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Does removal of invasives restore ecological networks? An experimental approach

Amanda D. Rodewald · Rudolf P. Rohr · Miguel A. Fortuna · Jordi Bascompte

Abstract Anthropogenic disturbance can alter the structure of ecological networks in ways that have population consequences. For example, bird-plant networks in forests surrounded by urban land were more likely to be dominated by strong interactions (i.e., less even in strength) than networks in rural landscapes, and these asymmetric interactions depressed avian nest survival. Based on this prior research, we hypothesized that invasion of urban habitats by exotic plants was the underlying mechanism driving changes in network structure. We tested this hypothesis using an in situ experiment where exotic Amur honeysuckle (*Lonicera maackii*) was removed from replicated 2-ha forest plots and compared bird-plant networks among urban removal forests, urban control forests dominated by honeysuckle, and rural forests with little honeysuckle. From 2005 to 2011, we surveyed densities of understory-nesting birds and nest predators, recorded information about nest location, and monitored nest survival. For each year and site network, we calculated evenness of interaction strengths. Despite post-removal vegetation resembling that in rural forests, removal of exotic honeysuckle did not restore network structure. Evenness of interactions between birds and plants was greatest in rural forests and least in urban control plots. Nest survival increased with evenness across all sites, but the relationship was strongest within urban removal plots, which had the lowest overall nest survival rates. Even though invasion by honeysuckle was a plausible driver of urban-associated network shifts in previous studies, the experimental removal suggested that factors other than invasion were responsible for network changes or that our system experienced hysteresis or time lags. Our study suggests that restoration of ecological networks may be more challenging than anticipated.

Keywords Birds · Evenness · Exotic plants · Honeysuckle · Invasive · Nest survival · Predation

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Introduction

Exotic plants can be among the most insidious of invasive species, disrupting ecosystem processes (Levine et al. 2003) and altering community composition (e.g., Hutchinson and Vankat 1997; Mack et al. 2000). Less well understood is how invasive plants affect networks of species interactions, especially those at higher trophic levels (Schmidt and Whelan 1999; Borgmann and Rodewald 2004, Rodewald et al. 2010). Ecological networks provide a powerful

framework for studying how invasive species can influence species interactions within a community (Bascompte and Jordano 2007; Bascompte 2009; Bastolla et al. 2009). For example, habitat changes in agricultural systems prompted shifts in networks of cavity-nesting bees, wasps, and their parasitoids by way of affecting species densities (Tylianakis et al. 2007). Such a holistic approach to understanding communities is critical in systems where habitat and/ or landscape modifications can change the nature of species interactions (Fortuna and Bascompte 2006; Albrecht et al. 2007; Tylianakis et al. 2007; Gagic et al. 2011).

Studies show that invasive plants can disrupt species interactions, especially in mutualistic networks of plants and pollinators (Richardson et al. 2000; Traveset and Richardson 2006; Montero-Castaño and Vilá 2012) and in ways that impact the reproductive success of native plants (Larson et al. 2006; Bartomeus et al. 2008). Aizen et al. (2008) suggested that the network asymmetries in invaded mutualistic networks might make the communities more resistant to restoration or other community-level change. Such changes in network structure, in turn, can have reproductive consequences, as has been demonstrated for individual-based networks of plants and pollinators (Gómez et al. 2011) and multispecies commensalistic bird-plant networks (Rodewald et al. 2014). From a conservation perspective, the restoration of a heavily invaded community should ideally involve recovering the typical suite of species interactions following eradication or control of invasives (Pimentel et al. 2000). There are cases of success, as Albrecht et al. (2007) reported that restored, rather than intensively managed meadows had higher interaction diversity, evenness, and linkage density of networks of host/prey and parasitoid/predator insects. However, the extent to which restoration influences network properties remains poorly understood.

In this paper, we build from our long-term research in Columbus, OH, USA, which provided evidence that (a) bird-plant networks in forests were more likely to be dominated by strong interactions (i.e., less even) as landscapes urbanized and (b) low evenness depressed nest survival among understory-nesting birds (Rodewald et al. 2014). Based on these initial findings, we suspected that exotic Amur honeysuckle (*Lonicera maackii*), an invasive and urban-associated shrub (Borgmann and Rodewald 2005), was responsible

for the urban-associated shifts in network properties. Honeysuckle was first introduced to North America from Asia in the 1800s as an ornamental plant and since then has become a dominant plant in many forest and shrubland systems, particularly in the eastern US (Hutchinson and Vankat 1997). Numerous studies have documented the negative consequences of honeysuckle to native plants (Gould and Gorchov 2000; Collier et al. 2002), animals (Schmidt and Whelan 1999; Watling et al. 2011), ecosystem processes (Ehrenfeld et al. 2001; Ehrenfeld 2003), ecological services such as pollination (McKinney and Goodell 2010), and even human health (Allan et al. 2010).

Honeysuckle also carries a number of consequences for breeding birds (Rodewald 2012a). First, although honeysuckle promotes high densities of certain generalist species (Leston and Rodewald 2006; Rodewald 2012b), others, such as the Acadian Flycatcher (*Empidonax virescens*), have lower densities and productivity when honeysuckle is abundant (Bakermans and Rodewald 2006; Rodewald 2009, 2012b). Second, honeysuckle can act as an early-season ecological trap, such that cardinals choosing to nest in honeysuckle for their first breeding attempt produce 20 % fewer young each year compared to birds nesting in other substrates (Rodewald et al. 2010). The ecological trap results from the fact that cardinals prefer to nest in honeysuckle, despite the fact that doing so increases risk of nest predation in understory-nesting birds, particularly early in the breeding season (Schmidt and Whelan 1999; Borgmann and Rodewald 2004; Rodewald et al. 2010). This trap also can manifest in a way that disadvantages the most colorful and presumably most competitive males (Rodewald 2012a). Third, honeysuckle increases risk of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) for Acadian flycatchers, which are then unable to fledge their own young (Rodewald 2009). Probably for this reason, cover by honeysuckle is the best predictor of, and negatively related to, annual reproduction by Acadian flycatchers (Rodewald 2012b). Further evidence of the ability of honeysuckle to alter species interactions came from our recent analysis of 10 years of bird-nest plant networks across 19 forested sites that showed how urbanization depressed network evenness, which in turn, was associated with reduced nest survival of understory birds (Rodewald et al. 2014).

The body of our previous work led us to hypothesize that invasion of urban habitats by exotic species was the mechanism of urban-associated changes in network structure. We tested this within the same study system and sites using the framework of an in situ experiment and compared bird-plant networks in four plots where exotic Amur honeysuckle (*Lonicera maackii*), an invasive and urban-associated shrub (Borgmann and Rodewald 2005), was experimentally removed from urban forests to eight plots in control urban forests and six rural forests with little honeysuckle.

Materials and methods

Field monitoring

Bird-plant interactions were studied in 18 mature riparian forests that were part of an invasive removal experiment in Ohio USA. Riparian forests ranged from 104 to 277 m wide and were comparable in width and configuration across the rural–urban gradient. Because the forests were relatively continuous along rivers in the study area, we could not delineate discrete patches of forest and, therefore, use width rather than area as our measure of size. Forests were located in landscapes that shared similar land use history as well as amount and spatial configurations of natural areas. However, landscapes differed in the dominant land use (agriculture or urban) within the matrix (see Rodewald and Shustack 2008 for more detail). Rural landscapes were dominated by cropland, pasture, managed grassland, and farms within 1-km of our study site, whereas urban landscapes were dominated by residential areas, commercial development, and roads.

The effect of invasive plants on networks was studied by using a replicated in situ experiment. Selection criteria ensured that sites were similar in topography, hydrology, and vegetation. Our six rural forests either lacked or contained small amounts of Amur honeysuckle, whereas all 12 urban forests were dominated by dense growth of Amur honeysuckle in the understory. Within four randomly chosen 2-ha plots, all honeysuckle was cut and removed from the site along designated haul trails to minimize impact to other vegetation. The 2-ha size was partly chosen based on logistics and cost, but it also is relevant for many breeding birds, which often have territories

$\leq$0.5 ha in size. Prior survey data indicated that 2-ha grids usually contained 2–5 territories per species for most common birds (AD Rodewald, unpublished data). Removal of honeysuckle was completed in January and February 2007 on three of the four sites. Removals on the remaining site, Rush Run park, were delayed due to an Ohio Department of Transportation mitigation project but were completed in Winter 2008. In each autumn following removals, remaining stumps and stems of honeysuckle were annually treated with a 50 % glyphosate isopropylamine salt solution (Roundup herbicide; Monsanto Company). Following honeysuckle removal, densities of understory woody stems >3 cm diameter breast height (dbh) were comparable to rural forests but half those at control urban plots (A.D. Rodewald, unpublished data). Each autumn any resprouting of honeysuckle shrubs was treated with glyphosate applied to individual plants.

From March to August 2005–2011 we monitored the fate of 3947 nests, represented by northern cardinal (*Cardinalis cardinalis*, n = 2469), American robin (*Turdus migratorius*, n = 644), Acadian flycatcher (*Empidonax virescens*, n = 409), gray catbird (*Dumetella carolinensis*, n = 232) wood thrush (*Hylocichla mustelina*, n = 168), indigo bunting (*Passerina cyanea*, n = 14), and red-eyed vireo (*Vireo olivaceous*, n = 11). Because our trained field crews mapped locations of territorial birds at sites, thereby allowing us to determine densities of focal species, we believe that differences in numbers of nests among species generally reflects the relative abundance of our focal species at sites. Acadian flycatcher, wood thrush, indigo bunting, and red-eyed vireos are Neotropical migrants that occurred at low numbers at urban sites, whereas the resident northern cardinal, temperate migrant American robin, and Neotropical migrant gray catbird were most abundant within urban landscapes (Rodewald and Bakermans 2006).

Each nest was checked at 2–4 days intervals by viewing nest contents or by observing parental behavior to track nest stage (e.g., onset of incubation behavior) 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.

Species known to be nest predators were surveyed at each site within 2-ha grids flagged at 50-m intervals at weekly intervals between May and July 2005–2011, totaling ten surveys each year. There were 21 species of known predators at our sites (i.e., video-confirmed in our system; Rodewald and Kearns 2011), including corvids, raptors, squirrels, common grackles (*Quiscalus quiscala*), brown-headed cowbirds (*Molothrus ater*), raccoons (*Procyon lotor*), opossum (*Didelphis virginiana)*, and domestic cats (*Felis catus*). During surveys a trained observer systematically traversed the entire marked grid over an approximately 45-min period between 0545 and 1000 and recorded all nest predators seen or heard. Although a few snakes were detected on surveys, they were too few to consider in analyses. Because (1) detections of nest predator species were positively correlated and (2) no predator dominated the system (i.e., even the most dominant predator still accounted for only 18 % of depredations; Rodewald and Kearns 2011), a single index of predator activity was created based on the total number of predator detections at a site each year. As this index is based upon number of detections, it better represents the relative activity of predators than actual densities at sites.

At each site, vegetation was measured at four systematically-located 0.04-ha plots that were regularly distributed across the plot. At each plot field teams estimated canopy height and then counted the number of small [diameter breast height (dbh) = 8–23 cm], medium-sized (dbh = 23.1–38 cm), and large trees (dbh > 38 cm) identified to species, as well as the amount of woody debris (i.e., numbers of logs and stumps) and numbers of snags (>12 cm dbh). Canopy cover and ground cover were estimated using ocular tubes at 20 points located at 2-m intervals along 2 perpendicular 20-m-long transects. The vertical structure of the stands was described by the number of contacts made by woody stems on a 3-m-tall vegetation pole at 2-m intervals along transects.

Analyses

Daily nest survival rates were estimated at each site in each year using logistic exposure models. The logistic 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). The logistic exposure model estimates probability of nest survival (either 0 for failed nests of 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).

We used weighted bipartite networks to represent the pattern of birds nesting on plants, where there was a link when a species of bird placed a nest in a given plant species. The weight of the link was represented by the number of nests on the plant species. Each site and year was represented by a separate matrix where each row represented a plant species and each column represented a bird species.

Evenness quantified the homogeneity or symmetry in interaction strength in a way that was standardized by network size. Evenness was calculated for the network for each site and year using the following equation:

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

where S_{plant} is the number of plant species, S_{bird} is the number of bird species and $p_{i,j}$ is the proportion of nests from bird j in plant i. Calculations were performed in R.

Using PROC MIXED SAS 9.2., we tested for differences among our experimental treatments (rural, urban control, urban removal) for the following response variables: evenness, detections of nest predators, and relative abundance of seven focal bird species. Sample sizes differed among treatments both because of numbers of sites but also in the years surveyed (e.g., removals were not implemented until 2007). Originally we used an interactive model with treatment and year as main effects and an interaction term between them. Both because interaction terms were not significant and there were no temporal trends in network changes (e.g., removal sites were not increasingly even over the years of our study), we opted to use a repeated measures regression with year as the repeated variable for subsequent analyses. The combined effect of honeysuckle removal and evenness on daily nest survival was tested using a repeated measures regression with experimental treatment and evenness as main effects and a treatment × evenness

interaction. We examined post-treatment differences in vegetation structure among the treatments using discriminant function analysis.

Results

Experimental removals successfully changed the habitat structure of our sites (Wilks' Lambda $F_{12,148} = 6.16$, $P < 0.0001$). In particular, removal and rural plots had lower amounts of honeysuckle, shrub cover, and total foliage density than urban controls (Table 1). In addition, all focal species of understory nesting birds differed significantly in abundance among sites (Table 2). Acadian Flycatcher, Indigo Bunting, Red-eyed Vireo, and Wood Thrush were most abundant on rural forests, whereas Northern Cardinal, American Robin, and Gray Catbird were most numerous in urban forests (Table 2).

Over the 7 years of our study, we quantified 103 bird-plant networks (42 rural, 45 urban control, and 16 urban removal). Rural networks were larger (i.e., a greater number of links) than either urban control or urban removal sites (rural $\beta = 1.92 \pm 0.962$ SE, urban control $\beta = -0.547 \pm 0.953$ SE, urban removal $\beta = 0$, $F_{2,100} = 6.44$, $P = 0.0023$; Table 1). Evenness of interaction strengths, referred to hereafter as interaction evenness, was greater for rural networks than urban removal or urban control networks (rural $\beta = 0.05 \pm 0.02$ SE, urban control $\beta = -0.04 \pm 0.02$ SE, urban removal $\beta = 0$, $F_{2,100} = 19.94$, $P < 0.0001$; Table 1). The fact that evenness remained lower on removal than rural plots suggests either that invasive plants were not solely responsible for altering

networks or that our system experience hysteresis or time lags such that recovery of the original network structure took many more years.

Daily nest survival was positively related to interaction evenness ($F_{1,97} = 10.68$, $P = 0.002$) and was lowest in the urban removal sites ($F_{2,97} = 6.52$, $P = 0.002$), but with a significant treatment × evenness interaction ($F_{2,97} = 5.62$, $P = 0.005$). The interaction indicated that the relationship between evenness and nest survival was most strongly positive in the urban removal sites (Fig. 1). We suspect that changes in activity of nest predators on urban removal sites specifically might have contributed to patterns in nest survival, as nest predators were detected at nearly twice the amount on urban removal sites (22.3 ± 2.66 SE) compared to either urban control (16.9 ± 1.12 SE) or rural (12.2 ± 1.50 SE) sites ($F_{2,117} = 7.52$, $P = 0.0008$).

Discussion

As part of an in situ experiment, removal of invasive honeysuckle from urban forests did not restore network structure to that of rural landscapes. Instead, networks from urban removal sites had levels of evenness that were intermediate between rural and urban control sites. This finding was not consistent with our original hypothesis that invasion of forests by the exotic Amur honeysuckle was responsible for the urban-associated changes in bird-plant networks documented in a related study (Rodewald et al. 2014).

Consistent with our prior observational study (Rodewald et al. 2014), changes to network structure

Table 1 Differences in habitat (within 0.04-ha plots) and network structure among rural, urban removal, and urban control plots in riparian forests in central Ohio

	Rural		Urban removal		Urban control		F	P
	Mean	SE	Mean	SE	Mean	SE		
Evenness	0.67	0.006	0.61	0.014	0.15	0.049	19.94	<0.0001
Network size	15.05	0.475	13.13	0.741	12.58	0.528	6.44	0.0023
Shrub cover (%)	11.03	1.358	13.97	0.927	32.75	2.391	34.8	<0.0001
Canopy cover (%)	81.82	1.774	85.2	1.366	87.42	1.26	3.62	0.0312
Number of:								
Snags	1.44	0.207	1.82	0.212	2.1	0.277	2.57	0.0826
Trees	27.59	1.342	33.89	2.632	42.02	2.621	9.24	0.0002
Honeysuckle stems	1.85	0.428	18.04	2.609	86.58	11.323	25.83	<0.0001
Total foliage density	37.41	4.234	30.01	2.642	30.01	2.642	6.31	0.0029

Table 2 Differences in relative abundance of understory-nesting birds among rural, urban removal, and urban control 2-ha plots in riparian forests in central Ohio

	Rural		Urban removal		Urban control		F	P
	Mean	SE	Mean	SE	Mean	SE		
Acadian flycatcher	1.53	0.117	0.31	0.083	0.56	0.071	43.18	<0.001
American robin	1.93	0.190	3.00	0.260	2.1	0.139	8.14	0.001
Brown-headed cowbird	1.00	0.082	1.06	0.097	0.86	0.060	1.80	0.170
Gray catbird	0.53	0.082	1.72	0.228	1.68	0.183	12.85	<0.001
Indigo bunting	1.48	0.163	1.31	0.198	1.03	0.11	2.70	0.072
Northern cardinal	1.68	0.12	4.47	0.357	4.32	0.314	24.72	<0.001
Red-eyed vireo	2.34	0.179	1.89	0.140	1.81	0.119	3.81	0.025
Wood thrush	1.33	0.125	0.69	0.161	0.77	0.151	4.53	0.013
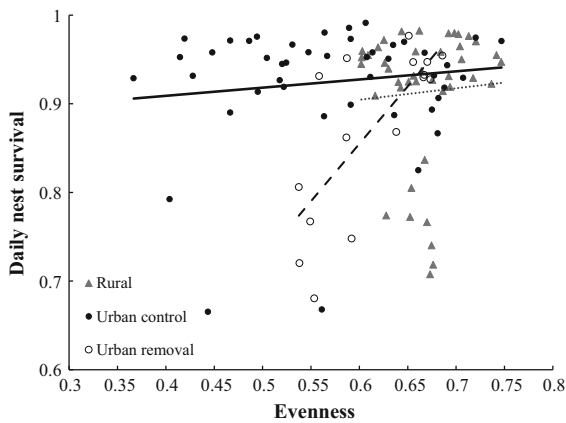
Fig. 1 The relationship between interaction evenness and avian nest survival differed among the experimental treatments, such that it was strongest in the urban removal (*dashed line*) compared to urban control (*solid line*) or rural (*dotted line*) sites, 2005–2011

had reproductive consequences for understory birds breeding within the community. Interactions between nesting birds and nest predators were mediated by the structure of the network, specifically the distribution and relative abundance of bird nests among plants. Avian nest survival improved when interactions between birds and plants were highly symmetric or even (i.e., nests were more evenly distributed among plants). This relationship was strongest in the urban removal plots, where plots with the lowest levels of evenness had approximately 20 % lower rates of daily nest survival than at higher levels of evenness, which translates to <1 % (lowest evenness) versus 27 % (highest evenness) of nests succeeding over a 21-day nest cycle. Although our previous work and this study showed that activity of nest predators alone or in

combination with evenness did not seem to drive nest survival rates, we question if there might be a consequence to high predator activity on removal sites alone. We suspect that evenness was most important at urban removal sites because they had both the highest levels of nest predator activity and reduced availability of potential nest locations given the removal of honeysuckle. Intuitively, this makes sense, as there are most likely be negative consequences to birds breeding at highly asymmetric sites that offer the fewest options for placing nests and when there also are abundant nest predators.

Although invasive honeysuckle did not seem to be the primary driver of urban-associated changes to bird-plant networks as originally suspected in our system, Aizen et al. (2008) showed that invasive species promote interaction asymmetries in mutualistic networks, potentially making invaded communities more resistant to restoration. Likewise, interaction evenness was greater for networks of host/prey and parasitoid/predator insects in restored than intensively managed meadows (Albrecht et al. 2007) and of cavity-nesting bees, wasps, and their parasitoids in less intensely managed agricultural systems (Tylianakis et al. 2007).

We suggest that the positive relationship between avian nest success and network evenness is the consequence of the pattern of distribution of nests among different locations and plants influences search efficiency of predators. Indeed, Martin (1988) demonstrated that when understory nests were less partitioned among vegetation strata and substrates, rates of nest predation were greater. Thus, the interrelatedness of nest partitioning and search efficiency of predators may drive the high risk of depredation associated with honeysuckle in early spring when the majority of nests

are placed either 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 et al. 2010). The nest-partitioning mechanism is further supported by the lack of seasonal changes in nest height within exotics and species composition of plants, birds, and predators at a site (Rodewald et al. 2010, A.D. Rodewald, unpublished data).

The reasons why removal of honeysuckle from urban forests partially, but not entirely, restores urban networks to those described in rural forest networks remain unclear. Hysteresis or time lags, whereby the recovery of the original network structure required much longer time periods, might have contributed to our inability to detect a post-removal return to networks typically found in rural landscapes; longer term studies could elucidate this. Two additional plausible mechanisms are differences in the community of understory breeders and nest predators among sites. Urban removal sites had comparatively greater numbers of resident and short-distance migratory species and of nest predators. Animal communities may take longer to return to those characteristic of uninvaded sites, especially compared to the immediate changes we provoked in the plant communities with our removals.

The degree to which native communities can be restored following removal of exotic plants remains unclear. For example, a recent review of 56 studies of exotic plant removals (157 exotic plant species) across 35 parks in 20 states within the USA found that although 87 % of studies reduced density of at least one exotic plant species, the response of native vegetation was highly variable (Abella 2014). Fewer studies have evaluated how ecological networks may respond to control of invasives (Devoto et al. 2012). Ferrero et al. (2013) showed that while the removal of an invasive weed from disturbed Mediterranean systems had little effect on the composition of a plant-pollinator network, reproductive success of some native species declined. Despite the inherent complexity associated with restoring heavily invaded ecosystems, our growing understanding of networks and community dynamics suggests that the desired ecological outcomes of restoration efforts may be linked to the our ability to restore species interactions (Strauss and Irwin 2004; Tylianakis et al. 2010).

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