

The effects of introduced plants on songbird reproductive success

Lani T. Stinson  · Liba Pejchar

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Abstract The effects of non-native plants on habitat use are well studied; however, whether introduced plants negatively influence reproductive output of animal populations has received much less attention. We conducted a systematic literature review to evaluate the influence of non-native plants on reproductive performance in songbirds. Our global search resulted in 32 relevant articles, from which we compiled a dataset of 133 songbird responses to nesting in or around non-native vegetation. Reproductive metrics examined included measures of nest survival/mortality, productivity, fledgling survival, adult survival, nestling condition, and brood parasitism. Thirty-five percent of songbird reproductive responses were negative ($n = 47$), with 31% positive ($n = 41$) and 34% neutral ($n = 45$) responses found. Only 15% of responses were statistically significant effects ($n = 20$), and of these, negative effects were reported three times as often as positive effects. Non-significant trends were more prevalent (51% of responses), and the frequency of negative and positive

trends was similar. The probability of finding a negative response (significant effect or non-significant trend) was higher for birds using introduced shrubs and wetland habitats. Mechanisms underlying responses were diverse, though similar drivers, such as differences in vegetation characteristics, predation pressure, and resource availability, were offered to explain both positive and negative effects. We found evidence for non-native plants as ecological traps in 39% of articles that assessed these phenomena ($n = 16$). This review highlights the sparsity of research targeting reproductive responses to plant invasion and synthesizes existing information to enhance our understanding of how birds respond to non-native plants. Our findings could be used to inform future research priorities in a world increasingly dominated by novel ecosystems.

Keywords Invasive exotic species · Non-native vegetation · Reproductive performance · Nest survival · Fitness · Ecological trap

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L. T. Stinson (✉) · L. Pejchar
Department of Fish, Wildlife and Conservation Biology,
Colorado State University, 1474 Campus Delivery,
Fort Collins, CO 80523, USA
e-mail: lani.stinson@colostate.edu

Introduction

The spread of non-native species is considered the second largest threat to biodiversity worldwide (Wilcove et al. 1998). The ecological impacts of non-native plant invasions are well-documented across diverse

ecosystems, taxa, spatial and temporal scales, and levels of biological complexity (Vila et al. 2011; Pyšek et al. 2012; Schirmel et al. 2016). Non-native plants can alter native species abundances, community composition, and species richness, as well as species interactions and community structure through alterations in food web dynamics (Richardson et al. 2007; Hladyz et al. 2011; Hajzlerova and Reif 2014). These changes can, in turn, result in negative consequences for ecosystem functioning and human well-being (Pejchar and Mooney 2009).

Much of the previous research on introduced plants has assessed impacts on habitat quality for native species, focusing primarily on changes in the use, abundance/density, species richness, and diversity of resident species (Vila et al. 2011; Bateman and Ostoja 2012; Schirmel et al. 2016). However, such habitat use metrics have been criticized as poor indicators of habitat quality (Van Horne 1983) or breeding success (Vickery et al. 1992). Invasion-mediated changes in habitat use, therefore, may not equate to negative effects on reproduction and survival for resident species (Safford 1997; Meyer et al. 2015). Thus, understanding the influence of non-native plant invasions on reproductive parameters is needed for effective conservation and management of native species in a world increasingly dominated by novel ecosystems (Hobbs et al. 2006, 2009).

Songbirds often play important ecological roles in ecosystems and serve as common indicators of ecological integrity (Carignan and Villard 2002; Sekercioglu 2006). Previous research indicates that songbirds regularly nest in habitats containing non-native vegetation and often use non-native plants as nesting substrates (Aslan and Rejmanek 2010; Smith and Finch 2014). Findings are mixed, however, as to whether and how nesting in non-native vegetation affects reproduction, with species-specific, context-dependent and often conflicting responses reported across studies (Lloyd and Martin 2005; Ludlow et al. 2015). Context-dependence, or variation in the strength and direction of impacts across different ecological contexts, arises from a variety of different abiotic and biotic factors operating in recipient ecosystems and has made uncovering general patterns of impact difficult (Pyšek et al. 2012; Hulme et al. 2013; Chamberlain et al. 2014).

The extent to which non-native plants serve as functional replacements for native vegetation, or

decrease habitat quality for nesting songbirds, remains unclear. Introduced plants may convert high quality habitat to ecological traps, habitats preferred by birds despite conditions that decrease fitness (Battin 2004; Robertson and Hutto 2006). This phenomenon arises as a result of an uncoupling of formerly reliable environmental cues and reproductive success (Schlaepfer et al. 2002, 2005). For birds, maladaptive behavioral decisions favoring lower quality habitats, including those with higher predation rates or reduced quantity or quality of prey resources to feed nestlings, can lead to negative reproductive consequences, such as decreased nest survival or productivity (Schmidt and Whelan 1999; Lituma et al. 2012). However, other studies suggest that non-native vegetation may provide quality nesting habitat, sometimes conferring equivalent or higher nesting success compared to native habitats (Schlossberg and King 2010; Meyer et al. 2015). To more effectively conserve songbird populations impacted by non-native plant invasions, we need a better understanding of non-native effects on songbird reproductive performance as well as the generality of these trends across various habitat types, growth forms of non-native vegetation, and plant and avian taxa.

The objective of this review was to synthesize all available literature on the effects of introduced plants on songbird reproductive success. We conducted a global systematic review of the peer-reviewed literature on this topic and characterized the direction and relative distribution of reported responses across different habitat types, vegetation forms, passerine taxa, and reproductive metrics. This work provides an in-depth analysis of reproductive responses at a global geographic scope and builds on recent syntheses that have addressed invasive plant impacts more generally (e.g. Schirmel et al. 2016; Nelson et al. 2017). We draw on the results of the review to evaluate the frequency and conditions under which non-native plants have a positive or negative influence on songbird reproductive performance. We also assess evidence for whether, and under what circumstances, non-native plants represent ecological traps characterized by decreased avian reproductive success, or functional replacements for native vegetation. Finally, we identify gaps in understanding and propose a research agenda for improving understanding of the relationship between introduced plants and songbird

reproductive success to help mitigate the effects of introduced plants on native bird communities.

Materials and methods

Literature search

We conducted a systematic search of peer-reviewed literature to obtain articles examining the effects of non-native vegetation on songbird reproductive success. A topic search of Web of Science combining three strings of search terms was used to characterize the various components of the search while excluding irrelevant articles. The first string included all possible combinations of adjectives to describe non-native species and nouns to describe vegetation forms (e.g. shrub, grass; Table A.1, Appendix A in ESM). The second string targeted papers studying reproductive success and the third string constrained the search to avian responses (Table A.1, Appendix A in ESM). The complete search syntax is included in Fig. A.1 of Appendix A in ESM. We searched for articles published in English across all years and geographic regions, but excluded review articles.

We reviewed titles and abstracts of the resulting 132 articles to identify papers that assessed effects of non-native vegetation on metrics related to songbird reproductive success. We included articles that met all of the following criteria: (1) article assessed non-native plant impacts during the nesting or postfledging periods, (2) article assessed effects on native songbird taxa (i.e. Order *Passeriformes*), and (3) article reported at least one reproductive measurement or comparison between native and non-native habitats (e.g. plots or study areas) or nest substrates. Effects of all non-native plants were considered, including species termed '*invasive*' (i.e. causing harm) as well as those considered non-native without specifying invasiveness. Herein, we use the terms '*non-native*', '*introduced*', and '*exotic*' synonymously, with '*invasive*' being reserved for those species described as such by authors of the reviewed articles.

As the objective of the review was to characterize reproductive effects of plant invasions, we excluded papers that focused solely on habitat selection (e.g. nest site selection) or habitat use (e.g. abundance, diversity). In addition to articles with a stated objective of investigating non-native plant impacts, we also

included papers that assessed the effect of exotic vegetation within a broader context, such as examining effects of urbanization or habitat management actions on avian reproductive parameters, provided that the authors reported relative levels of native and exotic plant presence within these areas. We reviewed the full text of the 28 articles that met the above criteria, and we conducted a forward–backward search of the literature using each of these articles to determine if any additional papers cited by, or citing, these articles met the inclusion criteria. The forward–backward search resulted in an additional 4 articles, bringing the total to 32 articles included in the review (Table 1, Appendix B in ESM).

Data extraction

For each article that met our criteria, we recorded the following data: years of study, geographic location, habitat type, non-native species, non-native vegetation form, and passerine species and family. We also assessed whether each article considered the phenomena of ecological traps, evolutionary traps, or habitat sinks (hereafter, 'ecological traps') and determined whether the authors found any support for these hypotheses. This determination was based on specific statements of support for these hypotheses or findings of non-native habitat preference resulting in negative reproductive outcomes relative to native habitats.

We extracted measures of avian reproductive success pertaining to the nesting and postfledging periods. We recorded a range of metrics (Table 2) which fell into two broad categories: (1) direct measures of reproductive success, or (2) correlates of reproductive success. Reproductive measures included responses related to nest survival and mortality, productivity (e.g. clutch size, # young fledged), fledgling survival, and adult survival; reproductive success correlates included responses related to brood parasitism and nestling condition. Because we aimed to assess effects of plant invasion on reproductive metrics, we excluded responses related to habitat use or selection, prey availability, parental care behavior, and other measures deemed only weakly or indirectly correlated to nesting success. We also excluded metrics reported based on artificial nest experiments because artificial nests are widely criticized as insufficient proxies for natural nests due to the inherent

Table 1 Summary of reviewed articles examining non-native vegetation effects on songbird reproductive success

Citation	Title	Location	Habitat	Form	Non-native species	Passerine family
Ausprey and Rodewald (2011)	Postfledging survivorship and habitat selection across a rural-to-urban landscape gradient	OH, USA	Forest	Shrub	<i>Lonicera maackii</i>	Cardinalidae, Tyrannidae
Borgmann and Rodewald (2004)	Nest predation in an urbanizing landscape: the role of exotic shrubs	OH, USA	Forest	Shrub	<i>Lonicera</i> spp., <i>Rosa multiflora</i>	Cardinalidae, Turdidae
Cristinacce et al. (2009)	Increasing use of exotic forestry tree species as refuges from nest predation by the critically endangered Mauritius fody <i>Foudia rubra</i>	Mauritius	Forest	Tree	<i>Cryptomeria japonica</i> , <i>Pinus</i> spp.	Ploceidae
de la Hera et al. (2013)	Exotic tree plantations and avian conservation in northern Iberia: a view from a nest-box monitoring study	Spain	Forest	Tree	<i>Eucalyptus globulus</i> , <i>Pinus radiata</i>	Paridae
Fisher and Davis (2011)	Post-fledging dispersal, habitat use, and survival of Sprague's pipits: Are planted grasslands a good substitute for native?	SK, Canada	Grassland	Grass	<i>Bromus inermis</i> , <i>Poa</i> spp.	Motacillidae
Gleditsch and Carlo (2014)	Living with aliens: effects of invasive shrub honeysuckles on avian nesting	PA, USA	Forest	Shrub	<i>Lonicera maackii</i> , <i>Lonicera morrowii</i>	Mimidae, multiple
Grant et al. (2006)	Nest survival of clay-colored and vesper sparrows in relation to woodland edge in mixed-grass prairies	ND, USA	Grassland	Grass	<i>Poa pratensis</i>	Passerellidae
Jones and Bock (2005)	The Botteri's sparrow and exotic Arizona grasslands: the role of exotic shrubs	AZ, USA	Grassland	Grass	<i>Eragrostis curvula</i> , <i>Eragrostis lehmanniana</i>	Passerellidae
Kennedy et al. (2009)	Effects of native and non-native grassland plant communities on breeding passerine birds: implications for restoration of northwest bunchgrass prairie	OR, USA	Grassland	Grass	<i>Phleum pratense</i> , <i>Poa pratensis</i> , <i>Thinopyrum intermedium</i>	Alaudidae, Icteridae, Passerellidae, multiple
King et al. (2009)	Habitat use and nest success of scrub-shrub birds in wildlife and silvicultural openings in western Massachusetts, USA	MA, USA	Shrubland	Unspecified	Unspecified exotics	Multiple
Leston and Rodewald (2006)	Are urban forests ecological traps for understory birds? An examination using northern cardinals	OH, USA	Forest	Shrub	<i>Lonicera maackii</i> , <i>Rosa multiflora</i>	Cardinalidae
Lituma et al. (2012)	Restoration of grasslands and nesting success of Dickcissels (<i>Spiza americana</i>)	TX, USA	Grassland	Grass	<i>Cynodon dactylon</i> , <i>Sorghum halepense</i>	Cardinalidae
Lloyd and Martin (2005)	Reproductive success of chestnut-collared longspurs in native and exotic grassland	MT, USA	Grassland	Grass	<i>Agropyron cristatum</i>	Cardinalidae

Table 1 continued

Citation	Title	Location	Habitat	Form	Non-native species	Passerine family
Ludlow et al. (2015)	Oil and natural gas development has mixed effects on the density and reproductive success of grassland songbirds	AB, Canada	Grassland	Grass	<i>Agropyron cristatum</i>	Cardinalidae, Icteridae, Motacillidae, Passerellidae, multiple
Maddox and Wiedenmann (2005)	Nesting of birds in wetlands containing purple loosestrife (<i>Lythrum salicaria</i>) and cattail (<i>Typha</i> spp.)	IL, USA	Wetland	Forb	<i>Lythrum salicaria</i>	Icteridae
Mcchesney and Anderson (2015)	Reproductive success of field sparrows (<i>Spizella pusilla</i>) in response to invasive Morrow's honeysuckle: does Morrow's honeysuckle promote population sinks?	PA, USA	Shrubland	Shrub	<i>Lonicera morrowii</i>	Passerellidae
Meyer et al. (2015)	Evaluating exotic plants as evolutionary traps for nesting veeries	NY, USA	Forest	Shrub	<i>Berberis thunbergii</i> , <i>Lonicera maackii</i> , <i>Rosa multiflora</i>	Turdidae
Miller et al. (2013)	Nest success and reproductive ecology of the Texas Botteri's sparrow (<i>Peucaea botterii texana</i>) in exotic and native grasses	TX, USA	Grassland	Grass	<i>Cynodon dactylon</i> , <i>Dichanthium annulatum</i> , <i>Pennisetum ciliare</i>	Passerellidae
Nordby et al. (2009)	Effects of a habitat-altering invader on nesting sparrows: An ecological trap?	CA, USA	Wetland	Grass	<i>Spartina alterniflora</i>	Passerellidae
Ortega et al. (2006)	Invasion of an exotic forb impacts reproductive success and site fidelity of a migratory songbird	MT, USA	Grassland	Forb	<i>Centaurea maculosa</i>	Passerellidae
Pearson and Knapp (2016)	Considering spatial scale and reproductive consequences of habitat selection when managing grasslands for a threatened species	OR and WA, USA	Grassland	Forb	Unspecified exotics	Alaudidae
Remes (2003)	Effects of exotic habitat on nesting success, territory density, and settlement patterns in the blackcap (<i>Sylvia atricapilla</i>)	Czech Republic	Forest	Tree	<i>Robinia pseudoacacia</i>	Sylviidae
Rodewald et al. (2010)	Exotic shrubs as ephemeral ecological traps for nesting birds	OH, USA	Forest	Shrub	<i>Lonicera maackii</i> , <i>Rosa multiflora</i>	Cardinalidae
Rodewald et al. (2014)	Community-level demographic consequences of urbanization: an ecological network approach	OH, USA	Forest	Shrub	<i>Lonicera maackii</i>	Multiple
Ruehmann et al. (2011)	Effects of smooth brome on Brewer's sparrow nest survival in sagebrush steppe	WY, USA	Grassland	Grass	<i>Bromus inermis</i>	Passerellidae
Safford (1997)	Nesting success of the Mauritius fody <i>Foudia rubra</i> in relation to its use of exotic trees as nest sites	Mauritius	Forest	Tree	<i>Citrus aurantium</i> , <i>Cryptomeria japonica</i> , <i>Eucalyptus robusta</i> , <i>Pinus elliotti</i>	Ploceidae

Table 1 continued

Citation	Title	Location	Habitat	Form	Non-native species	Passerine family
Scheiman et al. (2003)	Effects of leafy spurge infestation on grassland birds	ND, USA	Grassland	Forb	<i>Euphorbia esula</i>	Icteridae, Passerellidae
Schlossberg and King (2010)	Effects of invasive woody plants on avian nest site selection and nesting success in shrublands	MA, USA	Shrubland	Shrub	<i>Berberis thunbergii</i> , <i>Celastrus orbiculatus</i> , <i>Elaeagnus umbellata</i> , <i>Lonicera japonica</i> , <i>Rhamnus cathartica</i> , <i>Rosa multiflora</i>	Mimidae, Parulidae, multiple
Schmidt and Whelan (1999)	Effects of exotic <i>Lonicera</i> and <i>Rhamnus</i> on songbird nest predation	IL, USA	Forest	Shrub	<i>Lonicera maackii</i> , <i>Rhamnus cathartica</i>	Turdidae
Schmidt et al. (2005)	Invasive shrubs and songbird nesting success: effects of climate variability and predator abundance	NY, USA	Forest	Shrub	<i>Berberis thunbergii</i> , <i>Rosa multiflora</i>	Turdidae
Stoleson and Finch (2001)	Breeding bird use of and nesting success in exotic Russian olive in New Mexico	NM, USA	Forest	Tree	<i>Elaeagnus angustifolia</i>	Parulidae, Tyrannidae
Vander Haegen et al. (2015)	Avian abundance and reproductive success in the Intermountain West: local-scale response to the Conservation Reserve Program	WA, USA	Grassland	Grass	<i>Thinopyrom intermedium</i> , <i>Thinopyrom ponticum</i>	Icteridae, Mimidae, Passerellidae

biases associated with these approaches (Major and Kendal 1996; Moore and Robinson 2004).

As most articles presented data from multiple years of research (mode: 2 years; range 2–11 years), we recorded responses pooled across multiple years, except when a metric was only assessed in a single year of a multi-year study. Responses were recorded separately for each species of songbird or plant examined, unless analyses only reported responses grouped across multiple species. For each response, we recorded the predictor variable (e.g. % non-native cover) and response variable (e.g. nest survival).

We recorded the response direction as positive, negative or neutral and classified responses as ‘effects,’ or ‘trends’ based on the following criteria. Significant effects (i.e. ‘positive effect’ or ‘negative effect’) were identified based on *p* values, parameter estimates with confidence intervals (CI) not overlapping 0, odds ratios with CI not overlapping 1, or non-overlapping CI for group comparisons (e.g. mean clutch size compared between nests in non-native and native habitats). When authors only reported mean \pm SE, we calculated the CI using mean \pm 1.96 * (SE) to assess significance (approximately equivalent to the

95% confidence interval). For significant effects, we recorded effect sizes and measures of variance, when reported. We considered responses to have significant effects at the significance level reported by the authors (usually $\alpha = 0.05$). Non-significant trends (‘positive trend’ or ‘negative trend’) included author-reported directional patterns based on non-significant responses as well as those reported without any indication of significance (often in text). All other responses were recorded as neutral (‘no effect or trend’). Thus, for each response, non-native vegetation was classified as having (1) a significant positive effect, (2) a significant negative effect, (3) a positive trend (non-significant positive response), (4) a negative trend (non-significant negative response), or (5) no effect or trend (neutral response).

Data analyses

We tabulated the number of responses for each of the five response types within each of the response subcategories (Table 2). We summarized response direction for significant effects and trends combined to calculate the relative frequency of all negative,

Table 2 Response variables related to songbird reproductive success included in data extraction and analyses

Reproductive success measures	Reproductive success correlates
<i>Nest survival</i>	<i>Nestling condition</i>
# successful nests (# fledged \geq 1 young)	Nestling mass
Apparent nest success (% success)	Nestling tarsus length
Nest outcome (success or fail)	Nestling mass:tarsus ratio
Daily nest survival probability (rate)	Nestling wing length
Nest survival (to fledging)	Nestling outermost primary length
Nest stage-specific survival	Nestling culmen length
	Nestling rate of mass gain
	# days to fledging
<i>Nest mortality</i>	<i>Brood parasitism</i>
Nest predation rate (% predated)	Brood parasitism rate
Daily mortality rate (DMR)	
<i>Fledgling survival</i>	
Fledgling daily survival rate	
Postfledging survivorship	
<i>Productivity</i>	
Clutch size (# eggs laid)	
Brood size (# eggs hatched)	
# young fledged/nest	
# young fledged/successful nest	
Predicted fecundity (# female fledglings/female)	
Predicted # young fledged/season	
<i>Adult survival</i>	
Adult male apparent survival	
Adult female apparent survival	

positive, and neutral responses. Because of methodological inconsistencies and a lack of consistent reporting of effect sizes, we were unable to conduct a meta-analysis to address potential differences in the magnitude of significant positive and negative effects. To examine the influence of habitat types (i.e. grassland, forest, wetland) and non-native vegetation forms (i.e. shrub, tree, grass, forb) on songbird responses to non-native plants, we fit a mixed-effects logistic regression model using package ‘lme4’ (Bates et al. 2014) in the statistical program R (R Core Team 2016). We excluded one response with unspecified vegetation form from the dataset (n = 132). We modeled the probability of a songbird response being negative (significant effects and trends combined; coded as 1), or not (coded as 0) as a function of habitat and form (fixed effects) by fitting an additive model. To account for non-independence of multiple reported

responses from the same study, we varied the intercept by article (random effect). Data were too sparse to examine relationships among different passerine families.

Although we did not collect data on or analyze responses related to habitat use or habitat selection, we addressed the question of whether non-native plants serve as ecological traps for nesting birds by calculating the percentage of studies that tested this hypothesis and found support for it. We fit a logistic regression using the package ‘lme4’ (Bates et al. 2014) in the statistical program R (R Core Team 2016) to examine whether the probability that a study found support for ecological traps was related to habitat type or non-native vegetation form. We excluded one data point with unspecified vegetation form from the analyses (n = 16), and fit only univariate models due to the small sample size of the ecological trap dataset.

Results

Summary statistics

Articles measuring non-native plant effects on songbird reproductive success spanned two decades of research, five countries, 53 bird species within 12 passerine families, and 32 introduced plant species (Table 1). All but four studies were conducted in North America, and there was no representation from Oceania, South America, or Asia. Most studies examined the influence of non-native shrubs (34%) or grasses (34%) within grassland (47%) or forested (44%) habitats (Table 1). The dataset was comprised of 133 songbird responses to non-native vegetation, of which 89% were classified as direct measures of reproduction and 11% as reproductive correlates (Table 2). Of all responses, 128 (96%) pertained to the nesting stage (up to fledging), while 3 (2%) examined the postfledging period and 2 (1%)

addressed survival outside of the breeding season. Although 12 different passerine families were represented, the majority of responses were for sparrows (Passerellidae, 39%), cardinals (Cardinalidae, 15%) and thrushes (Turdidae, 12%). Fifty percent of all responses recorded were related to the effects of non-native grasses, while 31% were related to non-native shrubs. Non-native tree and forb effects were the focus of 10% and 8% of responses, respectively.

Songbird responses to nesting in non-native vegetation

The majority (65%) of songbird reproductive responses to non-native vegetation were either neutral ($n = 45$; 34%) or positive ($n = 41$; 31%), while the remaining 47 responses (35%) were negative ($n = 133$ total responses; Fig. 1). The negative reproductive responses were comprised of 15 statistically significant effects and 32 non-significant trends

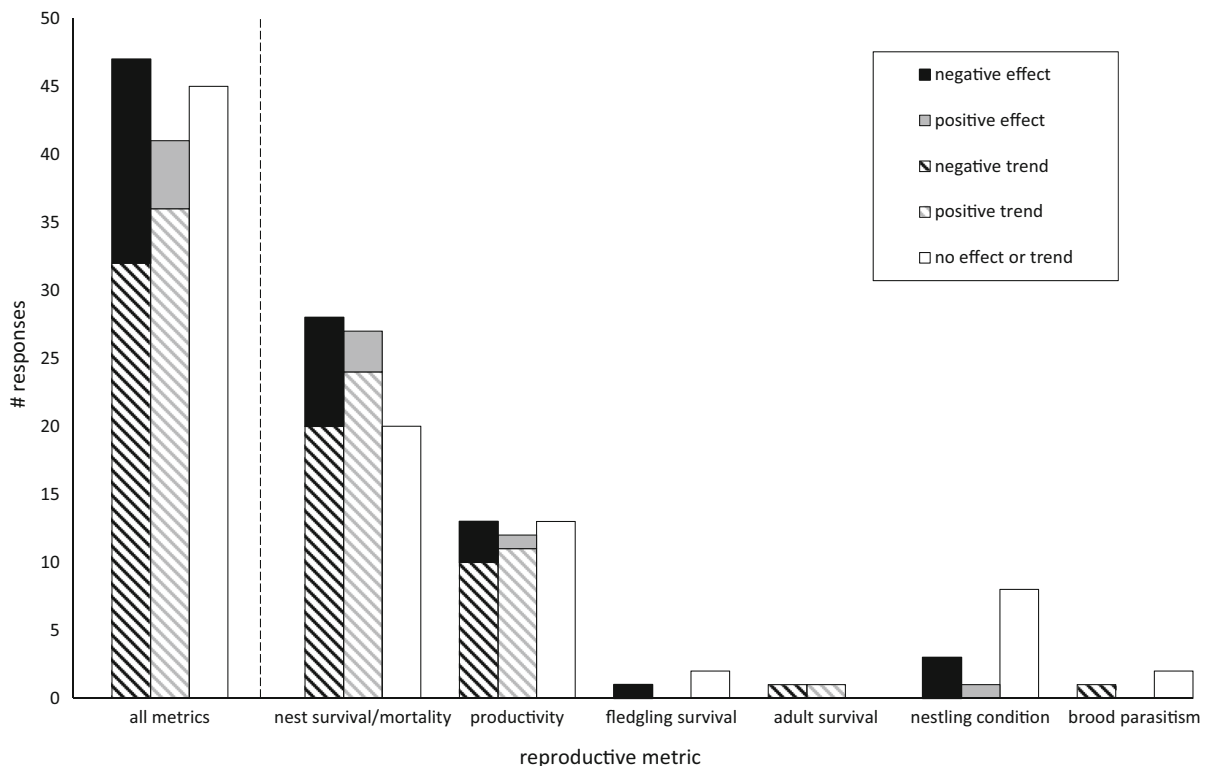


Fig. 1 Songbird responses to non-native vegetation ($n = 133$), including statistically significant effects ($n = 20$, solid shading), trends (directional patterns that are non-significant or of unknown significance; $n = 68$, hatched shading), and neutral responses (no effect or trend; $n = 45$, no shading). Reproductive

metrics examined included direct reproductive success measures (nest survival/mortality, productivity, fledgling survival, and adult survival; $n = 118$ responses) and reproductive success correlates (nestling condition and brood parasitism; $n = 15$ responses)

(Fig. 1). Negative responses were dominated by measures of nest survival/mortality (60%) and productivity (28%). The probability of finding a negative response (either effect or trend) was significantly influenced by non-native vegetation form and habitat type. We found a higher probability of negative responses to non-native shrubs than other vegetation forms and within wetland habitats than other habitats ($p = 0.023$ and $p = 0.0497$, respectively; Table 3). However, more than a third of articles reported mixed direction responses (i.e. positive and negative effects or trends) associated with different reproductive metrics, songbird species, or species of introduced plants within the same study.

Significant effects—Only 15% of all responses in our dataset were statistically significant ($n = 20$), with three times as many negative ($n = 15$) as positive ($n = 5$) responses. The majority of significant responses were related to nest survival/mortality metrics ($n = 8$ negative, $n = 3$ positive). Of all significant effects reported, negative effects dominated across all reproductive metrics (Fig. 1). Seven songbird species (within 5 passerine families) experienced significant negative impacts of nesting in or

around non-native vegetation, while only 3 species (within 3 families), experienced positive reproductive outcomes.

Non-significant trends—Non-significant directional trends were much more prevalent in our dataset than statistically significant effects (Fig. 1). Trends comprised about 51% of all responses and were found to be more balanced among positive ($n = 36$) and negative ($n = 34$) directions than the significant effects. Both positive and negative trends were dominated by responses related to nest survival/mortality.

Non-native plants as ecological traps

Just over half the articles examined ($n = 18$), addressed the question of whether non-native vegetation could represent ecological traps for nesting passerines. The majority of studies ($n = 11$) found no support for non-native habitats as ecological traps; however, 39% ($n = 7$) did provide some evidence for these hypotheses. In these studies, birds preferentially selected non-native habitats over native ones and suffered reduced reproductive success as a result. Of

Table 3 Coefficient estimates, standard errors (SE) and p values for linear models fit to songbird response data

Covariate	Estimate	SE	p value
Model 1: glmer (negative response ~ habitat + form + (1 article ID), family = binomial)			
(Intercept)	- 4.912	1.949	0.012
Grassland	1.94	1.255	0.122
Wetland	4.44	2.263	0.0497
Grass	1.992	1.464	0.174
Shrub	4.163	1.827	0.023
Tree	3.308	2.091	0.114
Model 2: glm (ecological trap ~ habitat, family = binomial)			
(Intercept)	- 0.693	0.707	0.327
Grassland	0.406	1.041	0.697
Model 3: glm (ecological trap ~ form, family = binomial)			
(Intercept)	- 0.406	0.913	0.657
Shrub	- 0.288	1.155	0.803
Tree	0.406	1.683	0.81

Model 1 is fit to the data set of all songbird responses to non-native vegetation ($n = 132$) with habitat type and vegetation form as fixed effects and article ID ($n = 31$) as a random effect. Negative responses (either significant or trend) were coded as 1 and all other responses were coded as 0. The reference category for habitat type is forest and the reference category for vegetation form is forb. Models 2 and 3 are fit to the dataset of articles that tested for ecological traps ($n = 16$), with studies that found support coded as 1 and studies that did not find support coded as 0. The reference categories for habitat type (Model 2) and vegetation form (Model 3) are forest and grass, respectively. Significant predictor variables are shown in bold ($p < 0.05$)

the studies that found evidence of traps, three evaluated the effects of non-native grasses in grassland habitats, two focused on exotic shrub effects in forested habitats, one addressed plantation trees in forested habitats, and the last examined non-native grasses in wetlands. Habitat type and non-native form did not have a significant influence on whether a study found support for an ecological trap (Table 3).

Discussion

Our systematic review of the effects of non-native vegetation on songbird reproductive performance uncovered relatively few studies ($n = 32$), with a strong focus on nest survival and productivity metrics, highlighting the lack of research on this topic and the need for more studies targeting a diversity of reproductive performance metrics. The limited number of investigations is consistent with the poor representation of research on fitness-related effects of invasive species on animals. A recent meta-analysis examining invasive plant impacts across diverse animal taxa ($n = 3624$ responses from 198 studies, Schirmel et al. 2016) reported only 5% of all animal responses were fitness-related, while 73% concerned animal abundances and 18% concerned diversity. The lack of information on reproductive performance likely results from the financial and practical challenges of collecting reproductive data. Despite the small number of papers included, our synthesis provides a novel contribution to the invasion biology literature. No previous reviews have focused specifically on reproductive responses and over one-third of the articles we reviewed do not appear in other recent reviews assessing invasive plant impacts more generally (i.e. Nelson et al. 2017; Schirmel et al. 2016; Pyšek et al. 2012; Vila et al. 2011).

The majority (85%) of responses in our dataset were non-significant trends or neutral responses. These findings suggest that (1) non-native plants do not significantly affect songbird survival and productivity in most cases, or (2) we lack the robust datasets and statistical power to detect significant effects where they exist. Further, authors' tendencies to group multiple seasons of data or responses from multiple passerine species in analyses may have reduced their ability to detect effects. In addition, many articles reported mixed responses (i.e. both positive and

negative effects or trends) across different reproductive metrics and species, which highlights the complex and non-uniform nature of non-native plant effects on avifauna, consistent with previous findings (Pyšek et al. 2012; Nelson et al. 2017). For example, higher cover of crested wheatgrass (*Agropyron cristatum*) was associated with decreased nest survival for Sprague's pipits (*Anthus spragueii*) but increased nest productivity for savannah sparrows (*Passerculus sandwichensis*) (Ludlow et al. 2015).

Of the 20 significant effects on reproductive performance that emerged from this review, the majority were negative (Fig. 1), consistent with findings from a broader global meta-analysis of animal responses (Schirmel et al. 2016). Mechanisms underlying negative effects were diverse, but lower reproductive success in non-native habitats was generally explained by interacting aspects of vegetation characteristics, resource availability and predation pressure that facilitated higher mortality and lower productivity in exotic habitats. One study suggested that a combination of lower nest height, an absence of sharp thorns, and specific branch architecture facilitating predator movement led to higher nest mortality in exotic shrubs (Schmidt and Whelan 1999). In addition to nest-patch characteristics, landscape context was also important. Borgmann and Rodewald (2004) found higher predation in urbanizing landscapes, where exotic substrates and nest predators were more abundant. Another study attributed the 17% lower odds of daily nest survival in introduced grasses to higher predation intensity and slower nestling growth rates in the exotic habitat (Lloyd and Martin 2005). Slower growth rates, which require nestlings to spend a longer time in the nest prior to fledging and result in lower mass at fledging, can increase predation risk during both nesting and postfledging periods (Lloyd and Martin 2005). Other negative effects on productivity included reduced clutch size for Brewer's sparrows (*Spizella breweri*) nesting in exotic grasses (Ruehmann et al. 2011) and 20% fewer young fledged throughout the breeding season for northern cardinals (*Cardinalis cardinalis*) that selected exotic *Lonicera* shrubs over available native substrates (Rodewald et al. 2010). These patterns may result from differences in prey availability, as native vegetation has been found to support more abundant and diverse insect communities than non-native plants (Litt et al. 2014).

Significant positive effects of nesting in non-native habitats were found for only 4% of all responses examined (Fig. 1) and responses were highly species-specific. The few papers that found significant positive effects pointed to differences in vegetation characteristics, predation rates, and resource availability between native and non-native habitats to help explain patterns; often multiple interacting factors were cited. For example, differences in foliage density affecting nest concealment and predator accessibility as well as foraging patterns of predators may help explain higher nest success of Mauritius fodies (*Foudia rubra*) using exotic plantation trees (Safford 1997). Schlossberg and King (2010) suggested that the dense cover provided by invasive shrubs may have benefited gray catbirds (*Dumetella carolinensis*) by concealing their large nests, blocking access by predators, and restricting foraging predator movements. Prolific fruits provided by some invasive shrub species (e.g. *Lonicera* spp.) may also provide enhanced food resources for feeding nestlings, which was offered to explain why catbird nestling condition was better in these non-native habitats (Gleditsch and Carlo 2014). Ludlow et al. (2015) examined responses to exotic crested wheatgrass cover for five grassland songbird species and found significantly higher fledgling success in areas of high wheatgrass cover, but only for savannah sparrow. The authors proposed a density-dependent mechanism where lower densities of nesting savannah sparrows in areas of high wheatgrass cover reduced competition for food resources and allowed these pairs increased opportunities to fledge more young. In the same study, however, significant negative effects were found for the primary endemic grassland specialist, Sprague's pipit, which may have experienced the exotic wheatgrass as lower quality habitat due to decreased biomass of preferred prey (Ludlow et al. 2015).

When significant effects and non-significant trends were considered together, we found a higher probability of negative responses to non-native shrubs and wetland habitats (Table 3). Thus, shrub-nesting species may be more susceptible to negative reproductive outcomes than birds that build nests in non-native trees, grasses, or forbs. In addition, our findings pertaining to invaded wetlands are consistent with previous findings that negative effects are most evident in riparian ecosystems (Schirmel et al. 2016). The fact that riparian zones are considered

some of the most susceptible ecosystems to invasion (Richardson et al. 2007) may help explain this pattern. However, we must caution that our inference is limited by the small sample sizes of some response types in our analysis, particularly for wetland habitats ($n = 4$). Nonetheless, these findings provide further evidence for the context-dependency of non-native plant effects, which has been a theme of previous syntheses of invasive plant impacts (Vila et al. 2011; Pyšek et al. 2012).

Of the 16 articles that assessed ecological traps, 39% found support for them, but vegetation form and habitat type were not important predictors of traps (Table 3). The small sample size of articles in our analysis ($n = 16$) likely hampered our ability to detect any general patterns. Also, because we relied on authors' designations of ecological traps which may not always be accurate, there is potential for false positives in our small dataset. A previous synthesis on the subject undertaken across diverse animal taxa found that only 11% of articles claiming support for ecological traps actually provided sufficient empirical evidence for them (Robertson and Hutto 2006; 45 articles, 3 in common with this review). Thus, the prevalence of ecological traps for songbirds may be even lower than reported. Several studies we reviewed concluded that non-native plants provided equally suitable or even enhanced resources compared to native species (Leston and Rodewald 2006; Schlossberg and King 2010; Gleditsch and Carlo 2014; Meyer et al. 2015). Even though songbirds may show preference for non-native habitats, the extent to which exotic vegetation actually threatens population persistence needs to be more rigorously examined.

Knowledge gaps and priorities for future research

We identified several knowledge gaps in our dataset. First, our review produced very few studies undertaken outside of North America, a pattern mirrored in the broader published literature on invasion biology (Pyšek et al. 2008). While limiting our search to papers written in English may have contributed to this finding, the lack of studies from the UK and Oceania is notable given the known prevalence of recent plant invasions in these English-speaking areas (Invasive Species Specialist Group ISSG 2015). One explanation might be that our search terms relied on non-native designations (e.g. exotic, alien; Appendix A in

ESM) that may not be relevant to geographic areas without a clear native/non-native dichotomy. In areas of the world that have been settled by humans for much longer than North America (e.g. Europe, Asia), it may be more difficult to distinguish between native and introduced species, and thus the dichotomy may be less meaningful. Research priorities surrounding non-native plants may also vary geographically. In addition, the general search terms we used may not have encompassed more specific references to introduced plants (e.g. scientific names).

A second knowledge gap uncovered was that only a handful of responses ($n = 5$, 4%) addressed reproductive performance outside of the nesting period, and only one article modeled demographic parameters to estimate population growth rates (λ) in native versus non-native habitats (Mcchesney and Anderson 2015). This shortcoming may stem from the effort and methodological difficulties inherent in collecting demographic data needed for population modeling. The bias in our dataset toward nest survival and productivity measures highlights the need for a broader understanding of how non-native plants influence population viability, including addressing parameters related to adult and fledgling survival (Anders and Marshall 2005; Mcchesney and Anderson 2015). Without comparative data on population growth rates, it will be difficult to fully characterize how non-native plants influence songbird populations.

The limited information on how non-native plants influence songbird reproductive output suggests a need for more research on this topic. Specifically, studies examining population productivity in non-native vegetation, across diverse ecosystems, taxa, and stages of invasion are needed. As nest success and nest productivity are generally poor metrics for comparing annual reproductive output across different habitats, restricting study to the nesting period provides an incomplete picture of non-native plant effects on songbird reproductive output (Thompson et al. 2001). Thus, we recommend researchers prioritize examining season-long productivity of marked pairs to better understand how presence of non-native vegetation influences songbird populations. In addition, a greater focus on habitats beyond forests and grasslands (e.g. wetland and riparian communities) is warranted to facilitate a broader understanding of non-native plant impacts across diverse ecosystems and resident species. It is also important to investigate the effects

of introduced plants across all stages of the invasion pathway, as impacts are expected to change as a non-native plant transitions through the stages of colonization, establishment, and landscape spread to potentially become invasive (Theoharides and Dukes 2007). Further, identification of the introduced plants producing the strongest negative impacts on native species will help prioritize management efforts for such invasive species and avoid allocating limited resources to control non-natives that serve as functional replacements or provide benefits to native species.

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