Community-level demographic consequences of urbanization: an ecological network approach

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Summary

1. Ecological networks are known to influence ecosystem attributes, but we poorly understand how interspecific network structure affect population demography of multiple species, particularly for vertebrates. Establishing the link between network structure and demography is at the crux of being able to use networks to understand population dynamics and to inform conservation.

2. We addressed the critical but unanswered question, does network structure explain demographic consequences of urbanization?

3. We studied 141 ecological networks representing interactions between plants and nesting birds in forests across an urbanization gradient in Ohio, USA, from 2001 to 2011. Nest predators were identified by video-recording nests and surveyed from 2004 to 2011.

4. As landscapes urbanized, bird–plant networks were more nested, less compartmentalized and dominated by strong interactions between a few species (i.e. low evenness). Evenness of interaction strengths promoted avian nest survival, and evenness explained demography better than urbanization, level of invasion, numbers of predators or other qualitative network metrics. Highly uneven networks had approximately half the nesting success as the most even networks. Thus, nest survival reflected how urbanization altered species interactions, particularly with respect to how nest placement affected search efficiency of predators.

5. The demographic effects of urbanization were not direct, but were filtered through bird–plant networks. This study illustrates how network structure can influence demography at the community level and further, that knowledge of species interactions and a network approach may be requisite to understanding demographic responses to environmental change.

Key-words: birds, demography, evenness, exotic plants, invasive species, nest success, predation, rural, urban development

Introduction

The need to understand and predict ecological responses to anthropogenic disturbance and land-use change has never been greater. Population and community responses to anthropogenic disturbance are usually quantified in terms of diversity, density and demography, with the latter widely regarded as the gold standard. Yet studies often report variation in demographic parameters across sites or years that proves difficult to explain directly with environmental variables (Grosbois *et al.* 2008; Schaub, Jako-ber & Stauber 2011; Salewski, Hochachka & Fiedler 2013). This difficulty may arise, in part, because studies seldom capture species interactions that can shape population processes across a wide range of spatial and temporal scales. A mechanistic understanding of the ecological and evolutionary consequences of anthropogenic change requires study of the drivers and outcomes of species interactions.

Although species interactions have traditionally been studied using pairwise approaches, species interact within the context of ecological communities that contain many species interacting directly or indirectly. These multispecies interactions have the potential for synergistic or antagonistic effects, and hence are difficult to understand or predict based on pairwise interactions (Strauss & Irwin

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2004). Ecological networks provide a powerful alternative approach to holistically examine the drivers and outcomes of species interactions (Bascompte & Jordano 2007; Bascompte 2009; Hagen *et al.* 2012). Network structure is already known to mediate ecosystem attributes, including community stability and ecological services (Bastolla *et al.* 2009). While reproductive consequences of individual-based networks of plants and pollinators (Gómez, Perfectti & Jordano 2011) and parasitism rates among multispecies networks of wasps and bees (Tylianakis, Tscharntke & Lewis 2007) have been recently described, we poorly understand the multispecies demographic consequences of interspecific network structure. Because demography underlies ecological and evolutionary responses, this link is key to elucidating how networks shape communities and selective environments.

Here, we assessed (1) how the structure of ecological networks changed with urbanization and (2) to what degree network structure explained the demographic consequences of that disturbance. Urbanizing landscapes were used as models to understand how shifts in resources and species composition influence interactions, as network structure may be affected by habitat modification (Albrecht *et al.* 2007; Tylianakis, Tscharntke & Lewis 2007; Gagic *et al.* 2011; Geslin *et al.* 2013; Lohaus, Vidal & Thies 2013; Spiesman & Inouye 2013) and invasive species (Aizen, Morales & Morales 2008; Spotswood, Meyer & Bartolome 2012). One of the most striking ways that urbanization influences forest ecosystems in our study area is that it promotes invasion by Amur honeysuckle, *Lonicera maackii*, an exotic woody shrub frequently planted as an ornamental in yards (Borgmann & Rodewald 2005). Although it differs architecturally and phenologically from native plants at our sites, honeysuckle is actively preferred as a nesting substrate by many birds nesting in our system (Leston & Rodewald 2006). However, nests in honeysuckle are at greater risk of depredation and therefore have lower probability of surviving and producing young than nests in native plants (Borgmann & Rodewald 2004), especially early in the breeding season when the majority of nests are placed in honeysuckle (Rodewald, Shustack & Hitchcock 2010). Our familiarity with these known and documented changes in bird and plant communities along a rural–urban gradient led us to hypothesize that networks of interactions between nesting birds and plants would be altered by urbanization in ways that impacted avian demography, as measured by nest survival. Specifically, we predicted that (1) urban networks would be dominated by strong interactions between nesting birds and a few exotic plants, resulting in networks that were less compartmentalized, less even, and by virtue of the super-dominant invader, more nested than rural networks, and (2) reductions in evenness would reduce avian nest survival because the simple nesting environment would improve the search efficiency of predators (Fig. 1).

Materials and methods

FIELD MONITORING

Study sites

Bird–plant interactions were studied in 19 mature riparian forests in Ohio, USA (Table 1). Forests (115–565 m wide) were located along a rural-to-urban gradient in landscapes that shared similar land-use history as well as amount and spatial configurations of natural areas. Landscapes in our system therefore differed primarily in the dominant land use (agriculture or urban) within the matrix. Building densities ranged from 10 to 727 buildings km^{-2}. The amount of urbanization was described within a 1-km radius area centred on each study site because the 1-km scale is known to be strongly associated with bird communities in our system (Rodewald & Bakermans 2006), is commonly used in conservation efforts and far exceeds average territory size of birds breeding at our sites.

As part of a complementary study, an index of urbanization was created based on a principal components analysis of landscape metrics within 1 km based on recent digital orthophotographs (Rodewald & Shustack 2008). The first principal component (hereafter termed the 'urban index') explained 80% of the variation among sites and was positively associated with number of buildings (0·92), per cent cover by roads (0·94), pavement (0·90) and lawn (0·88), but negatively associated with per cent cover by agriculture (−0·83). Rural landscapes were dominated by cropland, pasture, managed grassland and farms. Urban landscapes, in contrast, were dominated by residential areas, commercial development and roads.

An index of honeysuckle dominance was derived from vegetation measurements collected at four systematically located 0·04-ha plots at each site. The honeysuckle dominance index reflects the proportion of plots where honeysuckle was one of the three most abundant understorey woody plants at the site (Rodewald 2012). We were interested in this relative rather than absolute measure of honeysuckle at a site because our previous experience and research suggests that the impact of honeysuckle and the manner in which it affects the breeding birds is a function of dominance rather than abundance (Rodewald, Shustack & Hitchcock 2010; Rodewald 2012). Previous analyses showed that, with the exception of honeysuckle cover, forest structure among sites was comparable (Rodewald 2012).

Nest monitoring

From March to August 2001–2011, the fate of 4906 nests were monitored, represented by Northern Cardinal (*Cardinalis cardinalis*, n = 2924), American Robin (*Turdus migratorius*, n = 826), Acadian Flycatcher (*Empidonax virescens*, n = 563), Gray Catbird (*Dumetella carolinensis*, n = 285) Wood Thrush (*Hylocichla mustelina*, n = 232), Indigo Bunting (*Passerina cyanea*, n = 39) and Red-eyed Vireo (*Vireo olivaceous*, n = 37). Our trained field crews mapped locations of territorial birds at sites, thereby allowing us to determine densities of focal species, and we believe that differences in numbers of nests among species generally reflect the relative abundance of our focal species at sites. Acadian Flycatcher, Wood Thrush, Indigo Bunting and Red-eyed Vireos are urban-avoiding Neotropical migrants that occurred at low numbers at our sites, whereas the resident Northern Cardinal,
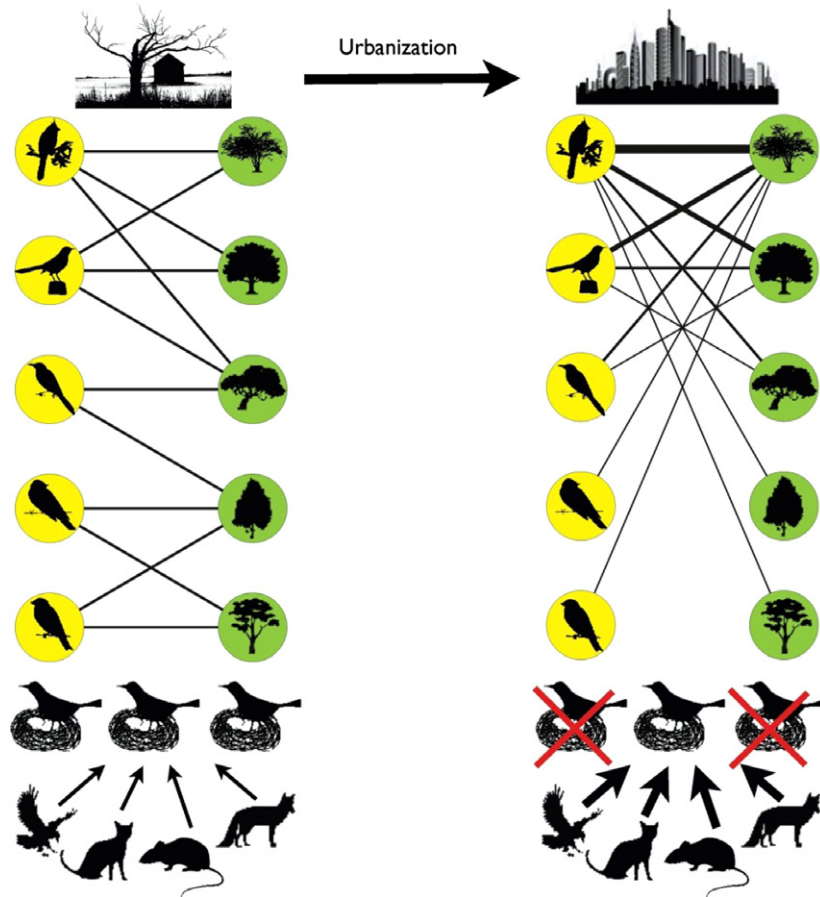
Fig. 1. The central hypothesis was that networks of interactions between nesting birds and plants would be altered by urbanization in ways that impacted avian demography, as measured by nest survival. Specifically, we predicted that (1) urban networks would be dominated by strong interactions between nesting birds and a few exotic plants, resulting in networks that were less compartmentalized, less even, and by virtue of the super-dominant invader, more nested than rural networks, and (2) these changes in network structure would reduce avian nest survival because the simple nesting environment would improve the search efficiency of predators.

temperate migrant American Robin and Neotropical migrant Gray Catbird were most abundant within urban landscapes and, with the exception of the catbird, bred in higher numbers at our urban than rural sites (Rodewald & Bakermans 2006).

Each nest was checked at 2- to 4-day intervals by viewing nest contents or by observing parental behaviour to track nest stage (e.g. onset of incubation behaviour) and locate young fledglings, when possible. To avoid exposing nests to predators as a consequence of our visits, we observed nests from as far a distance as possible (often >10 m), as briefly as possible, and from different routes each time. If a predator was observed in the vicinity, we delayed checking the nest. The plant species within which each nest was located was recorded.

Nest predators

Nest predators were surveyed at each site within 2-ha grids flagged at 50-m intervals at weekly intervals between May and July 2004–2011, totalling 10 surveys each year. During surveys, a trained observer systematically traversed the entire marked grid over an *c.* 45-min period between 0545 and 1000 and recorded all nest predators seen or heard.

To construct an ecologically meaningful measure of predator numbers, we determined which species were actual, not only

hypothetical, predators in our study system. This information came from a complementary study where nest predator species were identified at 99 incidents of nest predation that were video-recorded across the rural–urban gradient (Rodewald & Kearns 2011). While these data were insufficient to construct a plant–bird–predator network, the data allowed us to include only relevant species in our predator measure. There were 21 species of known predators at our sites, including corvids, raptors, squirrels, Common Grackles (*Quiscalus quiscala*), Brown-headed Cowbirds (*Molothrus ater*), raccoons (*Procyon lotor*), opossum (*Didelphis virginiana*) and domestic cats (*Felis catus*).

Because (1) detections of nest predator species were correlated and (2) most species were comparable in contribution to depredations with no single predator dominating the system (i.e. the most dominant predator still only accounted for 18% of depredations; Rodewald & Kearns 2011), detections were pooled across all known predator species within a 2-ha grid at each site in each year. Being based upon number of detections, the measure better represents the relative activity of predators than actual densities at sites.

ANALYSES

Daily nest survival rates were estimated for each species at each site in each year using logistic exposure models. The logistic

Table 1. Landscape composition surrounding 19 riparian forest study sites and the species for which nest survival was monitored in central Ohio, 2001–2011

	Forest width (m)	Number buildings	Proportion				Urban index
			Agriculture	Mowed	Paved	Road	
North Galena	135	34	0·36	0·05	0·01	0·01	−1·27
Pubhunt	194	210	0·32	0·08	0·01	0·01	−1·15
Prairie	148	58	0·47	0·12	0·03	0·02	−1·12
TNC	292	340	0·41	0·11	0·03	0·03	−0·96
Girlcamp	200	377	0·23	0·15	0·02	0·01	−0·82
Creeks	133	92	0·10	0·1	0·04	0·02	−0·71
South Galena	163	185	0·14	0·3	0·02	0·01	−0·57
Galena	277	360	0·15	0·22	0·04	0·02	−0·48
Elkrun	167	812	0·31	0·27	0·06	0·05	−0·16
Campmary	565	681	0	0·34	0·07	0·04	0·21
Woodside	104	1227	0·11	0·40	0·07	0·05	0·32
Rushrun	150	1611	0	0·41	0·09	0·06	0·75
Cherry	165	997	0·02	0·36	0·16	0·07	0·76
Kenny	126	1733	0	0·34	0·17	0·06	0·89
Bexley	133	1692	0	0·5	0·14	0·08	1·23
Casto	202	1776	0	0·42	0·20	0·08	1·25
Lou	156	2272	0	0·28	0·23	0·08	1·26
Big Walnut	115	2233	0	0·45	0·16	0·08	1·31
Tuttle	160	2285	0	0·34	0·30	0·09	1·61

exposure model is a generalized linear model that specifies a binomial error distribution and a link function similar to a logit link function adjusted for length of exposure for each nest (Shaffer 2004 in sas 9.2; SAS Institute, Inc., Cary, NC USA). The logistic exposure model estimates probability of nest survival (either 0 for failed nests or 1 for surviving nests) between each nest check, thereby eliminating potential bias due to different exposure periods. Predation was responsible for most nest failures (>95%), and we omitted the few nests whose failure was confirmed to be unrelated to predators (e.g. weather).

Over 10 years, 141 networks were quantified, comprised of a total of 71 plant species and seven species of understorey-nesting birds. Because several sites were added halfway through the study period (i.e. not monitored during the early years of the study), our sample of networks is fewer than the hypothetical maximum of 190. We considered the pattern of birds nesting on plants to be weighted bipartite networks in which a link between a plant and a bird species is established if that bird nests on that plant. To construct these networks, each site and year is represented by a separate matrix, where each row represents a plant species and each column represents a bird species. There is a link when a species of bird has placed a nest in a given plant species. The weight of the link is represented by the number of nests on the plant species. Five network statistics were computed for each site and year: nestedness, modularity, evenness for plants, evenness for birds and evenness for the whole network (see below for details). Nestedness measures how plants used by specialist birds for nesting are a subset of those plants used by the more generalist ones, and how birds nesting on specialist plants were a subset of those nesting on more generalist ones. Nestedness was based on the presence or absence of nests and calculated using the NODF measure (i.e. nestedness measure based on overlap and decreasing fills; Almeida-Neto *et al.* 2008; Guimarães & Guimarães 2006). Because NODF is dependent on network size and connectance, we relativized its value from what we could

expect from a similarly randomly built matrix (Bascompte *et al.* 2003). From a community perspective, generalist invaders can increase the amount of nestedness in a network because as the most connected species, they become the central nodes (Aizen, Morales & Morales 2008; Bartomeus, Vila & Santamaria 2008). Nestedness also may provide a buffer against secondary extinctions because if specialists are lost from a network, interactions among the remaining species will likely persist if the network is nested (Tylianakis *et al.* 2010). From the predator–prey standpoint of greatest interest to us, a more nested community should facilitate search efforts of predators given that certain plant–bird associations will be common to many, if not most, communities.

Modularity is a measure of how compartmentalized the network structure is in relation to a random occupancy pattern of plants by birds, that is, to what extent some groups of bird species tend to nest on some groups of plant species but not on plants associated with other groups. Modularity was computed in matlab (The MathWorks, Inc, Natick, MA USA) using the spectral algorithm adapted to bipartite graph (Barber 2007). Because modularity is partly a function of network size and connectance, we also calculated relative modularity as $(M - \overline{M}_{\text{random}})/\overline{M}_{\text{random}}$, where $\overline{M}_{\text{random}}$ was average modularity of the random runs. Compartmentalization is often thought to increase stability of networks because disturbances should spread more slowly, but empirical support for this idea is lacking (Tylianakis *et al.* 2010).

Evenness quantified the homogeneity or symmetry in interaction strength. This is similar to the standard Shannon diversity index, only applied to interactions rather than species and standardized by network size. We expected evenness to decline as sites were invaded by exotic shrubs that were used as nest substrate by many understorey-breeding birds in our study area. Moreover, we predicted that in more even sites (i.e. where nests are partitioned such that individuals and species nest in different locations), predators would have more difficulty locating nests than in sites with very asymmetric interactions. Evenness was

calculated for plants solely, birds solely and the complete network, respectively, using the following equations:

$$J_{\text{plant}} = \frac{-\sum\limits_{i=1}^{S_{\text{plant}}} p_i \log(p_i)}{\log(S_{\text{plant}})},$$

where S_{plant} is the number of plants and p_i is the proportion of nests in plant i.

$$J_{\text{bird}} = \frac{-\sum\limits_{i=1}^{S_{\text{bird}}} p_i \log(p_i)}{\log(S_{\text{bird}})},$$

where S_{bird} is the number of birds and p_i is the proportion of nests from bird i.

$$J_{\text{all}} = \frac{-\sum\limits_{i,j} p_{i,j} \log(p_{i,j})}{\log(S_{\text{plant}} \cdot S_{\text{bird}})},$$

where $p_{i,j}$ is the proportion of nests from bird j in plant i. These calculations were performed in R.

A different network was constructed for each year, and all analyses used repeated-measures regression with year as the repeated variable in PROC MIXED SAS 9.2 (SAS Institute, Inc.). For each site and year, daily nest survival rate was calculated by averaging across species. The relationship between evenness and nest survival was tested using a mixed model with site as a random-effects variable. An information-theoretic approach (Akaike Information Criterion; AIC) was used to compare the ability of network, habitat and landscape metrics to explain variation in nest survival among sites. AIC approaches allow one to evaluate the weight of evidence for multiple alternative hypotheses (a priori models), even in cases where predictor variables are correlated. Based on our previous research in the system, we hypothesized that avian nest survival might be influenced by relative intensity of urbanization within 1 km (i.e. the urban index), extent of invasion by the exotic shrub, *Lonicera maackii*, and the structure of the bird–plant network, as represented by qualitative (nestedness and modularity) and quantitative network measures (plant evenness, bird evenness, total network evenness).

Because predator numbers were positively correlated with urbanization ($r = 0.35$, $P = 0.0002$, $n = 108$) and negatively correlated with evenness of networks ($r = -0.417$, $P < 0.0001$, $n = 108$), we used the residuals of predator numbers regressed on evenness as our predator metric. The relationship between evenness and nest survival was expected to be partly a function of the number of predators at the site (e.g. evenness may only be important when predators are abundant, and unimportant when there are few predators). Therefore, with our reduced data set for which we had predator abundance data (108 networks), a mixed model was run with evenness and the residual of predator numbers as main effects and an evenness*predator residual interaction.

We also examined the possibility that the observed demographic outcomes of evenness were the consequence of shifts in the importance of certain predators. To do this, the proportions of recorded depredation events attributed to different predator groups (mesopredator, small mammal, raptor, corvid, small bird and snake) were calculated from the video-recorded depredation events. The predator identity data were analysed with a canonical correlation analysis to determine whether composition of the predator community was related to evenness of the network or to nesting success.

Results

As urbanization increased, the relative nestedness of bird–plant networks increased ($\beta = 0.09 \pm 0.036$ SE, $F_{1,139} = 6.79$, $P = 0.01$), though relative modularity was unchanged ($F_{1,139} = 0.85$, $P = 0.359$). In contrast, network size ($\beta = -1.03 \pm 0.30$ SE, $F_{1,139} = 12.20$, $P < 0.01$), absolute modularity ($\beta = -0.06 \pm 0.009$ SE, $F_{1,139} = 40.5$, $P < 0.01$) and evenness of interaction strengths, hereafter interaction evenness, decreased as landscapes surrounding forests urbanized (plant $\beta = -0.06 \pm 0.01$ SE, $F_{1,139} = 40.72$, $P < 0.01$; bird $\beta = -0.08 \pm 0.012$ SE, $F_{1,139} = 41.35$, $P < 0.01$; network $\beta = -0.04 \pm 0.006$ SE, $F_{1,139} = 34.05$, $P < 0.01$) (Fig. 2). Thus, urban networks were smaller, less compartmentalized, and were dominated by a few strong interactions compared with networks from rural landscapes.

Interaction evenness of the entire network was positively related to nest survival ($F_{1,139} = 4.90$, $P = 0.03$) and best explained variation in survival among sites, performing better than measures of urbanization or invasion (Table 2). The same pattern of model rankings persisted when the subset of sites for which we had predator abundance data ($n = 108$); predator numbers ranked as the lowest model ($\Delta AICc = 10$) and evenness for the entire network as the top-ranked model. The collective weight of evidence for evenness (for plant, bird and whole networks) was 0.914, providing strong support that evenness predicted nest success better than other metrics. Nest survival increased with interaction evenness for the network (95% confidence interval of $\beta_{\text{entire network}}$: 0.02–0.32) and showed similar trends for plants (95% confidence interval of β_{plants}: 0–0.19) and birds alone (95% confidence interval of β_{birds}: -0.01 to 0.16). This pattern held for both the resident and migratory birds in our system (Fig. 3).

When accounting for predator numbers with our reduced data set, daily nest survival remained positively related to evenness ($\beta = 0.151 \pm 0.086$ SE, $F_{1,104} = 3.04$, $P = 0.08$) but not significantly related to either predator numbers ($F_{1,104} = 2.29$, $P = 0.13$) or a predator*evenness interaction ($F_{1,104} = 1.56$, $P = 0.21$). Thus, the number of predators did not appear to drive the relationship that we observed between nest survival and network structure.

Shifts in the species composition of the predator community also are unlikely to drive observed patterns as the relative importance of different predator groups (e.g. mesopredator, raptor) was not significantly related to either evenness of networks (Wilks' Lambda $F_{6,5} = 0.28$, $P = 0.926$) nor to daily nest survival (Wilks' Lambda $F_{6,5} = 1.56$, $P = 0.322$). Likewise, when predator identifications (i.e. from nest videos) were pooled across years and sites to compare a rural to an urban predator–bird

network, the evenness scores were comparable with 17·86 for rural and 16·78 for urban.
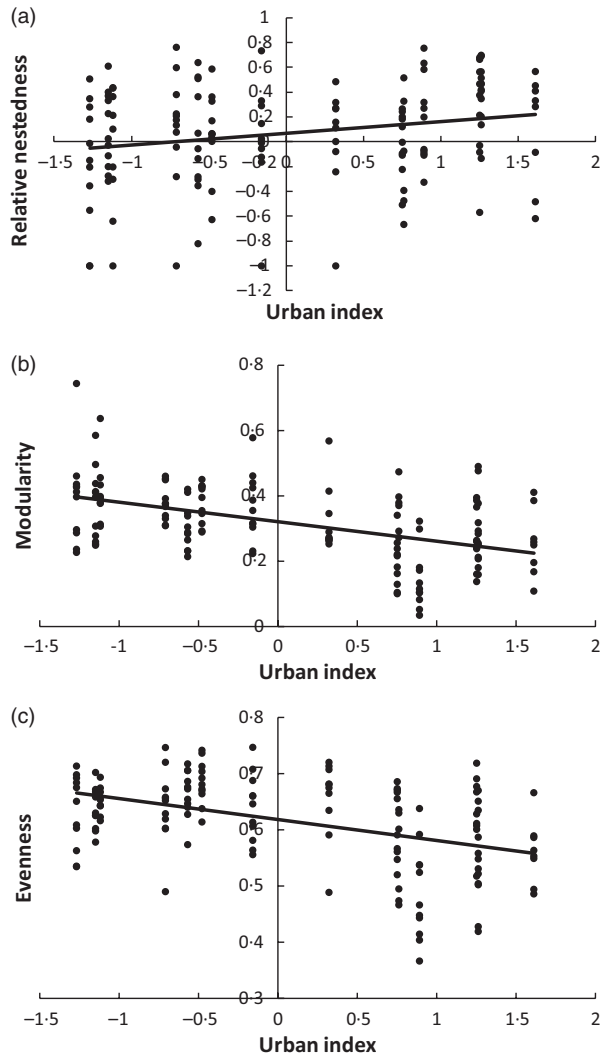

Fig. 2. Relationships between urbanization and (a) relative nestedness, (b) modularity and (c) evenness for 141 bird–plant networks in central Ohio forests, 2001–2011.

Discussion

Urbanization within landscapes surrounding riparian forests was associated with changes to ecological networks of birds and the plants in which they nested. As landscapes surrounding riparian forests urbanized, networks were smaller, more nested, less compartmentalized and dominated by stronger interactions than rural networks. These shifts in network structure are consistent with environmental changes known to occur in riparian forests as the surrounding landscapes become more urban (Rodewald 2012). Most notably, as landscapes urbanize, the understorey of forests becomes increasingly dominated by the exotic and invasive shrub, Amur honeysuckle (Borgmann & Rodewald 2005). Invasion by honeysuckle reduces the diversity and abundance of native plants (Gould & Gorchov 2000; Gorchov & Trisel 2003; Miller & Gorchov 2004), which would reduce network size in the heavily invaded urban forests. The higher nestedness and lower modularity of more urban forests likely reflects the fact that generalist invaders like honeysuckle become the most
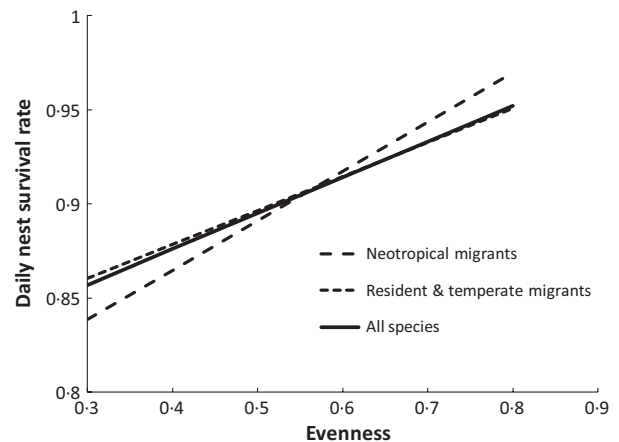

Fig. 3. Fitted relationships between network evenness and daily nest survival for residents and temperate migrants, Neotropical migratory species and all understorey birds combined at 141 networks studied from 2001 to 2011.

Table 2. Alternate hypotheses to explain variation in avian nest survival among 19 forest sites in Ohio, USA, 2001–2011 ($n = 141$). Models were ranked by AIC score, with ΔAICc = 0 indicating the best model). Akaike's weight (w) showed the weight of evidence for a particular model.

Model	AICc	ΔAICc	w	Parameter estimate	SE	P-value
Network evenness	−329·40	0·00	0·543	0·168	0·076	0·029
Plant evenness	−327·30	2·10	0·190	0·092	0·048	0·057
Bird evenness	−326·90	2·50	0·156	0·077	0·041	0·062
Modularity	−324·30	5·10	0·042	0·035	0·052	0·496
Relative modularity	−323·30	6·10	0·026	−0·021	0·016	0·237
Relative nestedness	−322·80	6·60	0·020	−0·018	0·015	0·237
Lonicera dominance	−322·00	7·40	0·013	0·005	0·020	0·796
Urbanization	−321·30	8·10	0·009	−0·008	0·006	0·204
Network size	−317·60	11·80	0·001	−0·001	0·002	0·495

connected species and the central nodes of sites (Aizen, Morales & Morales 2008; Bartomeus, Vila & Santamaria 2008). This becomes relevant to predator–prey interactions because when so many interactions are directed towards honeysuckle, predators can more easily form search images and patterns that increase their efficiency locating nests.

More important than describing shifts in network structure, our study shows that changes to network structure can have demographic consequences across multiple species within a community and is the first to demonstrate this with vertebrates. The strength of interactions at higher trophic levels (i.e. rate of predation reflects the outcome of interactions between predators and prey) was mediated by interactions at lower levels (i.e. the distribution and relative abundance of bird nests among plants). The evenness of the network, or the symmetry of interaction strengths, was positively related to avian nest survival – even after accounting for variation among sites in numbers of predators. Thus, when nests were more evenly distributed among plants, nest survival improved.

Our finding that network structure changed with urbanization is consistent with research on the response of parasite–parasitoid networks to habitat modification. Albrecht *et al.* (2007) reported that interaction diversity, evenness and linkage density of networks of host–prey and parasitoid–predator insects were higher in restored than intensively managed meadows, with interaction diversity declining more rapidly than species diversity. For networks of 33 species of cavity-nesting bees, wasps and their parasitoids, evenness of interaction frequencies declined with increasing intensity of habitat modification in agriculturally managed systems, likely due to differences in species density (Tylianakis, Tscharntke & Lewis 2007). Moreover, the decline in interaction evenness was associated with greater top-down pressures – in their case, parasitism rates. In contrast, others have reported higher evenness of interactions in the more highly modified sites, as with plants and pollinators in urban compared with agricultural or suburban sites (Geslin *et al.* 2013) and cereal aphid–parasitoid–hyperparasitoid communities in conventional vs. organic winter wheat fields (Lohaus, Vidal & Thies 2013).

The positive relationship that we found between interaction evenness and avian nest success may stem from the manner in which nest partitioning (i.e. when individuals and species nest in different locations) affects predator search efficiency. The pattern we report is consistent with field experiments with understorey-nesting birds showing that nest predation declines with greater partitioning of nests among vegetation strata and substrates (Martin 1988). Likewise, previous research in our system indicates that birds nesting in honeysuckle face a higher risk of depredation in early spring when the majority of nests were placed in early-leafing honeysuckle and multiflora rose (*Rosa multiflora*) (i.e. less partitioning in April and early May), as opposed to later in the season

(June-August) when nests were more widely distributed across strata and substrates (Rodewald, Shustack & Hitchcock 2010). The penalty for nesting in a common location was substantial; birds that nested in honeysuckle early in the season, when most nests were placed in honeysuckle, had 20% lower annual reproductive output than those nesting in other plants, even after renesting (Rodewald, Shustack & Hitchcock 2010). This difference in nest survival in our system was likely attributable to changes in search efficiency of predators, especially given that (1) the community of plants, birds and predators at a site was similar throughout the season, and (2) height of nests in honeysuckle and rose (i.e. accessibility) did not change over the season. In our current examination of networks, as bird–plant interactions became increasingly asymmetric and networks were dominated by a few strong links to exotic plants, predators were more successful locating the less partitioned nests. This reduction in daily nest survival rates can translate to half the apparent nesting success – from *c.* 22 to 11% of nests succeeding over a 21-day nest cycle across the range of evenness values we measured.

That evenness was a stronger determinant of nest survival than the number of predators detected at sites may initially seem counter-intuitive. However, this pattern likely reflects the effects of anthropogenic resources on predators. Sites with rich sources of human-provided food often support high densities of generalist predators (Marzluff, Bowman & Donnelly 2001; Gehrt 2004; Prange, Gehrt & Wiggers 2004), which frequently shift foraging behaviour to rely more heavily on those anthropogenic resources. This shift can result in a 'predator paradox', where high predator numbers in cities are not matched with correspondingly high rates of nest predation (Fischer *et al.* 2012). The predator paradox is consistent with patterns detected in empirical demographic studies (Rodewald *et al.* 2011; Stracey 2011) as well as in literature reviews (Fischer *et al.* 2012).

Our study shows that knowledge of landscape or habitat attributes, as typically measured in ecological studies, was not sufficient to predict the demographic consequences of environmental change. This finding is consistent with the equivocal support linking urbanization to rates of nest predation in other studies (Chamberlain *et al.* 2009). In our study, neither the amount of urbanization nor the degree of invasion by honeysuckle explained variation in nest survival. Rather, explicit knowledge of species interactions, as measured by interaction evenness, was necessary to explain patterns. Because urbanization was directly related to network structure but only indirectly to nest survival, we propose that inter-site variation in nest survival reflected how species interactions responded to urbanization. In this way, demographic effects of urbanization were filtered through the network.

Scientists and managers have long known that the complexity of ecological communities thwarts many efforts to predict the response of ecosystems to environmental

change. This study provides compelling evidence that knowledge of multispecies interactions is requisite to understand demographic responses to anthropogenic change. Network approaches, thus, offer elegant and practical means to describe and analyse the complexity of multispecies interactions within applied ecological research.

Acknowledgements

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