, USA.

Barabasi, A. L., and R. Albert. 1999. Emergence of scaling in random networks. Science 286:509–512.

Bascompte, J., and P. Jordano. 2007. Plant–animal mutualistic networks: the architecture of biodiversity. Annual Review of Ecology, Evolution, and Systematics 38:567–593.

Bascompte, J., P. Jordano, C. J. Melian, and J. M. Olesen. 2003. The nested assembly of plant–animal mutualistic networks. Proceedings of the National Academy of Sciences USA 100:9383–9387.

Bastolla, U., M. A. Fortuna, A. Pascual-Garcia, A. Ferrera, B. Luque, and J. Bascompte. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458:1018–1020.

Bommarco, R., J. C. Biesmeijer, B. Meyer, S. G. Potts, J. Poyry, S. P. M. Roberts, I. Steffan-Dewenter, and E. Ockinger. 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. Proceedings of the Royal Society B 277:2075–2082.

Csardi, G., and T. Nepusz. 2006. The igraph software package for complex network research. InterJournal, Complex Systems 1695.

Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecology Letters 5: 558–567.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Fortuna, M. A., and J. Bascompte. 2006. Habitat loss and the structure of plant–animal mutualistic networks. Ecology Letters 9:278–283.

Fründ, J., K. E. Linsenmair, and N. Blüthgen. 2010. Pollinator diversity and specialization in relation to flower diversity. Oikos 119:1581–1590.

Gathmann, A., and T. Tscharntke. 2002. Foraging ranges of solitary bees. Journal of Animal Ecology 71:757–764.

Grace, J. B. 2006. Structural equation modeling and natural systems. Cambridge University Press, Cambridge, UK.

Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153:589–596.

Guimera, R., D. B. Stouffer, M. Sales-Pardo, E. A. Leicht, M. E. J. Newman, and L. A. N. Amaral. 2010. Origin of compartmentalization in food webs. Ecology 91:2941–2951.

Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22:225–232.

Holyoak, M., M. A. Leibold, and R. D. Holt, editors. 2005. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, Illinois, USA.

Ievers-Landis, C. E., C. J. Burant, and R. Hazen. 2011. The concept of bootstrapping of structural equation models with smaller samples: an illustration using mealtime rituals in diabetes management. Journal of Developmental and Behavioral Pediatrics 32:619–626.

Inouye, D. W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. Ecology 59:672–678.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator–prey interactions. Nature 326:388–390.

Klein, A. M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B 274:303–313.

Kremen, C., N. M. Williams, R. L. Bugg, J. P. Fay, and R. W. Thorp. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. Ecology Letters 7:1109–1119.

Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences USA 99:16812–16816.

Laurienti, P. J., K. E. Joyce, Q. K. Telesford, J. H. Burdette, and S. Hayasaka. 2011. Universal fractal scaling of self-organized networks. Physica A: Statistical Mechanics and its Applications 390:3608–3613.

May, R. M. 1972. Will a large complex system be stable? Nature 238:413–414.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

Myers, R. L., and J. J. Ewel, editors. 1990. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

Newman, M. E. J., and M. Girvan. 2004. Finding and evaluating community structure in networks. Physical Review E 69:1–16.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2012. vegan: Community Ecology Package. Version 2.0-5. http://cran.r-project.org/web/packages/vegan/index.html

Okuyama, T., and J. N. Holland. 2008. Network structural properties mediate the stability of mutualistic communities. Ecology Letters 11:208–216.

Olesen, J. M., J. Bascompte, H. Elberling, and P. Jordano. 2008. Temporal dynamics in a pollination network. Ecology 89:1573–1582.

Outcault, L. W., and R. M. Scheffield. 1996. The longleaf pine forest: trends and current conditions. Resource Bulletin SRS-9. USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA.

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies, and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83:1421–1432.

Steffan-Dewenter, I., and T. Tscharntke. 1999. Effects of habitat isolation on pollinator communities and seed set. Oecologia 121:432–440.

Stys, B., R. Kautz, D. Reed, C. Keller, and A. Davis. 2004. Florida vegetation and land cover—2003. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida, USA.

Thébault, E., and C. Fontaine. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. Science 329:853–856.

Thies, C., I. Steffan-Dewenter, and T. Tscharntke. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. Oikos 101:18–25.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65–66.

Tylianakis, J. M., T. Tscharntke, and O. T. Lewis. 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. Nature 445:202–205.

Vazquez, D. P., and M. A. Aizen. 2004. Asymmetric specialization: a pervasive feature of plant–pollinator interactions. Ecology 85:1251–1257.

Vazquez, D. P., C. J. Melian, N. M. Williams, N. Blüthgen, B. R. Krasnov, and R. Poulin. 2007. Species abundance and asymmetric interaction strength in ecological networks. Oikos 116:1120–1127.

Weiner, C. N., M. Werner, K. E. Linsenmair, and N. Blüthgen. 2011. Land use intensity in grasslands: changes in biodiversity, species composition and specialisation in flower visitor networks. Basic and Applied Ecology 12:292–299.

Zhang, F., C. Hui, and J. S. Terblanche. 2011. An interaction switch predicts the nested architecture of mutualistic networks. Ecology Letters 14:797–803.

Supplemental Material

Appendix A

Habitat and study site information (*Ecological Archives* E094-250-A1).

Appendix B

Plant and pollinator species lists (*Ecological Archives* E094-250-A2).

Appendix C

Supplementary structural-equation model results (*Ecological Archives* E094-250-A3).