

Patterns and mechanisms of invasive plant impacts on North American birds: a systematic review

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Received: 2 June 2016 / Accepted: 30 January 2017
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Abstract Understanding how invasive plants affect biodiversity is a crucial conservation need. Numerous studies examine impacts of invasions on birds, but trends in these effects have not been synthesized. We reviewed 128 studies from North America to quantify the frequency of positive, negative, and neutral (non-significant) effects of invasive plants on avian ecology, and then evaluated support for proposed mechanisms of impacts. Our frequency-based approach enabled us to draw value from the full breadth of available literature, including articles that do not provide information necessary for meta-analyses and articles examining understudied phenomena. Total avian abundance and prevalence of individual bird species were usually unaffected by invasion, with 48.9 and 57.2% of tests showing neutral results, respectively. Avian richness decreased with invasion in

41.3% of tests. Although birds often preferred nesting in invasive vegetation (45.0% of tests), effects on nest survival were typically neutral (57.9%). Multiple metrics (e.g. body condition, fledgling survival) have received scant attention. Some of the patterns we highlight differ across ecological contexts, emphasizing the need to understand impact mechanisms. Several studies have directly linked invasion impacts to altered nest-site availability, habitat heterogeneity, and food supplies. There is mixed evidence that plant architecture impacts nest-site selection and nest predation. Our review highlights the nonuniform consequences of biological invasions. The high frequency of reported neutral effects suggests that invasions often have minimal impacts on birds, but positive and negative impacts certainly can arise. Managers considering eradicating invasive plants for avian conservation should monitor impacts locally to determine whether eradication will be beneficial.

Electronic supplementary material The online version of this article (doi:[10.1007/s10530-017-1377-5](https://doi.org/10.1007/s10530-017-1377-5)) contains supplementary material, which is available to authorized users.

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Keywords Avian ecology · Biological invasions ·
Habitat selection · Habitat structure · Nest predation ·
Trophic effects

Introduction

Invasive plants present a global challenge for conservation as they reshape ecosystem structure, composition, and function (Vitousek et al. 1996; Pyšek et al.

2012; Simberloff et al. 2013). Accordingly, it is critical to assess the extent to which they threaten biodiversity and the mechanisms of degradation (Vilà et al. 2011). Of the many taxa affected by invasions, few have received as much attention as birds. Avian distributions and fitness may be sensitive to plant invasions because vegetation structure often mediates habitat selection and nest predation (MacArthur and MacArthur 1961; Rotenberry and Wiens 1980; Martin 1993). Invasive plants can also affect birds through trophic pathways if they differ in nutrient quality from native plants (Ingold and Craycraft 1983) or support different arthropod communities (Flanders et al. 2006).

As authors have increasingly studied these impacts, the accumulating body of literature has enabled investigations of broad trends. For example, a recent meta-analysis presents evidence that invasive plants tend to reduce avian abundance, diversity, and fitness, providing valuable information on the threats posed by invasions (Schirmel et al. 2016). However, because these analyses only incorporated articles providing enough information to calculate effect sizes (29 avian studies; Schirmel et al. 2016, Appendix S1) they drew upon a relatively small fraction of the existing literature.

Different trends may emerge when the literature is examined through a wider lens. Indeed, although reports of negative impacts of invasion are common (e.g. Schmidt and Whelan 1999; Flanders et al. 2006; Ortega et al. 2006; Rodewald et al. 2011), some invasive plants have minimal effects on birds while others even appear to benefit them (e.g. Rosenstock and van Riper 2001; Chapman et al. 2004; van Riper et al. 2008; McCusker et al. 2010; Gleditsch and Carlo 2011). Although focusing on effect directions does not capture the magnitude of effects, determining the relative frequency of negative, positive, and neutral impacts on birds can clarify the risks posed by plant invasions, both in terms of the likelihood of negative impacts occurring and the aspects of avian ecology that invasions are likely to affect. Moreover, this approach allows for a review of understudied components of avian ecology, such as habitat preferences, body condition, and provisioning rates.

In addition to understanding patterns of effects, identifying the specific variables driving these patterns is important for decision-making in avian conservation. Despite the high volume of pertinent literature,

no current synthesis exists of the mechanisms underlying impacts of invasive plants on birds.

We address these knowledge gaps through a systematic review. We first present the frequencies of negative, neutral, and positive relationships between invasive plants and many metrics of avian ecology (e.g. abundance, species richness, nest survival, brood parasitism, body condition), and discuss additional patterns associated with specific habitat types, plant growth forms, and seasons. We then review and evaluate support for mechanisms proposed to explain these relationships, and finally discuss limitations and implications of the data, as well as key issues in need of further research.

Methods

Article selection

We identified relevant peer-reviewed articles published through 2014. To provide both an extensive and in-depth review of the literature, we restricted our scope to North America (i.e. Canada, United States, and Mexico; excluding islands). Because most pertinent studies investigate North American systems, examining these data provides a far-reaching, though not exhaustive, overview of existing knowledge. We searched the ISI Web of Science database using the keywords *invasive*, *exotic*, or **native AND plant or vegetation AND avian or *bird*. We reviewed relevant papers and examined citations within to identify additional studies. Study designs varied widely, but we considered articles relevant if authors related quantitative metrics of avian ecology to the presence or prevalence of invasive plants.

We defined plants as invasive if they have established populations outside of their native ranges *and* outside areas where humans have intentionally planted them (Davis 2009). We did, however, review studies of populations of exotic species planted by humans if the species in question are known to independently invade unplanted areas. Additionally, we included studies of native plants encroaching on habitats from which they have historically been excluded.

Determining patterns of invasive plant impacts

Articles reported relationships between plant invasions and a broad array of avian metrics. For each

reported statistical test we recorded the direction of the metric's response to invasion—specifically, whether the invasive plant had a negative, neutral, or positive impact according to authors' chosen significance criteria. If multiple articles were published using the same data (i.e. same species, location, and years), we counted overlapping tests only from the article published first. Some articles conducted multiple tests comparing avian metrics to several invasive plant species, or measured the same metric in multiple seasons or locations. We counted every test separately.

In some cases, avian responses to invasion were neither wholly negative nor wholly positive. For example, response directions sometimes varied between years or with invasion intensity. Additionally, relative responses of birds to invasive vegetation sometimes differed when compared to different types of native vegetation. We classified such responses as conditionally negative, conditionally positive, or conditionally negative-or-positive.

To provide a broad view of the literature, we reviewed results irrespective of the statistical criteria used to determine the significance of impacts (e.g. p -values, AIC scores, correlations with axes in multivariate ordinations). However, such criteria could influence the likelihood of tests achieving significance. To assess whether this decision affected our interpretation of the literature, we documented the criterion used for each test and graphically compared the frequencies of different effect directions between (1) all tests, and (2) only tests evaluated using $\alpha = 0.05$ —the most common criterion.

Variation in impacts across ecological contexts

For each reported test, we documented (a) the habitat type in which the study was conducted (e.g. grassland, woodland); (b) the species of invasive plant under consideration, and whether the species were woody or herbaceous; and (c) the season in which the data were collected (i.e. breeding, fall migration, winter, or spring migration). We highlight several notable context-specific patterns.

Influences of sample sizes, impact factors, and invasion magnitudes

A disadvantage of assessing patterns in the literature by counting the frequency of different effect directions

is that some tests might be more likely to show negative, neutral, or positive results based on underlying elements of the article in which they were reported. We examined the influence of three factors on these likelihoods: (1) test sample sizes, (2) impact factors of journals where tests were published, and (3) the degree of invasion intensity within study systems. We focused specifically on how these factors influenced tests examining invasion impacts on the abundance or density of individual bird species (by far the most commonly examined metric).

To assess the influence of sample size, we documented the number of replicate study sites or count stations used for each test. We then constructed a generalized linear mixed model (GLMM) with an unordered multinomial distribution in SAS 9.4 (SAS Institute Inc., Cary, NC) using PROC GLIMMIX. Sample size was the explanatory variable, and the outcome of each test (negative, neutral, or positive) was the response. We excluded the three conditional response categories from this analysis due to their rarity. We included the article in which each test was reported (ArticleID) as a random variable to control for non-independence of tests within individual studies. We determined significance of the model relationship based on $\alpha = 0.05$.

To assess whether test results are related to journal impact factors (Murtaugh 2002), we documented the most recent impact factor of journals represented in the review and compared them to the directions of tests published in each. We again constructed an unordered multinomial GLMM, including ArticleID as a random effect, and assessed the relationship at $\alpha = 0.05$.

Finally, we examined whether birds exhibit stronger responses to invasion as invasive plant prevalence increases. First, when it was quantitatively reported, we extracted data from each article on either the percent cover of invasive plants or the percent of total vegetation comprised by invasive plants in each study system. For articles that compared birds among groups of sites qualitatively categorized by invasion levels, we recorded invasion intensity as the average percent invasion in the most invaded category. For articles that compared birds across sites representing a continuous invasion gradient, we recorded invasion intensity as the average percent invasion across all sites (or the midpoint, if average was not reported). We constructed an unordered multinomial GLMM and evaluated the relationship between invasion intensity and avian responses at $\alpha = 0.05$.

Results

Reviewed articles

We identified 128 articles meeting our review criteria (Appendix A, Table A1 in Electronic Supplementary Material). The earliest article was published in 1980, and publication rates have increased since 1994 (Appendix B in Electronic Supplementary Material). Research was conducted in 8 Canadian provinces, 41 US states, and 3 Mexican states. These articles reported effects of invasive plants on 219 bird species (Appendix A, Table A2 in Electronic Supplementary Material). Invasive plant species included 26 graminoid, 13 forb, and 33 woody species. Studies were conducted in grasslands ($n = 46$), woodlands ($n = 25$), riparian woodlands ($n = 23$), wetlands ($n = 11$), shrublands ($n = 10$), and savannas ($n = 5$). Five articles focused on multiple habitat types and three were foraging studies conducted in aviaries.

Patterns of invasive plant impacts on birds

Abundance of birds and bird nests

The most commonly examined impact of invasive plants was on the abundance, density, or occurrence of individual bird species (single-species prevalence): 823 tests were reported across 60 articles (Fig. 1a). The majority (57.2%) indicated that invasive plants do not affect single-species prevalence, although some tests also showed decreasing (18.7%) and increasing (16.3%) prevalence. Patterns within studies often mirrored these basic distributions, with prevalence of most species unaffected by invasion, but some species increasing and some decreasing (e.g. Coppedge et al. 2001; Bakker and Higgins 2009; Gifford and Armacost 2012; Schneider and Miller 2014). However, some studies instead reported predominately negative (e.g. Flanders et al. 2006) or positive (e.g. Rosenstock and van Riper 2001; McCusker et al. 2010) effects.

In addition to impacts on individual species, 45 tests across 30 articles examined effects on total abundance or density of avian communities (Fig. 1b). Most frequently, tests detected no effects of invasion on these metrics (48.9%). Reductions in abundance or density were comparatively uncommon (23.4%), and increases were rare (10.6%).

Finally, 7 studies (19 tests) examined effects on abundances of nests of individual bird species or entire

communities (Fig. 1c). Most tests found neutral effects (57.9%), while fewer found reduced (26.3%) or increased (10.5%) nest abundances.

Avian richness, evenness, and diversity

Few studies reported effects on avian community evenness (3 neutral, 2 negative) or diversity (3 neutral, 4 negative, 1 conditionally positive). In contrast, 33 articles reported 46 tests examining invasion effects on species richness (Fig. 1d). Although neutral effects were the most common result (47.8%), many tests showed either negative (26.1%) or conditionally negative effects (15.2%) on richness. For example, richness decreased in wetlands invaded by common reed (*Phragmites australis*; Benoit and Askins 1999), and was lower in invasive saltcedar (*Tamarix ramosissima*) monocultures than in natural cottonwood (*Populus* spp.) woodlands (Keller and Avery 2014).

Habitat preferences

Site fidelity, distribution of dominant birds, and settlement timing may indicate avian habitat preferences between native and invasive vegetation (Robertson and Hutto 2006). While Botteri's sparrows (*Aimophila botteri*) had comparable site fidelity in exotic lovegrass (*Eragrostis* spp.) and native grass pastures, indicating no preference (Jones and Bock 2005), chipping sparrows (*Spizella passerina*) exhibited lower site fidelity in areas invaded by spotted knapweed (*Centaurea maculosa*), suggesting a preference for uninvaded habitats (Ortega et al. 2006).

Similarly, although dominant male chipping sparrows excluded younger subordinates from uninvaded patches, indicating preference for uninvaded areas (Ortega et al. 2006), dominant northern cardinals (*Cardinalis cardinalis*) preferred territories with abundant Amur honeysuckle (*Lonicera maackii*; Rodewald et al. 2011). Settlement patterns confirmed that cardinals preferred invaded territories since they selected them early in the season (Rodewald et al. 2011). In contrast, chestnut-collared longspurs (*Calcarius ornatus*) settled native grasslands and crested wheatgrass (*Agropyron cristatum*) monocultures at the same time, indicating no preference (Lloyd and Martin 2005). Avian preferences for invaded versus uninvaded habitats appear case specific, though evidence is currently sparse.

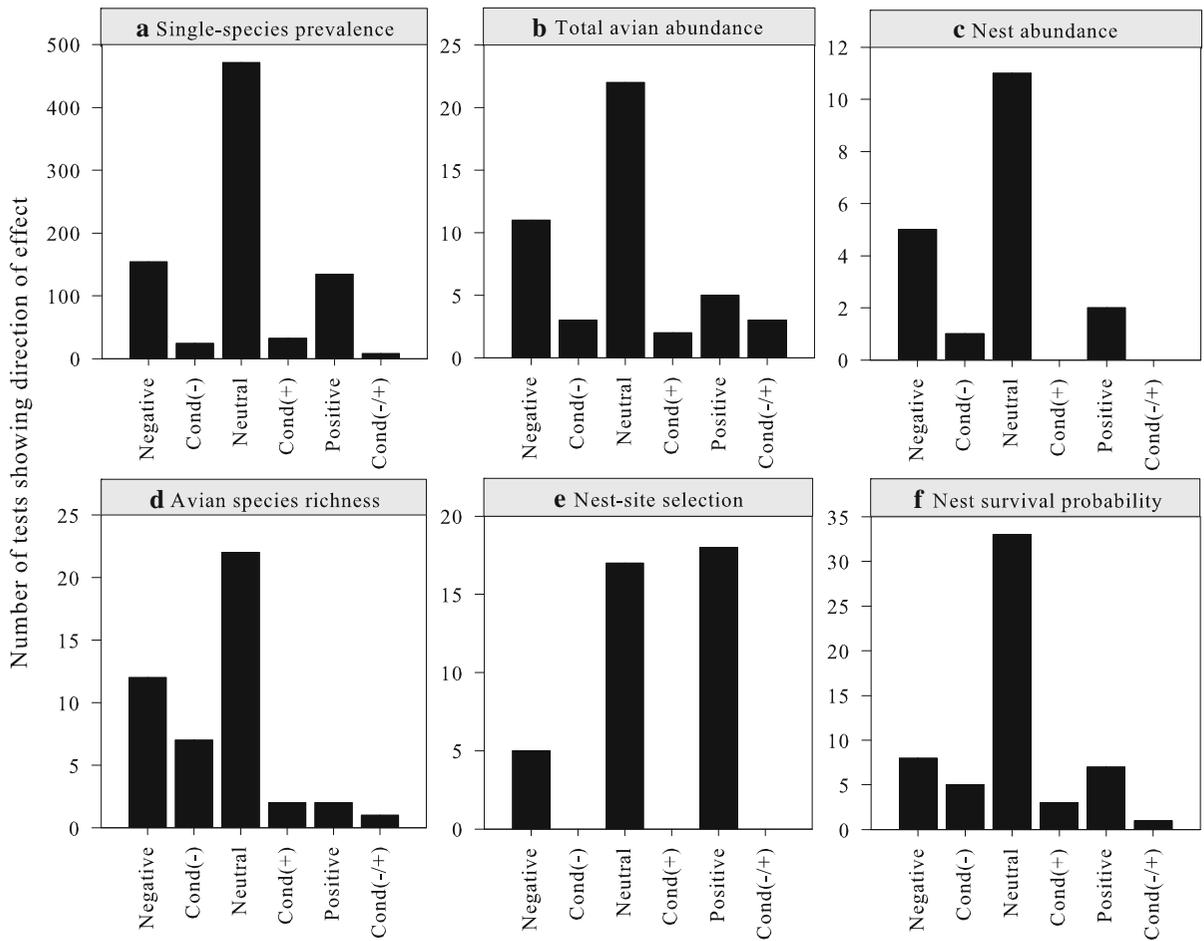


Fig. 1 The frequency of neutral (no effect), negative, positive, and variable effects (conditionally negative, conditionally positive, and conditionally negative-or-positive) of invasive vegetation on six metrics of avian ecology in North America. Y-axis scales differ among panels. Positive effects on nest-site

selection occurred when birds preferred to nest in invasive vegetation (negative effects represent avoidance). For all other metrics, a positive effect indicates an increase, a negative effect indicates a decrease, and a neutral effect indicates no change

Avian preferences for invaded or uninvaded habitats can have surprising effects. For instance, since older male chipping sparrows exclude first-year males from uninvaded habitats, first-year males have few older neighbors and thus do not learn their songs (Ortega et al. 2014a). Consequently, song diversity among young males is significantly reduced, potentially impacting lifelong reproduction.

Nest-site selection and fledgling habitat use

Forty tests from 16 studies (Fig. 1e) compared avian use of invasive plants as nest substrates relative to total substrate availability or compared invasive

plant prevalence near nests versus random points. Birds frequently preferred nesting in invasive substrates or invaded microsites (45.0% of tests); for example, gray catbirds (*Dumetella carolinensis*) preferred honeysuckle (*Lonicera* spp.) over native shrubs (Schmidt and Whelan 1999). Nearly as frequently though, birds showed no preference between substrates (42.5%). Only 12.5% of tests indicated avoidance of nesting in invasive plants. One study investigated how invasions affect fledgling habitat preferences: Northern cardinal and Acadian flycatcher (*Empidonax vireescens*) fledglings preferred dense patches of honeysuckle (Ausprey and Rodewald 2011).

Nest survival, fledgling survival, clutch size, and fecundity

Fifty-seven tests across 26 studies examined plant invasions' effects on nest survival (Fig. 1f). Some tests compared survival of nests in invasive versus native substrates, while others compared survival in invaded versus uninvaded microsites or study sites. Tests examined either individual bird species ($n = 48$) or pooled data from multiple species ($n = 9$). Most tests found neutral effects (57.9%), such as black-chinned hummingbirds (*Archilochus alexandri*) experiencing equal nest survival in saltcedar (*Tamarix* spp.), Russian olive (*Elaeagnus angustifolia*), and native plants (Smith et al. 2009). Still, invasion sometimes reduced (14.0%), increased (12.3%), or had conditional effects (15.8%) on nest survival.

Studies of impacts on fledgling survival were infrequent, with three studies reporting three neutral effects and one negative effect. Studies of clutch size and seasonal fecundity (offspring fledged per pair) were similarly rare, with only five tests reported on clutch size (4 neutral, 1 negative) and seven reported on seasonal fecundity (4 neutral, 3 negative). Effects on fecundity varied among species (e.g. Brand and Noon 2011).

Brood parasitism

Brood parasitism by brown-headed cowbirds (*Molothrus ater*) can reduce avian fitness because cowbirds compete with host chicks for food, reduce host juvenile survival, and increase parental energy costs (Hoover and Reetz 2006). Three studies have examined whether invasions affect parasitism rates, with mixed conclusions. Although parasitism on Acadian flycatchers increased with honeysuckle cover (Rodewald 2009), southwestern willow flycatchers (*Empidonax traillii extimus*) nesting in Russian olive only experienced elevated parasitism in some years (Stoleson and Finch 2001). Moreover, Russian olive and Eurasian grasses did not affect yellow-breasted chat (*Icteria virens*) or grasshopper sparrow (*Ammodramus savannarum*) parasitism, respectively (Stoleson and Finch 2001; Hovick and Miller 2013).

Offspring provisioning and body condition

Only one study examined effects on provisioning rates: gray catbirds delivered food more frequently to

their young as honeysuckle invasion increased (Gleditsch and Carlo 2014). In this case, increased provisioning led to higher catbird nestling quality (high mass-to-tarsus length ratios; Gleditsch and Carlo 2014). In contrast, chestnut-collared longspur nestlings in crested wheatgrass monocultures gained mass more slowly, fledged at lower mass, and took one day longer to fledge than nestlings in native grasslands (Lloyd and Martin 2005). Nestling masses of other species appeared unaffected by invasive cover (Jones and Bock 2005; Kennedy et al. 2009).

Adult body condition and survival

Even though the body condition of adult birds has strong effects on migration and reproduction (Smith and Moore 2003), only two articles reported whether plant invasions affect adult condition. Adult Wilson's warblers (*Cardellina pusilla*) occupying saltcedar stands did not differ from adults in native tree stands for some body condition metrics (e.g. body mass, fat scores), but triglyceride levels were greater in adults in saltcedar stands, while glycerol levels were greater in native vegetation (Owen et al. 2005; Cerasale and Guglielmo 2010).

Only one study has examined whether invasive plants affect adult survival: recapture rates of male and female northern cardinals between years were unaffected by honeysuckle invasion (Leston and Rodewald 2006). However, invasive plants can cause adult mortality either directly, such as when small birds (e.g. ruby-throated hummingbirds *Archilochus colubris*) become entangled in burdock (*Arctium* spp.; Hinam et al. 2004), or indirectly, such as when cyanobacteria (order: Stigonematales) growing on invasive *Hydrilla verticillata* cause outbreaks of Avian Vacuolar Myelinopathy (Wilde et al. 2005).

Variation in impacts among habitats, plant growth forms, and seasons

Examining how the impacts of plant invasions on avian ecology vary across different ecological contexts revealed several noteworthy patterns (Appendix C in Electronic Supplementary Material). One of the most salient is that negative impacts on total-community avian abundance were more common in grasslands than in woodlands and riparian woodlands (Fig. C3 in Electronic Supplementary Material).

Across all habitats, most effects on total abundance were neutral (48.9%), while negative effects were comparatively uncommon (23.4%). In grasslands, however, negative and neutral effects were equally common (45% each), whereas negative effects were rare in woodlands (0%) and riparian woodlands (10%). Similarly, negative effects on total abundance and species richness were more commonly associated with invasive herbaceous plants than with woody plants (Figs. C8, C9).

Interestingly, however, negative and conditionally negative effects on nest survival were proportionally more common in woodlands than in grasslands and riparian woodlands (54.6 vs. 13.8 and 25%, respectively; Fig. C5 in Electronic Supplementary Material). Given that birds in woodlands in most cases *preferred* to nest in invasive plants (87.5%; Fig. C6 in Electronic Supplementary Material), this pattern is particularly remarkable. In contrast, while birds in shrublands also often preferred to nest in invasive plants, they frequently experienced enhanced nest success there (Figs. C5, C6; note limited samples sizes). This underscores another pattern: woody plants, not herbaceous, accounted for most instances of birds preferring to nest in invasive plants (Fig. C11 in Electronic Supplementary Material), as well as for disproportionately more positive *and* negative effects on nest survival (Fig. C10 in Electronic Supplementary Material).

Examining patterns across seasons, negative and positive impacts of invasions on single-species prevalence were more common in winter than other seasons (Fig. C12 in Electronic Supplementary Material). Also, most negative effects on species richness occurred during the breeding season, though there are few tests reported in other seasons (Fig. C14 in Electronic Supplementary Material).

Influences of significance criteria, sample sizes, impact factors, and invasion magnitudes

To assess whether our choice to review results derived using a variety of significance criteria influenced our results, we compared the effects of plant invasions on six avian metrics while (1) including tests regardless of significance criteria used, and (2) only including tests evaluated based on $\alpha = 0.05$ (Fig. 2). These distributions reveal similar qualitative patterns, indicating that this choice did not bias our interpretation of the literature.

We also assessed whether test sample sizes, journal impact factors, or invasion levels within study systems influence the likelihood that tests examining invasion impacts on the prevalence of individual bird species will reveal negative, neutral, or positive responses. None of these factors significantly influenced response directions (GLMMs—*sample size*: $F_{2,625} = 1.46$, $p = 0.23$; *journal impact factor*: $F_{2,641} = 0.64$, $p = 0.53$; *invasion intensity*: $F_{2,527} = 1.42$, $p = 0.24$).

Mechanisms of invasive plant impacts on birds

As demonstrated, invasive plants can impact many patterns and processes in avian communities. These effects manifest through a broad suite of ecological pathways, including changes in habitat structure, predation risk, and food availability (Fig. 3). Many studies have evaluated specific mechanisms, shedding needed light on the processes shaped by invasive plants. We review these mechanisms here, and quantify the number of articles that support or contradict them (Table 1).

Invasive plants affect avian distributions by altering habitat structure

Avian responses to plant invasions often arise from changes in habitat structure, which mediate nest-site availability, refuge from predation, and ease of foraging. Avian responses to structural changes should depend on individual species' ecological requirements, and authors frequently invoke species-specific habitat needs to explain responses to invasion (e.g. Davis and Duncan 1999; Rosenstock and van Riper 2001; Gifford and Armacost 2012; Keller and Avery 2014). However, most authors simply assess correlations between changes in avian distributions and changes in habitat structure without explicitly assessing *why* birds respond the way they do. These studies provide limited mechanistic conclusions. In contrast, studies that assess the processes underlying avian responses to structural change are informative.

For example, some authors have examined whether avian abundance decreases when native plants that provide nest sites are displaced by invasive plants. For example, cavity- and canopy-nesting birds in southwestern riparian forests depend on native cottonwoods and willows (*Salix* spp.) for nesting, whereas

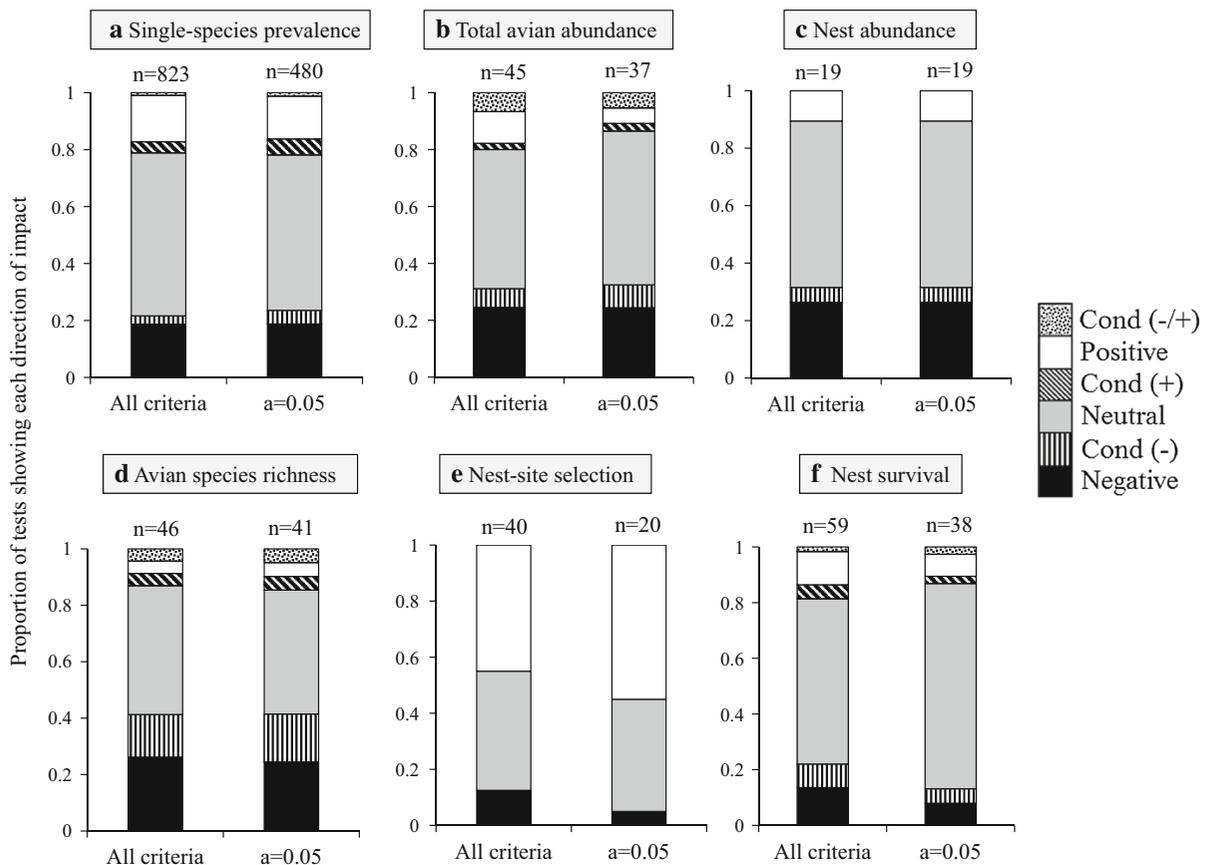


Fig. 2 Published relative frequencies of negative, neutral, positive, and variable effects (conditionally negative, conditionally positive, and conditionally negative-or-positive) of invasive vegetation on six metrics of avian ecology, compared between two groups: (1) all published tests, irrespective of

significance criterion used, and (2) published tests evaluated using the significance criterion $\alpha = 0.05$. Frequencies of effect directions are shown as proportions, but these distributions are based on unequal numbers of tests (n)

homogeneous saltcedar and Russian olive stands only support subcanopy- and shrub-nesters (Taylor 2003; Smith and Finch 2014). Similarly, sagebrush-dependent birds avoid nesting in patches where shrubs are scarce due to grass invasions (Reynolds and Trost 1980), and some wetland-dependent birds appear unable to nest in purple loosestrife (*Lythrum salicaria*) monocultures (Maddox and Wiedenmann 2005). Alternatively, invasive plants can provide nesting structures not supplied by native vegetation, such as crested wheatgrass enabling horned larks (*Eremophila alpestris*) to nest in sagebrush shrublands (Reynolds and Trost 1980). Novel nest sites may also explain why several bird species expanded their ranges into saltcedar-invaded areas that historically lacked mature trees (Hunter et al. 1988).

Although plant structure often determines nesting suitability, structure changes within seasons according to plant growth phenology. Invasive plants that leaf out early relative to native plants may be attractive to nesting birds—a hypothesis supported in some cases (Amur honeysuckle; Rodewald et al. 2010), but not others (crested wheatgrass; Lloyd and Martin 2005). In contrast, if invasive plants grow late in the season, birds may experience reduced fecundity due to delayed nesting (Maddox and Wiedenmann 2005).

In addition to affecting nesting, changes in habitat structure can alter avian foraging efficiency. Dense plant growth may inhibit access to arthropods, potentially reducing avian abundance (Osborne et al. 2012) or shifting diet composition (Kennedy et al. 2009). Alternatively, when invasive plants increase

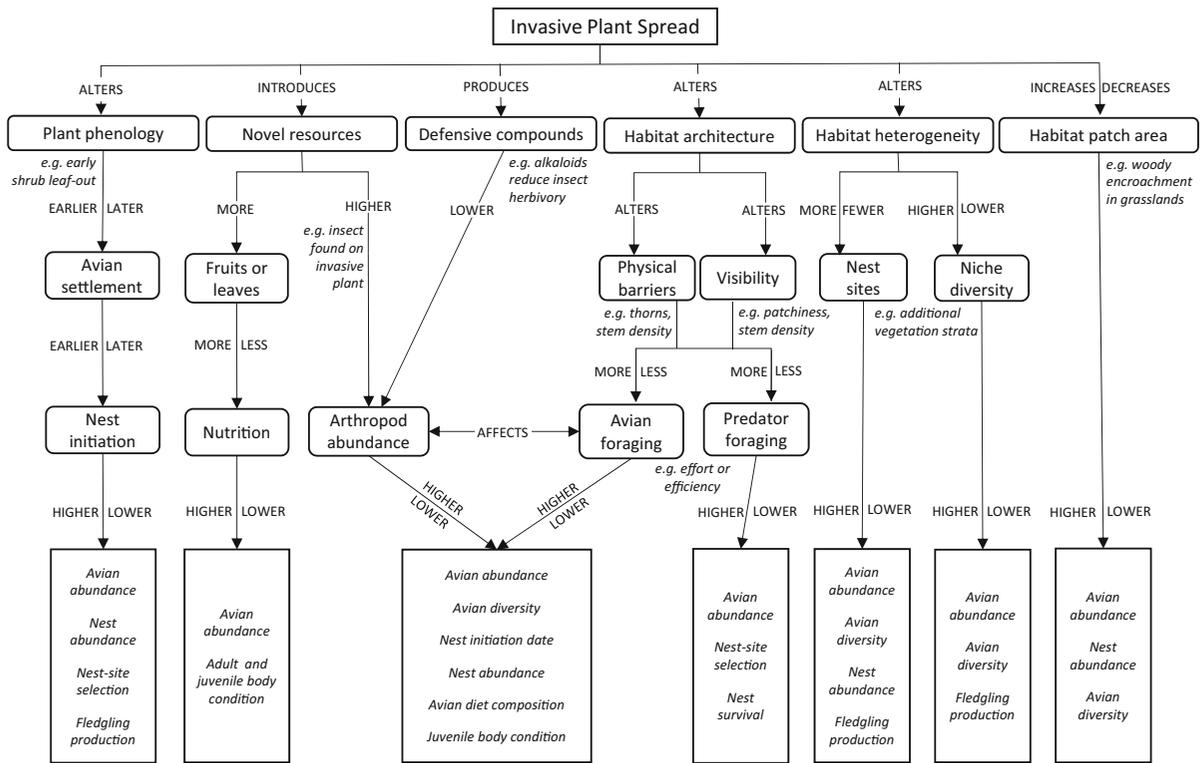


Fig. 3 A conceptual diagram depicting many of the mechanisms by which invasive plants can influence birds. Invasions can alter key habitat characteristics such as vegetation architecture, heterogeneity, patch size, and phenology, which in turn affect avian settlement timing, the ability of bird species to nest and forage, and the ability of predators to detect and

access nests and fledglings. Invasive plants may also mediate food availability directly or by altering arthropod abundance. Effects on resource availability and habitat characteristics lead to increases or decreases in avian abundance, richness, body condition, fledgling production, and more

vegetation patchiness, foraging opportunities for birds may improve as physical barriers decrease and visibility increases (Walker 2008).

Invasive plants may also affect richness by altering structural habitat heterogeneity, since patchiness often corresponds to niche availability (MacArthur and MacArthur 1961; Rotenberry and Wiens 1980). Supporting this, some studies have found that avian richness peaks at moderate invasion levels in association with increased structural heterogeneity (McAdoo et al. 1989; Van Riper et al. 2008; Fischer et al. 2012). Moreover, when invasive grass monocultures are more structurally homogeneous than native prairies, grassland bird richness and abundance are often lower (Wilson and Belcher 1989; George et al. 2013), whereas invasion may have few effects when structural heterogeneity is comparable (Sutter and Brigham 1998; Chapman et al. 2004).

Many birds also respond to habitat patch size, often only occupying patches of a minimum threshold area

(Johnson and Igl 2001). As such, if a bird cannot use invasive vegetation it may even avoid uninvaded remnants if remaining patches are too small. In contrast, as invaded patches expand, birds unable to use native vegetation may increase in occupancy. These mechanisms are illustrated in Great Plains avian communities: grassland birds have disappeared locally as eastern redcedar (*Juniperus virginiana*) encroachment has reduced the size of contiguous grassland patches, but woodland species have recently colonized expanding tracts of woody vegetation (Coppedge et al. 2001).

Invasive plants alter predator communities and foraging efficiency

Because vegetation structure can augment or inhibit predator foraging and nest detection (Martin 1993), authors commonly propose that changes in vegetation

Table 1 Mechanisms proposed to explain the impacts (or lack of impacts) of invasive plants on North American birds, and the number of reviewed articles that support or contradict each proposed hypothesis

Pattern and mechanism	DS	IS	DC	IC
<i>Mechanisms related to avian distributions</i>				
Changes in avian species richness and abundance are dependent on the effects of invasions on habitat structure (e.g. stem density, plant architecture, total vegetation cover, litter depth, litter and bare ground cover, vegetation height)	21	18	4	4
Changes in avian species richness and abundance are dependent on the effects of invasions on floristic composition	3	1	0	0
Changes in avian species richness and abundance are dependent on the effects of invasions on habitat heterogeneity	6	7	0	0
Abundances of area-sensitive species change because invasions reduce the size of uninvaded habitat patches but increase the size of invaded habitat patches	2	0	0	0
Impacts of invasive plants on avian species richness and nest abundance are mediated through their effects on nest-site availability	7	7	1	0
<i>Mechanisms related to nest-site selection and avian fitness</i>				
Some species of birds appear to prefer nesting in invasive plants because other species competitively exclude them from nesting in native plants	0	0	0	1
Birds prefer nesting in plants and habitats that grow leaves and accumulate biomass early in the breeding season	2	1	1	0
Changes in nest survival and parasitism are affected by invasion because high vegetation densities indicate to predators a high probability of areas containing nests, and predators thus increase their foraging efforts	0	2	0	0
Nests in monocultures of invasive plants tend to be placed in similar strata, increasing predator search efficiency	0	1	0	0
Birds prefer or avoid nesting in invasive plants because they select nest sites on the basis of vegetation density and concealment, and nest predation risk is mediated by these factors	2	5	1	1
When nests must be placed lower and fledglings must perch lower in the canopy because of invasions, accessibility by predators increases; this effect may be mediated by nest substrate structure	1	2	4	1
Invasions by thorny plants influence the survival of nests placed in them because thorns deter nest predators	2	0	2	0
Nests experience similar mortality rates when placed in invaded and uninvaded patches because invasions create functionally redundant habitats	0	2	0	0
Invasive plants create ecological and evolutionary traps	3	1	2	1
Invasion effects on nest and fledgling predation depend on predator responses to accompanying changes to habitat structure and composition; these responses may depend on the spatial scale of invasions	4	3	0	0
<i>Mechanisms related to food and foraging</i>				
Invasions change avian abundance, richness, body condition, and diets because invasive plants structurally inhibit birds from foraging on arthropods	0	2	0	1
Birds prefer to eat fruits and arthropods found on invasive plants	1	0	3	1
Birds prefer to eat fruits, leaves, and arthropods found on native plants	6	1	3	1
Invasive fruits are low in nutrition	3	0	1	1
Fruits and arthropods on invasive plants provide sufficient nutrients for birds to maintain normal or improved body condition	3	1	0	0
Consuming invasive fruits alters avian plumage coloration because nutritional content of invasive fruits differs from native fruits	3	0	0	0
Birds are more abundant in invaded habitats, expand their ranges to include invaded areas, and track seasonal availability of fruits because invasive plants increase the abundance of food available to herbivorous birds.	2	5	1	2
Avian abundance and species richness decrease with invasion because invasions reduce abundance of arthropods that insectivores require	1	8	0	4
Avian abundance and species richness increase with invasion because invasions increase abundance of arthropods or supply novel arthropods	0	5	0	1

Support and contradiction were classified as direct if all the variables involved in the mechanism were explicitly compared. Support and contradiction were classified as indirect if the variables involved were not all explicitly compared, but observations reported in the study were consistent (or inconsistent) with the mechanism. Citations for the articles examining these mechanisms are listed in Appendix D in Electronic Supplementary Material

DS articles directly supporting, *IS* articles indirectly supporting, *DC* articles directly contradicting, *IC* articles indirectly contradicting

structure accompanying invasions alter predation rates, though evidence for these hypotheses is mixed (e.g. Cook and Toft 2005; Leston and Rodewald 2006; Fisher and Davis 2011).

Several structural components may affect nest predation. Presence of thorns could mediate the relative protection provided by plants against predation, but although nests in thorny shrubs sometimes experience high survival (Schmidt and Whelan 1999) this effect is not ubiquitous (Borgmann and Rodewald 2004; Schlossberg and King 2010). Invasion may also mediate predation through nest concealment. Indeed, greater stem density sometimes reduces nest predation (Grant et al. 2006; Smith et al. 2009), but this effect has not manifested in all cases (Borgmann and Rodewald 2004). Finally, nests built in short invasive plants (or fledglings perching in such plants) may be situated relatively close to the ground, potentially increasing their detectability. This hypothesis is supported in some cases (Schmidt and Whelan 1999) but not others (Borgmann and Rodewald 2004; Rodewald et al. 2010; Ausprey and Rodewald 2011). In contrast, invasive plants enable some birds to nest off the ground, reducing predation by ground-dwelling predators (e.g. white-footed mice *Peromyscus leucopus*; Schmidt et al. 2005).

Invasion may also alter predator foraging effort and efficiency. Some authors propose that foraging efficiency may be low in densely-invaded stands due to the large number of potential nest sites that predators must examine (Martin 1993; Schlossberg and King 2010). Alternatively, predators may increase search effort if high vegetation density indicates a greater probability that patches will contain nests (Schmidt and Whelan 1999; Rodewald 2009). Moreover, birds in monocultures may be forced to nest in a single vegetation stratum, increasing predator foraging efficiency (Borgmann and Rodewald 2004). None of these hypotheses have been experimentally tested in an invasion context, and only the latter has observational support. Specifically, early in the breeding season northern cardinals overwhelmingly place nests in honeysuckle due to its early leaf-out, but nests in honeysuckle are depredated at very high rates until cardinals nest in more substrate species later in the summer (Rodewald et al. 2010).

Interestingly, invasion effects on nest survival may depend on the identity of predators and invading plants. For instance, predation of fledglings by

13-lined ground squirrels (*Spermophilus tridecemlineatus*) is high in exotic-grass-dominated fields relative to native grasslands (Fisher and Davis 2011), yet predation by ground squirrels decreases as invasive tree cover expands (Grant et al. 2006). This example complements other studies suggesting that predator-specific habitat use mediates effects of invasion on nest survival (Lyons et al. 2015) and cowbird parasitism (Rodewald 2009).

Invasive plants alter food availability and nutritional quality

Invasions can impact birds by altering food supplies. For instance, invasions may impoverish arthropod abundance and diversity if herbivorous arthropods cannot tolerate the defensive secondary compounds produced by invasive plants (Litt et al. 2014). While no studies have experimentally tested effects of reduced arthropod abundances on birds following invasions, observational studies indicate a linkage. Relatively low arthropod abundance and biomass in invaded habitats often coincides with low avian richness (Hickman et al. 2006; George et al. 2013) and abundance (Flanders et al. 2006; Hickman et al. 2006; Cerasale and Guglielmo 2010). Reduced arthropod numbers could also impact fitness if food limitation reduces offspring body condition—a hypothesis indirectly supported by Lloyd and Martin (2005). Moreover, birds that delay nesting because invaded patches support relatively few arthropods may be less likely to double brood, and thus produce fewer fledglings (Ortega et al. 2006).

It is important to note though that invasive plants do not always suppress arthropods (e.g. Kennedy et al. 2009), and may even support more, increasing avian abundance (Walker 2008). Moreover, when arthropod and avian abundances are lower in invaded areas, adult birds occupying those areas may still achieve excellent body condition—perhaps as a result of relatively low competition for food (Cerasale and Guglielmo 2010).

In addition to affecting total arthropod numbers, invasive plants may provide novel foods such as fruits (Ingold and Craycraft 1983), foliage (Baldwin and Lovvorn 1994), or arthropods associated with invasive plants (Yard et al. 2004; Ortega et al. 2014b). New food sources may allow species to increase in abundance or expand their ranges, as evidenced by populations of frugivorous birds (e.g. gray catbirds,

northern cardinals, northern mockingbirds *Mimus polyglottos*) increasing with fruit-bearing shrub invasions (Stiles 1982; Leston and Rodewald 2006; McCusker et al. 2010; Gleditsch and Carlo 2011). In some cases birds even appear to prefer eating invasive fruits (Lafleur et al. 2007; but see Whelan and Willson 1994; Smith et al. 2013), even though those fruits sometimes provide relatively poor nutrition (Ingold and Craycraft 1983; Smith et al. 2013; but see Greenberg and Walter 2010). Despite this, few studies assess whether consuming invasive fruits impacts avian body condition, and those that do have not shown detrimental effects (Witmer 1996; Gleditsch and Carlo 2014). It may be that the sheer abundance of invasive fruits allows birds to overcome nutritional deficits, or that invasive fruits improve body condition by providing useful secondary compounds and nutrients (Gleditsch and Carlo 2014). These hypotheses have not been tested.

Secondary compounds in invasive fruits are known, however, to affect adult plumage in some species. Witmer (1996) demonstrated experimentally that cedar waxwings (*Bombycilla cedrorum*) fed with honeysuckle berries develop red-tipped rather than yellow-tipped rectrices—an increase in erythrim resulting directly from high concentrations of the carotenoid rhodoxanthin in honeysuckle fruits. Subsequently, studies have linked honeysuckle fruits to increased erythrim in northern cardinals (Jones et al. 2010) and Baltimore orioles (*Icterus galbula*; Hudon et al. 2013). Erythrim has historically acted as an honest signal of male quality, with higher quality males being better able to acquire high-carotenoid foods and incorporate the pigments into their feathers. However, the easy availability of carotenoids in invasive fruits could reduce the usefulness of this cue for avian mate selection, potentially decreasing sexual selection and leading to poor mate choices (Jones et al. 2010).

Discussion

Awareness that invasive species are not categorically harmful is growing in conservation and management communities (Shackelford et al. 2013). Our review supports this perspective, showing that invasive plants in North America have varied effects on birds. In particular, effects on single-species prevalence, total avian abundance, nest abundance, and nest survival

are most frequently neutral, while invasive plants often reduce or conditionally reduce species richness and are regularly preferred as nest substrates (Fig. 1). These patterns sometimes vary across habitats, seasons, and with the growth form of invading plants (Appendix C in Electronic Supplementary Material).

Although we could not control for the effects of potential confounds within studies, such as landscape contexts and study-site sizes, we do not expect these factors to bias our results given the large number of articles reviewed. Moreover, we have demonstrated that low sample sizes are not responsible for the large number of reported neutral results, since sample sizes did not predict test outcomes.

The high frequency of neutral effects on species, whole-community, and nest abundances suggests that invasive plants do not consistently alter resource availability or habitat preferences for birds. This may indicate that invasive plants can be functionally equivalent to native vegetation, providing similar habitat structure and food supplies and thus having minimal effects on avian habitat selection. The preponderance of neutral effects of invasions on nest survival could also arise from functional equivalence, or if habitat alterations that increase predation are counteracted by changes in predator communities or foraging behavior. For instance, dense shrub thickets may impede predator mobility, but predators might increase foraging effort within them if nest density is higher. Regrettably, few studies have directly examined how invasions influence predators (but see Grant et al. 2006; Fisher and Davis 2011; Lyons et al. 2015).

Though neutral relationships are very common for many avian metrics, both positive and negative impacts certainly arise, and these directional effects can have strong impacts on avian communities when they occur. Positive impacts show that invasive plants can serve valuable ecological functions (Schlaepfer et al. 2011), acting as superior nest substrates (Schlossberg and King 2010), providing abundant foods (Baldwin and Lovvorn 1994; Gleditsch and Carlo 2011), or creating high-quality habitats for at-risk species (Cook and Toft 2005; Jones and Bock 2005). Importantly though, avian fitness must be monitored in invaded areas since they sometimes act as ecological traps (Lloyd and Martin 2005; Nordby et al. 2009; Rodewald et al. 2010).

Negative impacts reveal the challenges that invasions pose for avian conservation. Though relatively

uncommon, reduced avian abundances and nest survival increase vulnerability of populations to local extirpations. More frequently, invasions reduce avian species richness (e.g. Hickman et al. 2006; Klaus and Keyes 2007; Brand et al. 2008), which is especially concerning since declines or losses of even a few species can have outsized effects on plant and invertebrate communities by reducing pollination, seed dispersal, or arthropod numbers (Caves et al. 2013; Karp et al. 2013).

A recent meta-analysis highlighted the negative impacts of plant invasions, finding that, on average, invasive plants significantly reduce avian richness, abundance, and fitness (Schirmel et al. 2016). Our review provides a different perspective. Although our results align somewhat regarding effects on richness, we found that negative impacts on abundance and fitness were uncommon. Why might this be? First, we note that the meta-analysis included studies from islands, where avian populations are often disproportionately vulnerable (Szabo et al. 2012). Since our review was restricted to continental regions, we may have considered fewer high-risk systems, thus detecting fewer negative effects. Differences in methodology could also contribute. Since meta-analyses only consider studies from which effect sizes are calculable, we reviewed a larger pool of studies, exposing a greater variety of relationships. To illustrate this point clearly, Schirmel et al. analyzed 29 articles studying birds across the globe (Schirmel et al. 2016, Appendix S1), whereas we reviewed 128 articles from North America, including 16 included in the meta-analysis. Our methods thus counted many of the effects assimilated in Schirmel et al. However, since our assessment was not based on effect sizes, our divergent findings could be explained in part if most of the neutral effects that we reviewed in fact represented negative trends too weak to achieve statistical significance. We do not believe that the disparities can be ascribed to publication bias given our finding that journal impact factors were not related to the directions of reported effects.

Surprisingly, we found that the likelihood of observing negative, neutral, or positive effects of invasions on avian abundance does not differ across studies as a function of invasion intensity. This result runs counter to the expectation that negative effects should intensify with increasing invasion, and suggests that in many cases variability in impacts between

systems may be attributable to factors other than degree of invasion.

Variability across systems should compel scientists to discern the conditions under which different effects arise. Our review reveals that some of the patterns we have highlighted change depending on ecological context. For instance, invasions reduce whole-community avian abundances much more often in grasslands than in woodlands and riparian woodlands, even though negative impacts on nest survival have been more common in woodlands than in other habitats. Our findings also indicate that negative effects of invasions on species richness arise more often during the breeding season than other seasons, but both positive and negative effects on avian abundance are more common during winter. This seasonal variation could exist because birds garner different resources from plants through the year. For instance, invasive plants may primarily affect breeding birds via changes in nest-site and arthropod availability (Maddox and Wiedenmann 2005; George et al. 2013), whereas nonbreeding-season effects might depend more on fruit and seed availability (McCusker et al. 2010). Impacts on individual bird species could also vary with autecology, with some species being inherently more sensitive to habitat changes due to specialized diets or nesting requirements (e.g. Schneider and Miller 2014; Smith and Finch 2014). Finally, effects may vary as a function of time-since-invasion, since avian communities sometimes differ between patches of contrasting maturity (Gifford and Armacost 2012). Investigating the long-term dynamics of invasions could reveal whether some birds will learn to use novel resources, potentially increasing richness in invaded sites over time.

In addition to highlighting variability in invasion impacts, our review reveals critical knowledge gaps. Few studies have examined how invasions affect parental provisioning, juvenile body condition, or fledgling survival, even though the post-fledging stage represents a bottleneck in many populations and habitat composition frequently affects juvenile survival (Cox et al. 2014). Moreover, since several studies have indicated links between invasions, food supplies, and changes in avian communities (e.g. Yard et al. 2004; Flanders et al. 2006; George et al. 2013), experiments and mechanistic observational studies are needed to test these links across study systems (McCary et al. 2016). Another issue that warrants

greater attention is how invasions alter avian assemblages at continental scales. Invasive plants providing reliable food sources and nesting sites may be reshaping migration pathways (McCusker et al. 2010; Gleditsch and Carlo 2011) or expanding species' ranges (Stiles 1982; Hunter et al. 1988). Conversely, invasions could contribute to avian declines if they eliminate unique habitats required by avian specialists (Brand et al. 2008). Examining impacts at broad spatial scales requires high-quality data on invasive plant distributions, so investigators might consider using resources such as the USDA's National Invasive Species Data Center to address these questions.

It is clear that the effects of invasive plants on North American birds are neither simple nor uniform. The fact that invasions often appear not to change avian distributions and reproduction, and may in some cases benefit birds, suggests that we should not presume that removing invasive plants will universally advance avian conservation (Davis et al. 2011). Yet these patterns should not engender complacency about invasions, particularly given the negative effects reviewed here and the habitat-specific patterns we have reviewed (Simberloff et al. 2011). Furthermore, different trends could prevail in other continents, and we emphasize that our results are solely applicable to avian communities and may not speak to impacts on other taxa or ecosystem processes (Vitousek et al. 1996; Pyšek et al. 2012; Simberloff et al. 2013; Litt et al. 2014; Schirmel et al. 2016). Overall, because responses to invasion are inconsistent, it is incumbent upon scientists and practitioners to monitor birds in invaded habitats on a case-by-case basis (Appendix C in Electronic Supplementary Material). However, based on the data we have examined, invasive plants do not appear to ubiquitously degrade avian communities.

Supplementary material

A list of all articles meeting our review criteria is available online, organized by which ecological metrics were investigated in each article (Appendix A). This list includes a summary of the study seasons, locations, habitat types, and invasive plant species studied, as well as the number of tests reported and invasion intensities represented in each

article. Appendix A also includes a list of the bird species studied in reviewed articles, and citations for articles examining each species. A histogram is available showing publication years of reviewed articles (Appendix B), as well as figures showing the distributions of effect directions among different habitats, invasive plant growth forms, and seasons are available for five avian metrics (Appendix C). Lastly, Appendix D shows which of the studies we reviewed have supported or contradicted various mechanisms proposed to explain invasive plant impacts.

Acknowledgements Foremost, we would like to thank the many investigators whose investments of time and energy in collecting and publishing the reviewed data made this manuscript possible. Thank you to T.J. Benson for statistical advice, to C.R. Maresh for assistance with literature review, and to the "Bird Lab" avian discussion group at the University of Illinois at Urbana-Champaign for suggestions. E. Jongejans and two anonymous reviewers provided helpful comments to improve the manuscript. This material is based upon work that is partially supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, under Award No. ILLU-875-918.

Author contributions SBN wrote the manuscript, created online supplements, and conducted statistical analyses; SBN and JJC created the figures; SCS, SBN, CJD, JDF, CMP, and JRM designed the study; SBN, JJC, CJD, JDF, SJH, AJK, CMP, SCS, and TMS reviewed articles; SBN, JRM, JJC, TMS, CJD, AJK, and SJH edited the manuscript.

Compliance with ethical standards

Conflict of interest None.

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