THESIS

EFFECTS OF AN INTRODUCED TREE, NEW MEXICO LOCUST

(*ROBINIA NEOMEXICANA*), ON RIPARIAN BIRDS

Submitted by

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ABSTRACT

EFFECTS OF AN INTRODUCED TREE, NEW MEXICO LOCUST (ROBINIA

NEOMEXICANA), ON RIPARIAN BIRDS

Biological invasions are global drivers of environmental change and riparian ecosystems are particularly susceptible to the effects of non-native species. While much research has focused on understanding the impacts of non-native introductions from other biogeographic regions, effects of plant species that spread close to or within their native ranges are relatively understudied. My research investigated the effects of the near-range introduction of a non-native woody plant, New Mexico locust (*Robinia neomexicana*), on a variety of ecological responses within the Clear Creek drainage of northwestern Colorado, USA. I used riparian songbirds as model species to investigate invasion-mediated effects on 1) changes to avian habitat use, including species richness, occupancy, and abundance; 2) effects on songbird reproductive success, including nest survival and productivity; and 3) changes to aquatic insect subsidies and avian diet compositions.

My first chapter provides a general synthesis of fitness consequences of plant invasion through a global systematic review of introduced plant effects on songbird reproductive success. Only 16% of the 137 songbird responses examined resulted in significant effects, and these were predominately negative and highly context-dependent. However, non-significant trends were much more prevalent and mixed in direction. The literature review highlighted the lack of study on fitness-level impacts of invasion, uncovered a strong geographic bias for North American

studies, and identified knowledge gaps, such as the lack of studies on juvenile survival during the postfledging period.

In chapter two, I examine the effects of New Mexico locust invasion on the habitat use and reproductive success of breeding songbirds in the Clear Creek drainage of northwestern Colorado. Despite evidence of biotic homogenization of the vegetation community with increasing invasion intensity, I found few negative impacts on the songbird community. Rather, the introduced locust provided quality breeding habitat to support diverse assemblages of riparian birds. Not only did I find increased bird species richness with increasing invasion intensity, but nest productivity was significantly higher in invaded habitats compared to those where locust was absent. Overall, I found that environmental characteristics other than invasion (*i.e.,* elevation and shrub density) were more important predictors of avian habitat use. There was also no evidence of reduced nest survival in nests built in locust or in nests in native plants situated in locust-invaded habitats.

My third chapter, a collaboration with Colorado State University M.S. student Hannah Riedl, uses stable isotope analysis of avian fecal samples and insect prey to investigate invasion-mediated changes in the aquatic resource subsidies provided to avian insectivores. We quantified the amount of terrestrial- and aquatic-derived insect prey consumed by a riparian songbird assemblage and assessed whether relative prey contributions differed between non-invaded reference sites and sites invaded by New Mexico locust. We found that songbird diets were comprised of approximately one third aquatic resources and two-thirds terrestrial resources, highlighting the importance of aquatic resource subsidies for riparian consumers. Although differences in diet composition between reference and locust habitats were highly species-

specific and inconsistent across years, we found significant diet shifts towards more aquatic-derived prey at locust sites for two species of avian insectivores.

Collectively, my findings provide little support for negative impacts on riparian bird communities associated with the near-range introduction and establishment of New Mexico locust within Clear Creek drainage. Similar or stronger effects might be expected for invasive alien species introduced from more geographically isolated native ranges. Combining multiple ecological response variables to obtain a more complete and mechanistic understanding of invasion impacts is critical for advancing invasion biology and facilitating effective conservation of native communities.

ACKNOWLEDGEMENTS

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CHAPTER ONE

A SYSTEMATIC REVIEW OF THE EFFECTS OF INTRODUCED PLANTS ON SONGBIRD

REPRODUCTIVE SUCCESS[1]

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

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[1] At time of submission (June, 2017), this chapter was in revision at Biological Invasions.

resident species (Safford 1997; Meyer et al. 2015). Thus, understanding the fitness consequences of non-native plant invasions 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 fitness consequences, such as decreased nest survival or productivity (Schmidt and Whelan 1999; Lituma et al. 2012). However, other

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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 fitness 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 effects across different habitat types, vegetation forms, passerine taxa, and reproductive metrics. This work provides an in-depth analysis of fitness effects 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 positive or negative effects on songbird reproductive success. 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.

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; Appendix 1.1). The second string targeted papers studying reproductive success and the third sting constrained the search to avian responses (Appendix 1.1). The complete search syntax is included in Appendix 1.2. 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 review articles.

As the objective of the review was to characterize fitness 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 (Appendix 1.3).

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. In addition, we noted the context within which each study was framed to categorize articles as having either 1) a primary objective of evaluating the effects of non-native vegetation on birds, or 2) other primary objectives. The articles with other primary objectives included research comparing nest success among habitat management treatments as well as investigations of effects of fragmentation, urbanization and energy development, where non-native plants were a component of the vegetation community. Although non-native effects were not the main focus, these studies still included some quantification or categorization based on non-native vegetation. 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

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statements of support for these hypotheses or findings of non-native habitat preference resulting in negative reproductive effects 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 1.1) 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 nesting timing, brood parasitism, and nestling condition. Because we aimed to assess fitness consequences of plant invasion, 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 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 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 direction of each effect and criteria used to determine significance. We considered responses to have directional effects (*i.e.,* positive or negative) at the significance level reported by the authors. Significant responses were identified based on p-values, parameter

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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 ± SE, we calculated the CI using mean ± 1.96*(SE) to assess significance (approximately equivalent to the 95% confidence interval). For significant responses, we recorded the effect sizes and measures of variance, when reported. Responses were recorded as non-significant when significance tests indicated p-values above the chosen alpha level (usually α = 0.05), overlapping CI of parameter estimates or group comparisons, or language in the text indicating no significant difference. Directional trends (positive and negative, herein 'trends') included both non-significant effects as well as trends reported without any indication of significance (often in text). Thus, for each response, non-native vegetation was classified as having 1) a significant positive effect, 2) a significant negative effect, 3) a non-significant effect, 4) a positive trend, or 5) a negative trend. It was possible for responses to be classified as both a non-significant effect and trend when effect directions were presented despite statistically non-significant findings.

Data Analyses

Responses were tabulated for each of the five response types and summarized within each of the response subcategories (Table 1.1). In order to provide an overall characterization of effects of nesting in non-native habitats, we summarized responses across subcategories and across main categories of direct measures and correlates. 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 the documented effects of non-native species, we fit mixed-effects logistic regression models with intercepts varying by article to account for non-independence of multiple reported responses from the same study. We conducted analyses using the 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=136). We conducted analyses for two different binary response variables: 1) whether a response had a significant negative effect (coded as 1) or not (coded as 0), and 2) whether a response was negative (significant effects and trends combined; coded as 1), or not (coded as 0). To assess the probability of a response being negative, we fit univariate models, with fixed effects as either form or habitat and random effects of article ID (analyses 1 and 2). The significant effects dataset (analysis 1) was too sparse to accommodate additive or interactive models; however, we were able to fit an additive model for habitat and form to the dataset of all negative responses (analysis 2). 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 were able to address the question of whether non-native plants serve as ecological traps for nesting birds by calculating the proportion of studies that tested this hypothesis and found support for it. We fit a logistic regression in the statistical program R to examine whether the probability that a study found support for ecological traps was related to either the habitat type or the non-native vegetation form examined. We fit only univariate models on the ecological trap dataset, and excluded one data point with unspecified vegetation form from the analyses (n=16).

RESULTS

Temporal, Geographic, and Ecological Context

Articles measuring the effects of non-native plants on nesting birds spanned two decades of research (1997-2016), with the majority (69%) published in the last decade. While a few articles grouped multiple songbird species in their analyses, most (88%) assessed species-specific responses of passerines. Species-specific data were collected on 32 species of songbirds, representing 12 different families within the Order Passeriformes. There was a substantial geographic bias in the publications, with all but four papers reporting research conducted in the United States and Canada. The North American research was undertaken in 25 different states and two provinces. Of the four studies conducted outside of North America, two were based in European countries, and the remaining two from the country of Mauritius. There was no representation from Oceania, or any country in South America or Asia.

Most studies investigated the effects of introduced shrub (34%) or grass (34%) species, with effects related to trees (16%), forbs (12%), or unspecified exotic invasive plants (3%) comprising the remainder of vegetation forms examined. Studies were split fairly evenly between grassland (47%) and forested (44%) habitats, with the remaining studies conducted in wetlands (6%) and scrub-shrub (3%). Studies quantified introduced plants as either discrete variables, including classifications based on non-native nesting substrate (8 studies) and non-native dominated habitat (11 studies), or continuous variables, such as percent non-native cover (6 studies). In addition, 6 articles measured responses based on a combination of continuous and categorical variables (*i.e.,* interactive effects) and one study quantified exotic cover based on an index of non-native dominance.

Summary Statistics of Songbird Reproductive Responses

The final dataset compiled across all reproductive measures and correlates was comprised of 137 songbird responses to non-native vegetation. The vast majority of responses (96%) pertained to the nesting stage (up to fledging) with only 3 responses related to the postfledging period. Although 12 different passerine families were represented in the dataset, the majority of responses were for sparrows (Emberizidae, 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.

Approximately 86% of the responses we recorded represent direct measures of reproduction, while we considered the remaining 14% to be reproductive correlates (Table 1.2). Of all the direct reproductive measures we investigated, 64% were related to nest survival or mortality, which was commonly measured by calculating daily nest survival probability or daily nest mortality rates using variations on the Mayfield method (Mayfield 1961, 1975; Johnson 1979) or logistic exposure modeling (Rotella 2004; Shaffer 2004). Productivity metrics, such as number of young fledged and clutch/brood size, comprised about 32% of all reproductive measures. The remaining responses assessed fledgling or adult survival, which comprised 3% and 2% of direct reproductive measures, respectively. The reproductive correlates were dominated by various measures of nestling body condition, but also included nest initiation and timing variables, and brood parasitism rates (Table 1.2).

Effects of Songbird Nesting in Non-native Vegetation

Significant Effects. – Only 16% of the responses in our dataset were statistically significant and negative (n=17) or positive (n=5). Of all the significant effects reported, negative

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effects dominated across all reproductive metrics (Figure 1.1). Six passerine families and 9

different species of songbirds experienced significant negative impacts of nesting in or around

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

The probability of finding a negative effect was not significantly influenced by habitat type or

vegetation form (Appendix 1.4).

Non-significant Trends. – Non-significant trends (n=70) were much more prevalent in

our dataset than statistically significant effects (n=22). Trends comprised about 51% of the

responses in the dataset and were found to be more balanced among positive (n=36) and negative

(n=34) directions (Figure 1.2) than the significant effects.

All Effects and Trends Combined. – Together, effects and trends comprised 67% of

responses. More than one third of articles reported mixed effects (*i.e.,* positive and negative

effects or trends) associated with different reproductive metrics, songbird species, or species of

introduced plants within the same study. The probability of finding a negative effect (either

significant or trend) was not significantly influenced by habitat type or vegetation form when

these predictor variables were examined alone (*i.e.,* single variable models); however, when

additive effects of habitat and form were considered, we found a higher probability of negative

effects for non-native shrubs and wetland habitats (p=0.049 and p=0.026, respectively; Appendix

1.5).

Non-native Plants as Ecological Traps

Just over half the studies examined (n = 18), addressed the question of whether non-

native vegetation could represent ecological traps for nesting passerines. The majority of articles

(61%, 11 studies) found no support for non-native habitats as ecological traps; however, 39% (7

studies) 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 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 (Appendix 1.6).

DISCUSSION

Our global systematic review of the effects of non-native vegetation on songbird reproductive success uncovered relatively few studies (n=32), highlighting the lack of research on this topic. Significant effects of non-native vegetation on fitness were primarily negative, which is consistent with findings from a broader global meta-analysis of animal responses (Schirmel et al. 2016), but contrasts with the primarily neutral effects of invasive plants found for North American birds (Nelson et al. 2017). Our consideration of non-significant trends, however, uncovered a greater balance between positive and negative effects. More than one third of articles reported mixed effects (*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). Patterns of response did not appear to be related to habitat types or vegetation forms; however, when significant effects and non-significant trends were grouped, we found higher probabilities of negative responses for non-native shrubs and wetland habitats. Of the articles that assessed ecological traps, 39% found support for this hypothesis, but as with

significant effects, vegetation form and habitat type were not important predictors of traps (Appendix 1.6).

The limited number of investigations on reproductive consequences for songbirds nesting in non-native vegetation is consistent with the poor representation of research on fitness-related effects of invasive plants, in general. A recent meta-analysis examining invasive plant impacts across diverse animal taxa (*e.g.,* insects, arachnids, birds) reported only 5% of all animal responses were fitness-related, while 73% concerned animal abundances and 18% concerned diversity (n=3624 responses from 198 studies, Schirmel et al. 2016). There are several potential explanations for the lack of information on fitness-level effects. First, nest monitoring studies are time-consuming and expensive compared to other observational techniques (*e.g.,* point audio-visual surveys). Second, practical limitations may render reproductive data inaccessible for some species. Not only is it difficult for researchers to locate nests of many cryptic bird species, but placement of nests in inaccessible areas (*e.g.,* forest canopies, private lands) adds to the difficulty of monitoring reproductive outcomes for songbirds. Third, because of the challenges of reproductive data collection, sample sizes are often small and data more sparse compared to habitat use metrics, which produce richer datasets for statistical analyses. Thus, researchers interested in effects of non-native plants may opt for ecological metrics and methodologies that provide greater return on investment, especially in areas of the world with fewer resources to fund ecological research.

The resource-intensive nature of reproductive data collection may also explain biases in our dataset. First, we found very low representation of studies outside of North America and Europe (n=2). This strong geographic bias for research conducted in North America mirrors broader trends in the published literature on invasion biology (Pyšek et al. 2008). Second, we

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encountered only two studies that examined differences in juvenile survival following hatching (*i.e.,* the postfledging period), despite the great potential of this period to influence population viability (Anders and Marshall 2005). This knowledge gap may be a result of the immense effort required and methodological difficulties inherent in following young birds (*e.g.,* using radio-transmitters).

Of the studies that overcame the aforementioned research challenges and were included in our review, few reported significant findings (Table 1.2). One interpretation of this result is that in many cases non-native plants do not cause significant effects on songbird survival and productivity. Another interpretation is that we lack the robust datasets and statistical power to detect significant effects where they exist. The fact that we found over three times more non-significant trends than we did significant effects in our review could lend support to the latter interpretation. In addition, many studies conducted analyses on datasets combined across multiple seasons or passerine species, which may have increased variation in response variables as a result of environmental stochasticity or differences in species-specific responses, respectively. The decisions to lump responses across years and species likely arose from data deficiencies related to the previously noted challenges of obtaining large, species-specific datasets with nest monitoring methodologies.

Of the significant findings that emerged from this review, most were related to nest survival/mortality and the majority were negative (Figure 1.1); however, a variety of mechanisms were proposed to explain these negative impacts. One study suggested that a combination of characteristics of exotic shrubs, including lower nest height, absence of sharp thorns, and specific branch architecture facilitating predator movement, were responsible for higher nest mortality rates for American robins (*Turdus migratorius*) (Schmidt and Whelan

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1999). In addition to characteristics of the nest substrate, Borgmann and Rodewald (2004)

suggested that nest-patch characteristics and landscape context were important. They found

higher predation in urbanizing landscapes, where exotic substrates and nest predators were more

abundant (Borgmann and Rodewald 2004). Another study comparing nest success of chestnut-

collared longspurs (*Calcarius ornatus*) in introduced crested wheatgrass (*Agropyron cristatum*)

monocultures and native prairie habitats, 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). In summary, 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.

Significant positive effects were found for only 4% of all responses examined (Figure

1.1) and responses were highly species-specific. The few papers that found significant positive

effects of nesting in non-native habitats pointed to differences in vegetation characteristics,

predation rates, resource availability, and density-dependence affecting competition 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 invasive shrubs may have benefited gray catbirds (*Dumetella carolinensis*) disproportionately compared to other species because catbirds had larger nests than most other species in their study. Extremely dense cover provided by the invasive shrubs helped conceal the large nests, block access by predators, and restrict foraging predator movements (Schlossberg and King 2010). Prolific fruits provided by some exotic 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 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 (*Passerculus sandwichensis*). 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 *(Anthus spragueii)*, which may have experienced the exotic wheatgrass as lower quality habitat due to decreased biomass of preferred prey (Ludlow et al. 2015). Despite the complexity and species-specific nature of many reproductive effects, the broad categories of mechanisms suggested to explain positive effects, such as differences in vegetation characteristics, predation, and resource availability, are the same presumed drivers of negative fitness effects.

Given these findings of mixed effects and interacting underlying mechanisms, we explored potential generalizations across habitat types and non-native vegetation forms in our dataset. We found some evidence that birds using non-native shrubs and wetland habitats were more likely to experience negative fitness consequences. However, these patterns only held when all effects and trends were analyzed together in an additive model including both habitat and form as predictor variables. The fact that neither single covariate model in isolation identified significant predictors suggests a more nuanced interpretation. That is, the effects of non-native form depend on the type of habitat that a plant invades. This finding provides 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). Interestingly, of the 20 negative effects or trends associated with non-native shrubs, 90% were related to shrubs deemed '*invasive*,' species specifically known to cause economic or environmental harm. However, caution should be taken in interpreting wetland habitat type as an important predictor, as the dataset only included a very small sample of responses from wetlands (n=4). Despite this caveat, these results are consistent with findings from a recent review on invasive plants showing negative effects to be most evident in riparian ecosystems (Schirmel et al. 2016), which are considered some of the most susceptible ecosystems to invasion (Richardson et al. 2007). Finally, the lack of consistent patterns for significant effects alone may be a result of small sample sizes which precluded fitting an additive model for these data.

Those studies that assessed the potential for non-native plants as ecological traps combined both reproductive metrics and habitat preference data to test this hypothesis. Our finding that non-native plants are associated with ecological traps in almost 40% of studies is notable, especially given the multiple data types required to test for ecological traps and the

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difficulties inherent in collecting robust fitness-related datasets. Further, previous synthesis on the subject across diverse taxa suggests that little empirical evidence for ecological traps exists in the published literature, in general (Robertson and Hutto 2006). Thus, this outcome of our review suggests that, in at least some cases, nesting in exotic vegetation may threaten the persistence of certain songbird populations. One important caveat, however, is that authors may not always accurately characterize ecological traps. This was found to be the case in the vast majority of studies claiming support for ecological traps in Robertson and Hutto's (2006) review. As we relied mainly on authors' designations of traps, there is potential for false positives in our relatively small (n = 18) dataset.

Priorities for Future Research

The lack of information on the effects of non-native plant invasions on songbird reproductive success suggests the need for more studies targeting fitness consequences. Specifically, studies examining fitness effects during the postfledging period, across diverse ecosystems, taxa, geographic regions and stages of invasion are needed. Although examination of postfledging parameters was beyond the scope of most studies we reviewed, several authors acknowledged postfledging survival as a critical and understudied component of avian productivity (Jones and Bock 2005; Ausprey and Rodewald 2011). Future studies should specifically target the postfledging period to determine if non-native plant invasion influences demographic parameters during this sensitive stage of the avian life cycle. In addition, greater research 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. Further, increased study of non-native plant impacts is warranted in underrepresented geographic regions outside of North America to ensure

a more robust global characterization of effects. 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).

Importantly, future studies on non-native invasions should test for ecological traps and examine the magnitude of effects in addition to characterizing effect directions. Increased examination of non-native plants as ecological traps, including consistent and robust characterization of these phenomena based on specific criteria (*e.g.*, as Robertson and Hutto 2006) will be particularly important for mitigating non-native plant impacts on native fauna. 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.

Conclusions

As non-native species become increasingly prevalent in ecosystems across the globe, understanding the impacts of introduced plants is one of the greatest challenges facing conservation biologists. In our systematic review of non-native plant effects on nesting songbirds, we found that significant effects on reproductive parameters were predominately negative and highly-context dependent. The findings of this review highlight the lack of study on fitness-level impacts, despite the importance of these metrics for accurately assessing habitat quality and population persistence of resident species. The lack of study, together with the species- and site-specific nature of non-native impacts, leaves many unanswered questions about

the generality of non-native plant effects on songbird fitness and highlights the need for additional study of reproductive responses.

The scope of this review focused on songbird reproductive responses, but our findings contribute more broadly to the larger body of knowledge on fitness impacts of non-native species invasions. Future studies aimed at filling specific research gaps, including targeting understudied periods of animal life cycles, underrepresented habitats, species, and geographic regions, as well as lesser-known species of invading plants across all stages of the invasion pathway, will help broaden inference across diverse contexts to elucidate more general global trends in non-native plant effects. That being said, the complexity and nuanced nature of non-native plant effects should not be overlooked as we strive to identify more general global patterns across diverse contexts.

TABLES

Table 1.1. Response variables related to songbird reproductive success included in data extraction and analyses. Reproductive metrics are divided into 2 main categories (measures and correlates), each with subcategories displayed in italic font.

Reproductive Success Measures	**Reproductive Success Correlates**
nest survival / mortality	*nesting timing*
apparent nest success (# or % success)	egg laying date (1st clutch)
nest outcome (success or fail)	nest initiation date (1st clutch)
daily nest survival probability (rate)	
nest survival rate	
apparent nest predation rate (% predated)	*brood parasitism*
daily nest mortality rate	brood parasitism rate
productivity	
clutch size (# eggs laid)	*nestling condition*
brood size (# eggs hatched)	nestling mass
# young fledged/ nest	nestling tarsus length
# young fledged/ successful nest	nestling mass:tarsus ratio
predicted fecundity (# female fledglings/ female)	nestling wing length
predicted # young fledged/ season	nestling outermost primary length
	nestling culmen length
fledgling survival	nestling rate of mass gain
fledgling daily survival rate	# days to fledging
postfledging survivorship	
adult survival	
adult male apparent survival	
adult female apparent survival	

Table 1.2. Reproductive effects of songbird nesting in non-native vegetation, summarized by reproductive metric types (direct measures and correlates) and subcategories. Significant responses were based on author-determined significance levels. Trends include both non-significant directional effects as well as stated trends where no indication of significance was provided.

Reproductive Metrics	# articles	# responses	Effects of Non-native Vegetation				
			+ significant	− significant	non-significant	+ trend	− trend
Direct Measures	**32**	**118**	**4**	**12**	**87**	**36**	**32**
nest survival/mortality	28	75	3	8	56	24	20
productivity	14	38	1	3	27	11	10
fledgling survival	2	3	0	1	2	0	1
adult survival	1	2	0	0	2	1	1
Correlates	**10**	**19**	**1**	**5**	**12**	**0**	**2**
nesting timing	4	4	0	2	1	0	1
brood parasitism	2	3	0	0	3	0	1
nestling condition	4	12	1	3	8	0	0
All Metrics	**32**	**137**	**5**	**17**	**98**	**36**	**34**
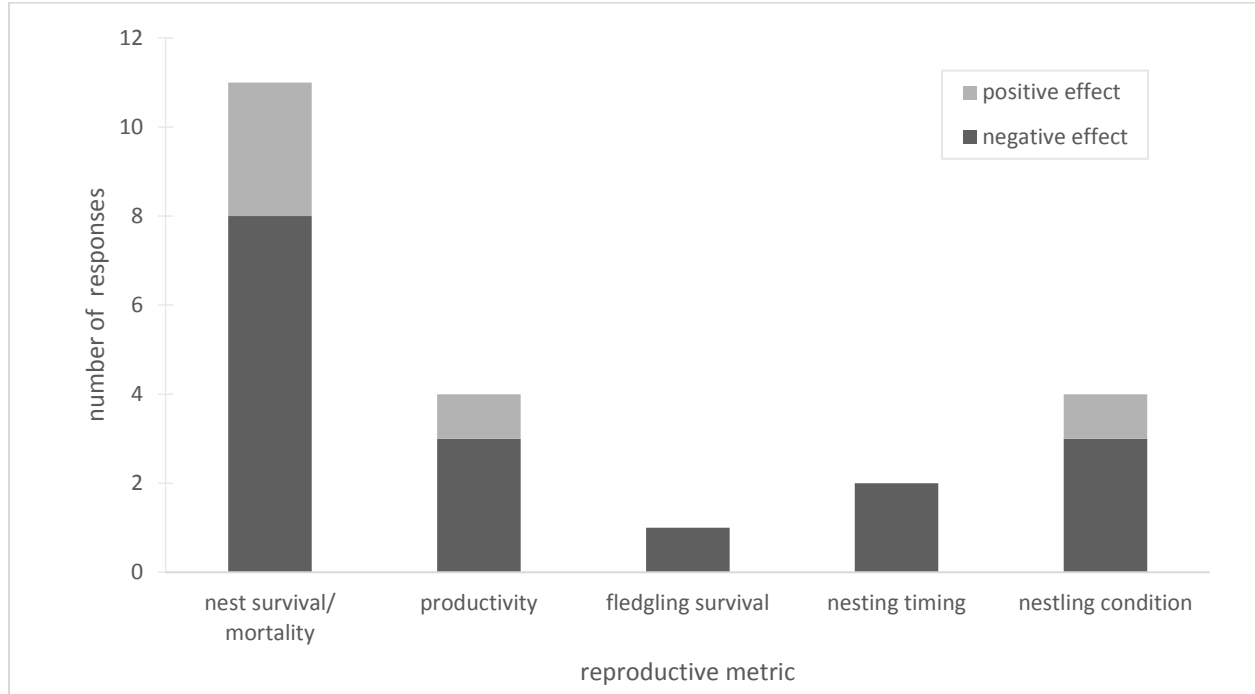
Figure 1.1. Significant positive (n=5) and negative (n=17) effects of songbird nesting in non-native vegetation. Direct reproductive success measures included survival/mortality (n=11), productivity (n=4), and fledgling survival (n=1). Reproductive success correlates included nesting timing (n=2) and nestling condition (n=4).
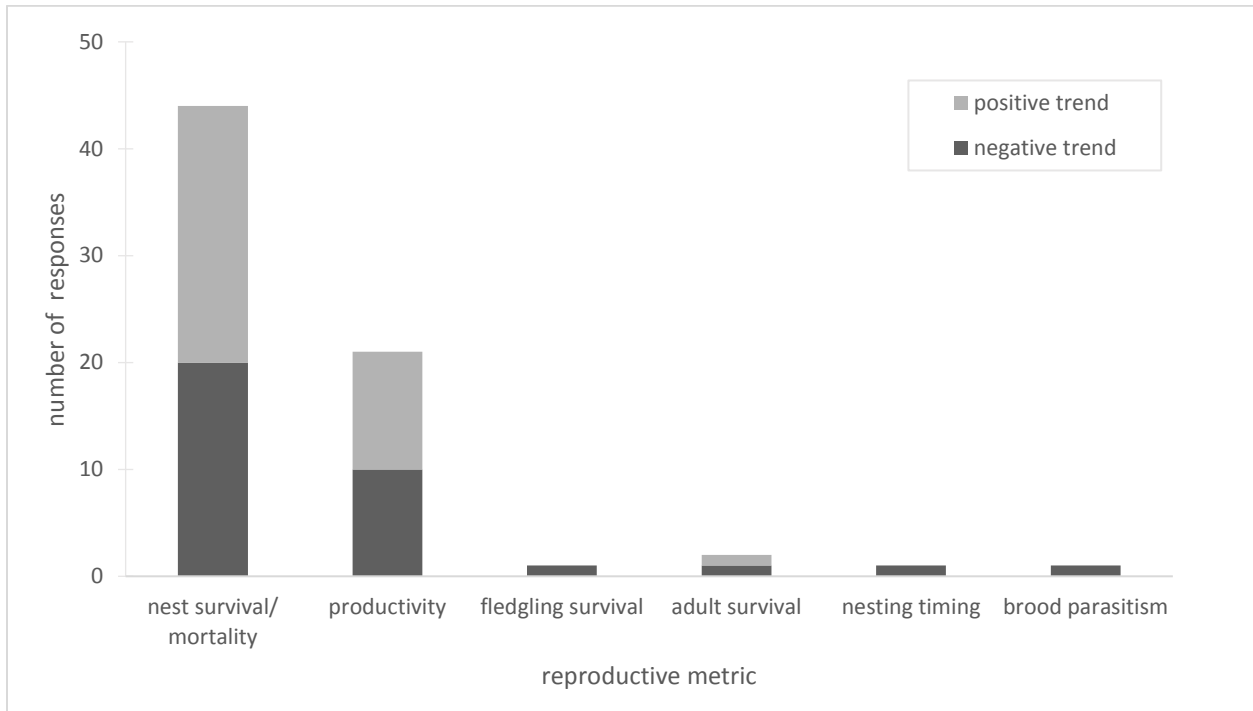
Figure 1.2. Non-significant or directional trends of unknown significance reported in articles examining effects of songbird nesting in non-native vegetation. Trends were balanced between positive (n=36) and negative (n=34) responses to non-native plants. Direct reproductive success measures included survival/mortality (n=44), productivity (n=31), fledgling survival (n=1) and adult survival (n=2). Reproductive success correlates included nesting timing (n=1) and brood parasitism (n=1).

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CHAPTER TWO

A NEAR-RANGE PLANT INVASION HAS NEUTRAL OR POSITIVE EFFECTS ON

RIPARIAN BIRD HABITAT USE AND REPRODUCTIVE SUCCESS

INTRODUCTION

Biological invasions are a global driver of environmental change and the second leading

cause of biodiversity loss worldwide (Vitousek et al., 1996; Wilcove et al., 1998). Through

synergistic interactions with other anthropogenic drivers, such as land use and climate change,

the rate and impact of invasions is expected to increase, leading to a greater prevalence of novel

ecosystems (Hellmann et al., 2008; Hobbs et al., 2006; Walther et al., 2009). In addition to the

long-distance invasion of species from other biogeographic regions, species that spread within or

close to their native ranges (*e.g.,* native invaders, near-range invaders), also have potential to

transform communities (Carey et al., 2012; McGeoch and Latombe, 2016; Simberloff, 2011).

Yet, the consequences of these local invasions for native ecosystems have received much less

attention than long-distance invaders (Carey et al., 2012).

Plant invasions can alter communities in a variety of ways, resulting in changes to the

abundance, species richness/diversity, and fitness of resident flora and fauna, as well as broader

ecosystem-level processes and functions (Ehrenfeld, 2010; Schirmel et al., 2016; Vila et al.,

2011). Invasion-mediated ecosystem changes can also impact delivery of important ecosystem

services, with consequences for human health and well-being (Millennium Ecosystem

Assessment, 2005; Pejchar and Mooney, 2009). However, there is growing recognition that non-

native plant impacts are complex, diverse, and highly context-dependent (Pyšek et al., 2012) – not all plant invasions result in negative impacts, and many can even produce positive effects (Schlaepfer et al., 2011). Recent reviews suggest that the effects of non-native plants vary across invading taxa, ecosystems, spatial and temporal scales, and levels of biological complexity (Pyšek et al., 2012; Schirmel et al., 2016; Vila et al., 2011). Variation in the direction and magnitude of effects arises from a combination of the specific characteristics of introduced plants and conditions in their recipient environments (MacDougall and Turkington, 2005).

Plant invasions affect animal communities through diverse pathways and understanding the mechanisms underlying these changes is critical for informing conservation and management decisions. One way that introduced plants affect animals is by altering the structure and composition of vegetation. For birds, vegetation changes can influence availability of suitable foraging and nesting substrates, result in changes to arthropod prey communities, and alter the distribution and abundance of predators (Litt et al., 2014; Nelson et al., 2017; Schmidt and Whelan, 1999), all of which have potential to impact the habitat use, fitness, and persistence of avian populations. While much research focuses on how non-native plants alter bird occupancy, abundance, and species richness/diversity, the fitness consequences of plant invasion remain relatively understudied (Schirmel et al., 2016; Stinson and Pejchar, *in review*). Thus, research characterizing the effects of plant invasion on bird fitness, especially in the case of near-range invaders, is needed for effective avian conservation and management.

The objective of this study was to investigate the effects of an introduced woody plant, New Mexico locust (*Robinia neomexicana*; Family: Fabaceae), on habitat use and fitness of riparian birds in the Piceance Basin of northwestern Colorado, USA. New Mexico locust is a deciduous tree native to the southwestern US, where it exists as a minor component of riparian

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forests (Pavek, 1993). The northern boundary of the plant's native range enters into southern Colorado; however, it does not extend as far north as our study area in the Clear Creek drainage of northwestern Colorado (Little, 1976). The plant was introduced to Clear Creek over a century ago and has since become well-established, likely as a result of its ability to fix nitrogen and spread quickly by rhizomatous growth (Pavek, 1993). Landowners have tried repeatedly to control the plant's spread using a variety of methods, but attempts have been largely unsuccessful (C. Tysse, personal communication).

To characterize the effects of this near-range plant introduction on riparian bird communities, we examined differences in measures of songbird habitat use, including species richness, occupancy, and abundance, across a gradient of invasion intensity within our study area. Based on previous findings of relatively depauperate insect and bird communities in invaded compared to native habitats (Holland-Clift et al., 2011; Litt et al., 2014; Schirmel et al., 2016), we expected to find decreased habitat use in highly invaded areas. We examined variation in vegetation characteristics across a gradient of invasion intensity as a way of identifying potential mechanisms (*e.g.,* biotic homogenization) underlying patterns in avian habitat use. In addition, because habitat use does not always indicate habitat quality (Van Horne, 1983; Vickery et al., 1992), and use differences may not necessarily translate into fitness consequences, we also investigated reproductive responses to invasion. We hypothesized that invasion would reduce fitness of riparian songbirds, resulting in lower nest survival and productivity in locust-invaded sites compared to non-invaded reference sites.

METHODS

Study Area

 The study was conducted along a ~25 km reach of Clear Creek and its tributaries, situated on privately owned lands within the Piceance Basin of northwestern Colorado, USA (Figure 2.1). The area contains diverse and rugged terrain, characterized by high mesas and steep canyons surrounding a low lying riparian corridor, which spans an elevation gradient of approximately 1700-2200 m. The landscape has undergone oil and gas development, with well pads and other energy infrastructure present, including a gravel access road that parallels much of the mainstem of Clear Creek. The higher elevation tributary sites remain isolated from development. Other land uses include agricultural crop production and seasonal cattle grazing in areas adjacent to Clear Creek. Streams are perennial but experience dynamic seasonal fluctuations in flow, especially following annual spring runoff, and are not known to contain fish. Stream width is variable throughout the area, measuring on average 2.07 ± 0.10 m (mean $\pm$ SE; n=125), with tributaries slightly narrower (1.45 ± 0.11 m; n=57) than sites within the mainstem of Clear Creek (2.59 ± 0.12 m; n=68).

 The vegetated riparian corridor averages 52 ± 3.55 m in width (range: $6.5 - 155$ m; n=125) and is dominated by an overstory of native box elder (*Acer negundo*), narrow-leaf cottonwood (*Populus angustifolia),* and Gambel oak (*Quercus gambelii*), as well as the introduced New Mexico locust. The understory vegetation within the riparian corridor is dominated by native shrub species, including Saskatoon serviceberry (*Amelanchier alnifolia*), mountain snowberry (*Symphoricarpos oreophilus.*), skunkbush sumac (*Rhus trilobata*), rabbitbrush (*Chrysothamnus spp.)*, and big sagebrush (*Artemisia tridentata*).

Sampling Design

Bird and Vegetation Surveys. – Sites for sampling bird and vegetation communities were established throughout the study area using a systematic sampling design and ~200 m spacing between sites (Figure 2.1). Using ArcGIS, we randomly selected starting points centered along the mainstem of Clear Creek and each of the five tributaries within the study area. Subsequent sites were systematically spaced at 200 m intervals along the steam centerline in upstream and downstream directions of the mainstem and tributaries. Sampling sites were verified for accessibility in spring 2015 and a total of 125 sites were established within the riparian corridor. Final sampling sites were placed in accessible locations of the corridor, located at varying distances from the stream edge (mean: 13.18 m, range: 1-32 m) to maximize visual and auditory detection of birds. Sites were situated on both sides of the stream, depending on access, with 52 sites established on the north/east side of the stream and 73 sites established on the south/west side.

Nest Monitoring. – We established 8 plots centered along the stream centerline within which to intensively search for and monitor passerine songbird nests. The plots measured approximately 2 ha in size and were placed in sites established previously for a complimentary project examining food web dynamics (see Chapter 3, Figure 3.1). Four of the plots were in areas invaded by locust and each was paired with a reference plot situated in similar habitat where locust was absent. Plots were separated by a minimum of 300 m.

Field Data Collection

Bird Surveys. – We conducted avian point count surveys at the 125 sampling sites within Clear Creek and tributaries during the breeding seasons in 2015 and 2016. Line transects and point counts are both effective bird sampling techniques for use in linear riparian habitats,

yielding similar species richness and relative abundance estimates (Dobkin and Rich, 1998). Line transects, however, require continuous navigation and movement in a straight line during surveys, which can reduce ability to detect birds, especially when moving through dense vegetation. Given the thick riparian vegetation and difficult terrain of the study area, point counts were selected as the preferred method for this study.

Five-minute, unlimited radius point count surveys were conducted from sunrise to 11am during May through early July of each year. Upon arrival to the point count station, the observer waited 1-2 minutes to allow birds to settle; however, birds that flushed during approach were included in the first minute of the survey. We identified and recorded the species of all individual birds observed visually and/or aurally throughout the survey. For each detection, we also recorded minute of first detection, initial detection method (visual or aural), cardinal direction, and detection distance (m) estimated using a range finder.

During each survey, we collected data on the following environmental variables hypothesized to influence detection: precipitation, wind and gusts using the Beaufort scale, % cloud cover, and stream noise level (rated 0-3). Surveys were never initiated during rain or if wind was greater than Beaufort scale level 3 (8-12 mph). Additional survey-level covariates collected included % crown cover of locust trees within a 10 m radius of the survey station and distance to nearest locust stem (m). Each point count station was visited a total of 3 times during each season. These replicate visits were conducted a minimum of 2 weeks apart and spanned a range of start times, alternating between early-, mid-, and late-morning hours for a given station to account for potential temporal variation in bird activity and detection.

Vegetation Surveys. – We conducted vegetation surveys at each sampling site during mid-June through early August to assess the structure and composition of vegetation and

generate variables to characterize the gradient of locust invasion throughout Clear Creek. Sampling effort was allocated evenly across years and latitudinal/spatial gradients to reduce bias associated with inter-annual variation. Each survey comprised 2 main components: 1) stem counts of live trees, live saplings, snags, and live shrubs within a 50 m x 2 m belt transect, and 2) line point intercept measurements taken at 1 m increments along a 25 m transect to assess percent cover (Elzinga et al., 1998). All transects were placed perpendicular to the riparian corridor with starting points positioned on the stream edge either 5 m upstream or downstream from each point count station (direction selected randomly).

Live trees and snags were defined as single stems $\geq$ 1.4 m height and $\geq$ 4 cm diameter at breast height (DBH). All trees and snags encountered within the belt transect were assigned to one of three height classes: 1.4 - 5 m, >5 - 10 m, or > 10 m. Live stems of tree species < 4 cm DBH were recorded as saplings and assigned to one of five height classes: 0.5 - 1.4 m, >1.4 - 2 m, >2 - 3 m, >3 - 5 m, or > 5 m. Shrubs were counted and assigned to one of the same five height classes used for saplings. When individual shrub boundaries were unclear, only stems spaced $\geq$ 12 in apart were considered different individual shrubs for the count.

For the line point intercept survey, we recorded vegetation intercepts within the following six height classes: < 0.5 m, 0.5 - 1 m, >1 - 2 m, >2 - 5 m, >5 - 10 m, or > 10 m. Intercepts were recorded to species only for trees and shrubs; forbs and grasses were recorded generally to assess percent cover by growth form.

Nest Monitoring. – To assess fitness consequences of invasion, we searched for and monitored nests of riparian songbirds within locust and reference plots within Clear Creek and tributaries during two breeding seasons (May-August, 2015 and 2016). We conducted walking transects and visual observation of adults to identify individuals flushing from nest locations as

well as adults demonstrating nesting behaviors (*e.g.,* carrying nest material). We standardized effort across the two site types and targeted nests of low-shrub to mid-canopy nesting species, focusing primarily on two riparian-dependent songbirds, MacGillivray's warbler (*Geothylpis tolmiei*) and yellow warbler (*Setophaga petechia*). We also opportunistically located nests of a variety of other passerines throughout the course of field activities. We visited nests every 2-5 days and photographed nest contents to assess status and monitor progress throughout the incubation and nestling stages. An extendable monopod attached to a camera was used to photograph nests above eye level.

We determined the fate of each nest as successful (fledged ≥ 1 nestling), or failed using a combination of 1) nestling age estimations from photos and observations collected at each nest visit, 2) estimates of hatching and fledging dates, and 3) physical evidence of nest failure, such as damaged or dismantled nests and missing contents prior to estimated fledge dates. We considered hatching date to be the date that the first egg hatched and fledging date to be the date that the first nestling left the nest. The exact date of hatching was known when eggs and newly hatched nestlings were both present in the nest during a single visit. Exact fledging date was known when the nest was observed mid-fledging (≥ 1 nestling missing with ≥ 1 near fledged nestling remaining in the nest). When hatching and fledging dates were not exactly known, we estimated them based on species-specific durations of incubation and nestling periods obtained from the literature (Baicich and Harrison, 2005; Rodewald, 2017; Appendix 2.1). In addition to documenting nest fates, we also recorded productivity measures, including clutch size, brood size, and number of young fledged. We collected environmental covariates associated with each nest, including substrate type and height, nest height, and elevation (Appendix 2.2).

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Statistical Analyses

Locust Intensity Index. – We used principal components analysis (PCA) to generate an

index of locust intensity based on 11 locust-related variables collected during point count and

vegetation surveys. PCA is an ordination method used to create composite variables from

multiple correlated variables and is often used to summarize plant traits and other aspects of the

environment (McCune et al., 2002). We measured variables at 3 spatial scales, including 1) 10 m

scale: % locust crown cover (averaged across replicate point count surveys), 2) 25 m scale: %

locust cover at each of 6 height classes (from line point intercept surveys), and 3) 50 m scale:

stem density (# stems/100 m^2) of locust trees, saplings, and snags (from belt transect counts). In

addition, we estimated distance to the nearest locust stem from each point count station using

either direct measurement (stems <100 m) or estimation in ArcGIS. All variables included in the

PCA were standardized to have a mean of 0 and standard deviation of 1. We used the first

principal component, which explained 52% of the variation in locust variables across sites, to

generate a locust intensity index. In addition, we used the locust intensity index to classify each

site into one of three groups: no locust, low intensity, or high intensity (Figure 2.1). Groups

contained approximately the same number of sites (n=41 or 42) and were based on tertiles from

ordered locust index values (n=125). Because of the nature of locust invasion within the area, 'no

locust' sites were spatially isolated from 'low intensity' and 'high intensity' sites and were

generally located at higher elevations within tributaries, while the invaded sites dominated the

mainstem of Clear Creek.

We examined relationships between invasion intensity and broader vegetation

characteristics using generalized linear models, assuming a Poisson distribution appropriate for

count data. We constructed a separate model for each vegetation variable hypothesized to vary as

a function of invasion intensity, including tree species richness, shrub species richness, total

density (#stems/100 m^2) of all trees, snags, and saplings and total density (#stems/100 m^2) of

native trees, snags, and saplings. We used model results to predict mean richness and density

measures across the range of locust intensity index values. All statistical analyses were

conducted in the statistical program R (R Core Team, 2016).

Species Richness. – For each sampling site, we calculated the raw species richness of

passerine and near-passerine species (excluding flyovers) based on the maximum number of

different species detected within 100 m of each site over the course of each season. We fit

generalized linear models to examine the relationship between songbird species richness and

locust intensity. For each year, maximum species richness at each site was modeled as a function

of the locust index, assuming a Poisson distribution appropriate for count data. We used model

results to predict mean songbird species richness across the range of locust intensity index

values. All statistical analyses were conducted in the statistical program R (R Core Team, 2016).

Single Species Occupancy Modeling. – We examined the influence of locust invasion

intensity and other environmental covariates on songbird habitat use using single-species, single

season occupancy models (MacKenzie et al., 2002) fit to point count data collected in the

breeding seasons of 2015 and 2016. Occupancy models allow for estimation of the probability of

occupancy (proportion of sites occupied; occupancy: 'psi') while accounting for imperfect

detection probability (detection: 'p'). We fit models for 12 riparian songbird species with

sufficient detections across our 125 sampling sites (>50 individuals detected within 100 m in

both years; Appendix 2.3). We did not pursue dynamic occupancy models because we did not

expect strong invasion-driven dynamics between the two years. Because locust has been

established for >100 years in the riparian corridor, we expected its effects to be similar between years. However, we anticipated other environmental variables to vary between years.

For each of the 12 species in each year, we modeled occupancy as a function of locust intensity index and other environmental variables hypothesized to influence habitat use. We modeled occupancy as a function of five site-level covariates collected during point count and vegetation surveys: 1) locust intensity index, 2) elevation, 3) riparian corridor width, 4) total density of all trees, saplings, and snags, and 5) total shrub density. Site-level covariates were constant across replicate site visits and years. We modeled spatial and temporal variation in detection probability as a function of five observation-level covariates collected during the three replicate point count surveys: 1) stream noise, 2) % cloud cover, 3) wind, 4) survey date (Julian), and 5) survey time (calculated as decimal hours after 12 a.m.). Observation-level covariates varied across replicate visits and years. All environmental variables were scaled to have a mean of 0 and standard deviation of 1. We calculated Pearson's correlations among all pairwise combinations of both site-level and observation-level covariates and all correlations were less than 0.5 in both years.

We conducted analyses using the 'occu' function in the 'unmarked' package (Fiske and Chandler, 2011) in the statistical program R (R Core Team, 2016). Because we constructed a single model for each species in each year, with additive effects of all covariates of interest, there was no need to undertake model selection and we simply interpreted the parameter estimates in each fully parameterized model for each species in each year. We summarized effect sizes and directions across species and years and considered effects with $p < 0.05$ to be significant (non-significant relationships are not discussed). For some species with very high naïve occupancy, our models incorporating detection probability estimated occupancy at or very near 1.0. Thus,

making inference on the influence of locust or other environmental covariates on occupancy for these species was not very informative. To complement our occupancy analyses and provide more information about associations for the more widespread songbird species, we also modeled songbird abundance.

Abundance Modeling. – To estimate songbird abundance as a function of locust intensity and environmental covariates, we fit hierarchical binomial N-mixture models, assuming a Poisson distribution, to the point count data. N-mixture models allow for estimation of abundance of unmarked animals based on temporally replicated count data, while simultaneously accounting for imperfect detection (Kéry et al., 2005; Royle, 2004). Like occupancy models, these models assume independence of sites and demographic closure, such that no changes in abundance are assumed to occur throughout the sampling period (*e.g.*, breeding season). To ensure equal survey areas for comparisons across stations and maintain independence of detections between adjacent sites, data were truncated to include only detections ≤ 100 m. Thus, our abundance estimates can also be interpreted as density estimates (# birds/100 m^2).

Using the same procedure as for occupancy modeling, we modeled songbird abundance as a function of locust intensity index and environmental covariates, while accounting for differences in detection among replicate visits and survey sites. We investigated the effects of the same site-level and observation-level covariates used for occupancy modeling on abundance and detection, respectively. Thus, for each species in each year, the model structures for abundance and occupancy analyses were identical. We fit abundance models to data for the same 12 songbird species to allow species-specific comparisons between the covariate effects on occupancy and abundance. We considered effects with $p < 0.05$ to be significant and do not discuss non-significant relationships. We conducted analyses using the 'pcount' function in the

'unmarked' package (Fiske and Chandler, 2011) in the statistical program R (R Core Team, 2016).

Nest Productivity and Survival Analyses. – We examined fitness consequences of invasion using two broad sets of analyses: 1) statistical comparisons of nest productivity measures and 2) nest survival modeling. Both sets of analyses compared nest outcomes between nests located in locust and reference sites. To examine effects of invasion on nest productivity, we compared clutch size, brood size, and number of young fledged between site types. We conducted two-sample Wilcoxon tests, a non-parametric alternative to t-tests used to compare samples that do not follow a normal distribution, to assess significant differences in productivity between locust and reference nests.

Daily nest survival rates can be used to calculate nest survival (the probability that ≥ 1 nestling hatches) over the duration of the nesting period. We modeled daily nest survival in program MARK (White and Burnham, 1999), which uses a maximum-likelihood estimation approach. We estimated daily nest survival rates as a function of individual covariates hypothesized to influence survival, while accounting for variation in nest exposure periods between successful and failed nests (Dinsmore et al., 2002; Dinsmore and Dinsmore, 2007). This represents a large improvement over apparent nest success, which fails to account for detection differences between successful and failed nests, and often results in biased high estimates because nests that fail early in incubation are underrepresented (Dinsmore et al., 2002; Mayfield, 1961).

We conducted two sets of nest survival analyses: 1) a community analysis based on nest monitoring data combined across 12 songbird species (Appendix 2.3) and 2) species-specific analyses for two riparian-dependent songbirds (MacGillivray's warbler and yellow warbler). To

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examine patterns in nest survival of the riparian songbird community, we modeled nest survival

across all nests for which there was sufficient data to determine nest fate (n=92). Although we

anticipated species-specific responses to locust invasion, we were unable to incorporate species

as a covariate in our community survival models because of parameterization limitations

associated with the large number of species and small sample size. However, we tested for

species differences using a subset dataset (n=78 nests) comprised of data from the six most data-

rich species (sample sizes ranging from 7 to 27). We used the second-order Akaike Information

Criterion (AICc) for small sample sizes (Anderson, 2008) to compare performance of a 'species

+ site type' model to our null model (site type) and found little support for the 'species + site

type' model (ΔAICc > 5). Furthermore, no significant differences existed in the species-specific

nest survival estimates obtained from the 'species + site type' model (all 6 sets of 95%

confidence intervals overlapped). Thus, we proceeded with our community survival modeling on

the complete dataset (n=92 nests) without incorporating species as a covariate.

Because invasion impacts were our main interest, we retained site type (locust or

reference) as the base of all models and added covariates to construct additive models based on

specific a priori biological hypotheses. We examined the influence of year and four nest

covariates: substrate ID (locust or other), nest height, substrate height, and elevation. We

constructed models with all possible combinations of the five covariates added to the base model

(32 candidate models), ranked models using AICc, and interpreted model coefficients in the top

model (lowest AICc value). To estimate nest survival rate from daily nest survival for the

community, we used a 23-day nesting period (incubation + nestling periods), based on the

average across all nests (12 species: range 21-31 d; Appendix 2.1).

We tested species-specific responses to locust invasion and nest characteristics for two riparian-dependent songbirds, MacGillivray's warbler and yellow warbler. Because of small sample sizes and a desire to avoid over-parameterization, we constructed a candidate set of single covariate models for each species. Covariates included site type (locust or reference), year, substrate ID (locust or other), substrate type (low shrub/forb or tree/high shrub), nest height, substrate height, and elevation. Substrate ID was excluded from yellow warbler models because only one nest was built in locust and substrate type was excluded from MacGillivray's warbler models because all nests were built in low shrub/forb substrates. We ranked models using AICc and interpreted model coefficients in the top model (lowest AICc) for each species.

RESULTS

Characterizing Locust Intensity and Vegetation Across Sites

The locust intensity index values generated from our PCA of 11 locust variables ranged from -2.24 to 8.14 (mean = 0) and mean values for the no locust, low intensity and high intensity groups were -1.77, -1.13, and 2.88, respectively (Appendix 2.4). Based on loading coefficients from PC1, higher index values were positively correlated with higher percent cover of locust, higher densities of locust trees, saplings, and snags, and smaller distances to the nearest locust stem. All sites in the no locust group (n=42) lacked locust at all scales examined and were also spatially very isolated from locust (mean distance to nearest stem = 1.3 km; Figure 2.1; Appendix 2.4). Sites within the low intensity group (n=41) were characterized by mean locust crown cover of 4%, locust cover within each height class of 1% or less, locust sapling stem densities around 6 stems/100 m^2, and a mean distance to nearest locust stem of about 26 m. Sites within the high intensity group (n=42) averaged 28% locust crown cover, 32% cover within the 2

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- 5 m height class, and about 26 times the density of locust trees and 7 times the density of locust saplings as low intensity sites. The mean distance to nearest locust stem averaged only 1 m for these high intensity sites (Appendix 2.4).

We found strong variation in shrub species richness, total shrub density, total tree density and native tree density as a function of invasion intensity, but tree species richness showed little variation across sites. The species richness and density of shrubs decreased significantly with increasing invasion intensity (p<0.001 for both; Figure 2.2; Appendix 2.5). While there was a significant increase in total tree density with increasing invasion intensity (p<0.001), this relationship was strongly driven by locust presence, as evidenced by the opposite pattern for native tree density (p<0.001; Figure 2.2; Appendix 2.5).

Effects of Invasion Intensity on Songbird Habitat Use

Species Richness. – We detected a total of 2,939 and 2,768 passerine and near-passerine birds within 100 m of point count stations (excluding flyovers) in 2015 and 2016, respectively. There were 50 species detected in total, with 43 and 41 species represented in the 2015 and 2016 datasets, respectively (Appendix 2.3). Raw species richness at sampling sites ranged from 3 to 19 species in 2015 and 3 to 17 species in 2016. Total species richness of passerines and near-passerines increased significantly with increasing locust intensity in both years (both p<0.001; Figure 2.3; Appendix 2.6).

Occupancy and Abundance. – Locust invasion intensity did not significantly affect songbird occupancy for 10 of 12 species examined; however, spotted towhee (*Pipilo maculatus*) occupancy decreased (p=0.026) and chipping sparrow (*Spizella passerine*) occupancy increased (p=0.044) with invasion intensity (Table 2.1). Similarly, locust intensity was not an important predictor of abundance for 11 of 12 songbird species examined (Table 2.2). Chipping sparrow,

the one species whose abundance was significantly influenced by locust intensity, showed a positive response.

Effects of Environmental Characteristics on Songbird Habitat Use

   Occupancy and Abundance. – Environmental characteristics, particularly elevation and shrub density, were more important predictors of songbird occupancy and abundance than invasion intensity. Effects were generally consistent between these two response variables; however, a greater number of significant effects were found for abundance compared to occupancy (Table 2.1; Table 2.2). Elevation and shrub density had significant effects on occupancy for 7 and 5 species, respectively (Table 2.1), but significant effects on abundance were even more widespread, with 8 species responding to each of these environmental variables (Table 2.2). Consistent across both years, the occupancy and abundance of Cordilleran flycatcher (*Empidonax occidentalis)* and hermit thrush (*Catharus guttatus*) were higher at higher elevation sites, while spotted towhee and song sparrow (*Melospiza melodia*) occupancy and abundance were higher at lower elevation sites. In addition, elevation had a consistent negative effect on abundance of house wren and lazuli bunting. As for shrub density, *Empidonax* flycatcher and spotted towhee had higher occupancy and abundance in areas of higher shrub density in both years. The effect of shrub density on abundance was consistently negative for Cordilleran flycatcher.

   Width of the riparian corridor and tree density had greater influence on songbird abundance than occupancy. While there was a negative effect of riparian corridor width on both measures of habitat use in both years for green-tailed towhee (*Pipilo chlorurus*), two additional species, yellow warbler and warbling vireo (*Vireo gilvus*), showed consistently positive effects

for abundance only. Total tree density showed no significant effects on occupancy and only influenced abundance of two species in 2016 only.

Estimates of Occupancy and Abundance

Study-wide estimates of occupancy and abundance varied among the 12 species of songbirds we examined; however, both measures of habitat use were lowest for song sparrow and highest for yellow warbler in both years (Appendix 2.7; Appendix 2.8). Song sparrow occupancy was estimated at 0.409 ± 0.024 and 0.463 ± 0.026 in 2015 and 2016, respectively, while abundance was <1.0 individual per site (100 m^2) in each year. Three species, yellow warbler, MacGillivray's warbler, and house wren, occupied almost all sites regardless of locust invasion or other site characteristics (all psi >0.90 in both years), and also attained some of the highest abundances (Appendix 2.7). Mean occupancy within high intensity invasion sites was consistently higher than within low intensity or no locust sites for Cordilleran flycatcher, house wren, yellow warbler, lazuli bunting, chipping sparrow, and song sparrow. The opposite was true for hermit thrush, warbling vireo, and MacGillivray's warbler, which all had lower occupancy in highly invaded sites. Inconsistent trends between years were found for the remaining species, which included *Empidonax* flycatcher, green-tailed towhee, and spotted towhee.

Detection Probability. – Because detection probability can strongly influence estimates of occupancy and abundance, it was an important consideration in accurately characterizing habitat use patterns in our system. Detection probability varied across sites and replicate visits for all species examined and estimates were generally much lower for abundance models than occupancy models (Appendix 2.9). Our models for MacGillivray's warbler and lazuli bunting estimated detection to be so low (<0.03) that abundance estimates were driven unreliably high

for these species (*e.g.,* >20 individuals/site), and thus were not considered biologically relevant (Appendix 2.8).

Significant environmental covariates influencing detection differed among species and years but effect directions between occupancy and abundance models were generally consistent (Appendix 2.10; Appendix 2.11). The most influential covariates on detection were stream noise and survey date. For 10 of 12 species, detection probability decreased significantly with increasing stream noise. Survey date had a significant effect on detection of 9 species, most of which were easier to detect as the breeding season progressed. The remaining survey-level covariates, including wind, cloud cover, and survey time, had little influence on detection probability for most species. Further discussion of the effects of detection probability is included in Appendix 2.9.

Invasion Effects on Songbird Reproductive Success

Locust Use and Effects on Nest Productivity. – We monitored 92 nests (n=52 locust, n=40 reference) of 12 species of riparian songbirds during May-August in 2015 and 2016. Songbirds commonly used locust as a nest substrate, with 44% of nests from locust sites incorporating the introduced plant as a supporting structure, either in its shrub or tree form (Appendix 2.12). All measures of nest productivity examined were higher in locust habitats, with significantly higher mean brood size, number of young fledged per nest and number of young fledged per successful nest in locust sites (all $p < 0.05$, Wilcoxon tests; Figure 2.4). Apparent nest success in locust sites (65%) was slightly higher than in reference sites (58%). Based on nest observations, predation was the main cause of nest failure in both site types, and there was no evidence of brood parasitism observed during the study. We found no differences in nest heights or substrate heights between site types; however, nests in locust sites were located at lower

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elevations than those in non-invaded reference habitats (p<0.001, Wilcoxon tests; Appendix 2.12).

Songbird Community Nest Survival. – Community nest survival estimates were similar for nests in locust and reference sites. We estimated the daily nest survival rate as 0.975 ± 0.006 SE for nests in locust-invaded habitats and 0.967 ± 0.009 SE for nests in reference habitats. Based on an average 23-day nesting period, community nest survival rate for locust nests was 55% (n=52), which was slightly higher than the 47% survival rate estimated for reference nests (n=40). Our top community model included additive effects of site type, substrate ID, nest height, substrate height, and elevation; however, only nest height and substrate height were significant predictors. Nest height had a positive effect on nest survival, while substrate height had a negative effect on nest survival (Appendix 2.13; Appendix 2.14).

Riparian-Specialist Nest Survival. – Based on results from our best supported model, which included site type, MacGillivray's warbler daily nest survival rate was 0.995 ± 0.005 SE in locust sites and 0.953 ± 0.027 SE in reference sites. MacGillivray's warbler nest survival over the 21-day nesting period was estimated at 91% for our sample of locust nests (n=17) and 36% for nests in non-invaded areas (n=10). All other single covariate models in our set were not well supported (all ΔAICc >2, Appendix 2.14), suggesting little influence of the specific nest characteristics investigated. Parameter estimates from the top model suggest locust has a slightly positive effect on nest survival for this species; however, the relationship is not statistically significant (Appendix 2.13). For yellow warbler, the intercept-only model was best supported (Appendix 2.14), suggesting no difference in nest survival between site types (0.979 ± 0.010 SE daily nest survival; 64% survival over the 21-day nesting period). Likely due to the small sample size, there was substantial model uncertainty, with support for six of the seven models in our

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candidate set (ΔAICc <2, Appendix 2.14); however, none of the parameter estimates in these single covariate models suggested significant effects of the specific nest characteristics we examined.

DISCUSSION

The near-range introduction of New Mexico locust had neutral or positive effects on riparian bird habitat use and reproductive success. Most songbird species showed no significant effect of invasion intensity on occupancy or abundance. Despite evidence of biotic homogenization of the vegetation community at highly invaded sites, total bird species richness increased with increasing invasion intensity. Locust was commonly used as a nesting substrate, and nests placed in locust did not show increased failure. Estimates of nest survival did not differ between locust and reference sites and nests in locust sites were more productive, yielding larger broods and fledging significantly more nestlings. Collectively, these findings suggest that the near-range introduction and establishment of New Mexico locust within Clear Creek has not had negative impacts on the bird community; rather, locust appears to provide quality breeding habitat for many riparian songbirds.

We found little evidence for negative effects of locust invasion on occupancy and abundance of songbird species in our study. We are confident in these findings because our modeling accounted for variation in 1) site-level covariates, such as elevation and shrub density, which influenced bird habitat use and 2) survey-level covariates, such as stream noise and date, which influenced the detection process. Cordilleran flycatcher, house wren, and yellow warbler were so widespread that they occupied every high intensity invasion site, suggesting no negative influence of invasion on their habitat use. Further, none of the songbird species we examined

showed significant reductions in abundance with increased invasion intensity; only spotted towhee occupancy decreased significantly with increasing invasion intensity and only in one year of the study (Table 2.1). Occupancy and abundance of spotted towhees, like most species in our assemblage, showed stronger associations with elevation and shrub density. These significant effects were larger in magnitude than the effect of locust intensity and were found in both years of the study (Appendix 2.10; Appendix 2.11). As towhees prefer open, shrubby habitats (Bartos Smith and Greenlaw, 2015), it is reasonable that they would preferentially occupy non-invaded or low intensity invasion sites, which were characterized by higher shrub densities. Based on Breeding Bird Survey data, spotted towhees have shown declining trends in both Colorado and the Southern Rockies during 1966-2015 (Sauer et al., 2017); however, we did not detect invasion-mediated effects on abundance in our study area, perhaps due to the availability of preferable habitat outside of highly invaded areas.

Another species that has shown regional population declines over the last several decades is the chipping sparrow (Sauer et al., 2017); however, our results of positive effects of invasion on occupancy and abundance suggest that their populations may be bolstered by the resources provided at invaded sites (Table 2.1; Table 2.2). We observed chipping sparrows foraging on tent caterpillar outbreaks within young locust stands at our site, which may help explain why we saw a positive association between locust intensity and the occupancy and abundance of chipping sparrows. These sparrows may have been capitalizing on this high quality, protein-rich food source, as they are known to supplement their plant-based diets with insect prey, including Lepidoptera larvae, during the breeding season (Middleton, 1998).

Although invasion had neutral effects on occupancy and abundance of most bird species, vegetation characteristics varied with invasion intensity, suggesting differences in habitat

conditions across the invasion gradient. Sites with higher cover and stem densities of locust also had lower total shrub species richness, shrub densities, and native tree densities (Figure 2.2), consistent with the observation that biotic homogenization of vegetation is often driven by the spread of invasive species (McKinney and Lockwood, 1999). However, we found no accompanying reduction in bird species richness as might be expected; rather, avian richness was lower at sites without locust and increased with invasion intensity (Figure 2.3). While several previous studies have found reductions in bird species richness and diversity associated with invasive plants (Aravind et al., 2010; Hajzlerova and Reif, 2014), others report little influence of non-native vegetation (Fischer et al., 2012; Fleishman et al., 2003). For example, in a study of saltcedar (*Tamarix ramosissima*) impacts on riparian bird communities, Fleishman et al. (2003) found that total vegetation volume, rather than vegetation diversity or non-native plant dominance, was the best predictor of bird species richness. The authors suggested that increased vegetation volume may support higher prey abundances as well as a greater diversity of feeding strategies. Despite reduced vegetation diversity, locust-invaded sites in our system may still support high structural diversity, which has been previously shown to drive avian diversity patterns (MacArthur and MacArthur, 1961). This structural heterogeneity could be maintained in part by the fact that New Mexico locust takes multiple growth forms, ranging from low shrubs and small saplings to mature trees and snags.

In addition, the pattern of increasing bird species richness with higher invasion intensity may be influenced by variation in other site characteristics, such as elevation and riparian width. The decline in biodiversity with increasing elevation is a foundational pattern in ecology. Global analysis of bird elevational diversity suggests that middle and lower elevations often support more diverse avian communities than higher elevations (McCain, 2009). In our study, these

patterns are likely driven by differences in abiotic and biotic conditions that interact with species

habitat requirements to result in lower bird richness at high elevation 'no locust' sites. Smaller

riparian width at non-invaded sites may also have excluded more area-sensitive species and

reduced the overall amount of riparian habitat available to support diverse bird communities. We

also recognize that the spatial segregation of the 'no-locust' sites from the 'low intensity' and

'high intensity' invasion sites within the mainstem of Clear Creek (Figure 2.1) may have

influenced our findings in other ways that we could not account for through modeling.

We found no evidence of negative effects of invasion on avian reproductive success. This

suggests that the introduced locust provides suitable habitat for nesting songbirds, rather than

acting as an ecological trap with negative fitness consequences (Battin, 2004), as has been found

for numerous other exotic and invasive plants (Nordby et al., 2009; Rodewald et al., 2010;

Schirmel et al., 2016; Schmidt and Whelan, 1999). Daily nest survival rates in locust and

reference sites were not statistically different, which is consistent with findings of generally

neutral effects on nest survival reported in a recent synthesis of invasive plant effects on North

American avifauna (Nelson et al., 2017). Other reviews have found few significant effects on

nest survival, but suggest that when they are found, they are mainly negative (Schirmel et al.,

2016; Stinson and Pejchar, *in review*). Surprisingly, nests in locust sites produced larger broods

and fledged more young per nest on average, despite having similar clutch sizes to nests in

reference sites (Figure 2.4). Because New Mexico locust is a near-range introduction, perhaps

the pattern of reduced insect prey typically associated with alien invasive species (Litt et al.,

2014) does not apply to this species. If so, higher productivity in invaded sites could be

explained by enhanced quantity or quality of food resources that might result in better nestling

condition (Gleditsch and Carlo, 2014), and thus more young fledged. Our observation of tent

caterpillar outbreaks in locust stands during both years of the study lends some support to this idea, since caterpillars are known to be important prey items for breeding insectivores (Greenberg, 1995). While we were unable to directly assess prey availability in this study, it is feasible that a near-range plant introduction might have less pronounced effects on arthropod assemblages, because of shared evolutionary histories with resident species as well as greater similarities in environmental conditions between native and introduced ranges (Mitchell et al., 2006).

The few previous studies that have investigated invasive plant impacts on nesting productivity have shown mixed negative, neutral and positive effects (Nelson et al., 2017). Negative effects of invasive plants on the number of young fledged were found for chestnut-collared longspurs (*Calcarius ornatus*) nesting in crested wheatgrass (*Agropyron cristatum*) monocultures (Lloyd and Martin, 2005) and northern cardinals (*Cardinalis cardinalis*) nesting in exotic honeysuckle shrubs (*Lonicera maackii*) (Rodewald et al., 2010). Conversely, invasive grass cover had a positive effect on the number of young fledged per successful nest for savannah sparrows (*Passerculus sandwichensis*) (Ludlow et al., 2015). Still other studies report little effect of invasive cover on productivity measures (Jones and Bock, 2005; Kennedy et al., 2009). Thus, more research is needed on productivity outcomes (and fitness measures, in general; Stinson and Pejchar, *in review*) for songbirds nesting in invaded habitats to better understand how plant invasion affects avian population persistence across different ecological contexts. In addition, we were unable to examine adult or post-fledging juvenile survival in this study; thus, it is unknown whether this plant invasion could negatively influence these other stages of the avian life cycle, which also influence population dynamics.

Conclusions

The near-range introduction of New Mexico locust has resulted in few negative impacts on the songbird community, despite evidence of vegetation homogenization with greater invasion intensity. In contrast to our hypothesis that invasion would reduce avian habitat use, we found mainly neutral effects on songbird occupancy and abundance and a positive impact on bird species richness. The pattern of increased bird species richness with increasing invasion intensity suggests that locust-invaded areas are providing habitat to support diverse bird assemblages. These findings lend support for the importance of structural diversity rather than plant species richness for influencing bird species richness. We found no evidence of reduced survival for nests built in locust substrates, nor for those placed in other substrates within locust-invaded sites. Thus, there was no support for our hypothesis that locust invasion would result in negative fitness consequences for breeding songbirds. Rather, there appeared to be reproductive benefits associated with nesting in invaded sites, namely increased nestling fledging rates. By examining both habitat use and reproduction, we sought a more complete understanding of the potential consequences of plant invasion on songbird population health and persistence. Investigating the effects of lesser-known invading species (*e.g.,* near-range invaders, native invaders) using such multi-faceted approaches as these is important for broadening our understanding of plant invasions and facilitating effective conservation and management of native communities.

TABLES

Table 2.1. Significant effects (p < 0.05) of an introduced plant (locust intensity index) and other environmental covariates on occupancy for 12 species of riparian songbirds in 2015 and 2016. Effect directions are based on coefficient estimates of covariates from single-season occupancy models (Appendix 2.10). Covariate relationships for which p ≥ 0.05 (blanks) were considered to have little or no effect. Species are listed in taxonomic order.

species code	species common name	locust index		elevation		riparian width		tree density		shrub density	
		2015	2016	2015	2016	2015	2016	2015	2016	2015	2016
EMPI	*Empidonax* Flycatcher									+	+
COFL	Cordilleran Flycatcher			+	+					−	
HOWR	House Wren				−						
HETH	Hermit Thrush			+	+						−
WAVI	Warbling Vireo										
YWAR	Yellow Warbler										
MGWA	MacGillivray's Warbler										
LAZB	Lazuli Bunting			−							
GTTO	Green-tailed Towhee			−		−	−			+	
SPTO	Spotted Towhee		−	−	−					+	+
CHSP	Chipping Sparrow		+								
SOSP	Song Sparrow			−	−						

Table 2.2. Significant effects (p < 0.05) of an introduced plant (locust intensity index) and other environmental covariates on abundance for 12 species of riparian songbirds in 2015 and 2016. Effect directions are based on coefficient estimates of covariates from N-mixture models (Appendix 2.11). Covariate relationships for which p ≥ 0.05 (blanks) were considered to have little or no effect. Species are listed in taxonomic order.

species code	species common name	locust index 2015	locust index 2016	elevation 2015	elevation 2016	riparian width 2015	riparian width 2016	tree density 2015	tree density 2016	shrub density 2015	shrub density 2016
EMPI	*Empidonax* Flycatcher								−	+	+
COFL	Cordilleran Flycatcher			+	+					−	−
HOWR	House Wren			−	−						−
HETH	Hermit Thrush			+	+				+		−
WAVI	Warbling Vireo					+	+				
YWAR	Yellow Warbler					+	+				
MGWA	MacGillivray's Warbler				+					+	
LAZB	Lazuli Bunting			−	−						−
GTTO	Green-tailed Towhee			−	−	−				+	
SPTO	Spotted Towhee			−	−					+	+
CHSP	Chipping Sparrow		+								
SOSP	Song Sparrow			−	−						
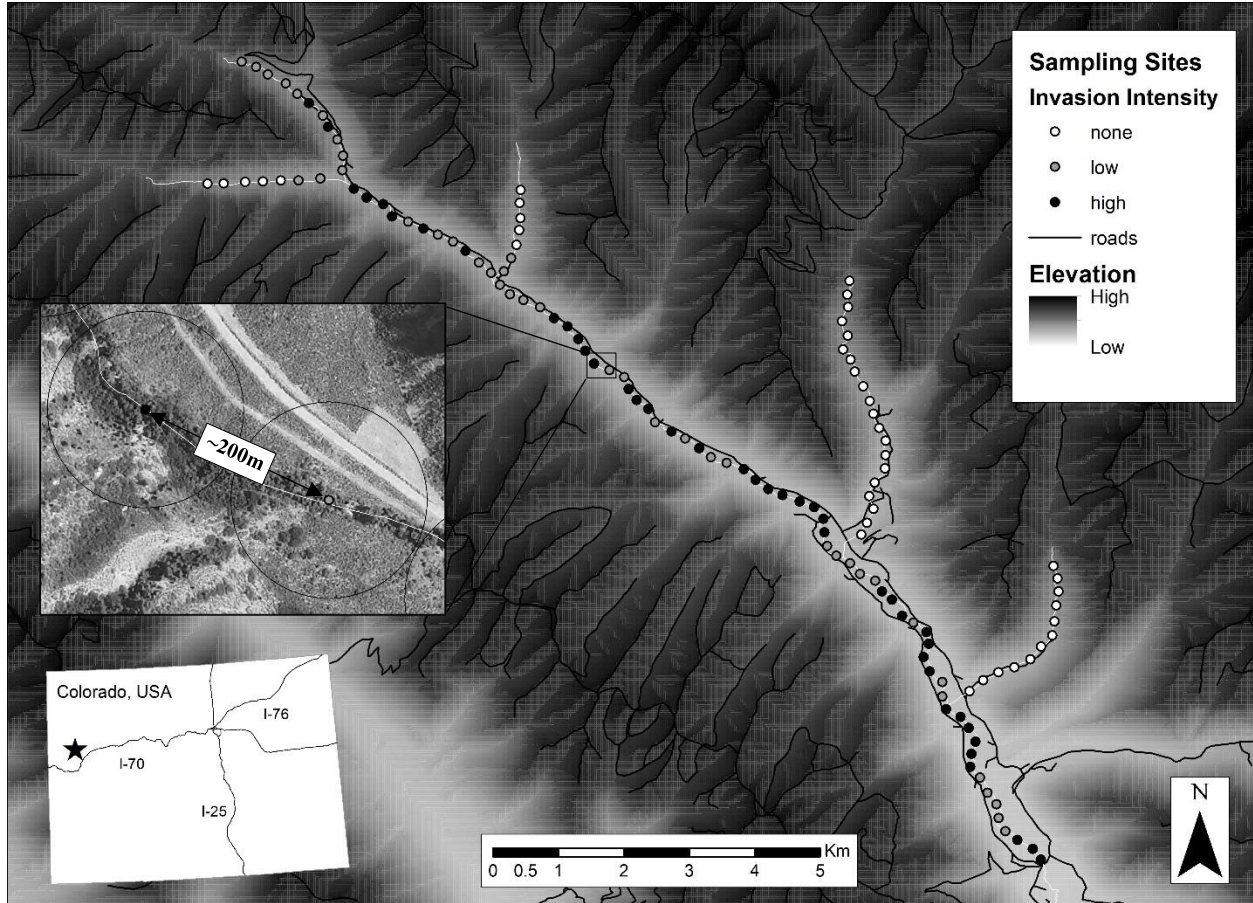
Figure 2.1. Bird and vegetation sampling sites (n=125), established to evaluate the ecological effects of an introduced plant, were placed systematically throughout the study area in the Clear Creek drainage of northwestern Colorado, USA. Symbol color corresponds to invasion intensity group, determined using principal components analysis of 11 locust-related variables collected at each site. White symbols depict sites with no locust present (n=42), gray symbols depict low intensity invasion sites (n=41), and black symbols depict high intensity invasion sites (n=42). The inset shows 200 m site spacing and placement within the riparian corridor.
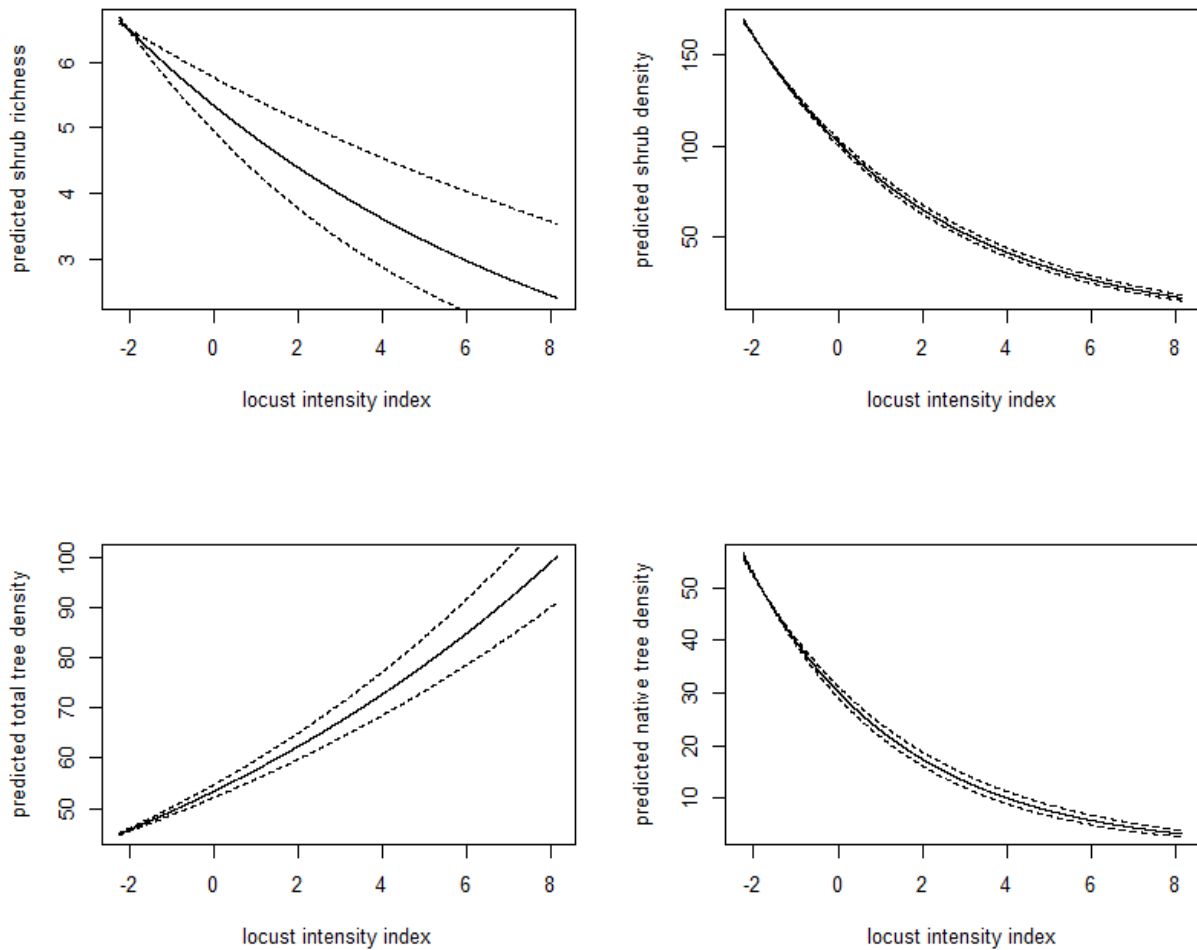
Figure 2.2. Patterns of shrub species richness, shrub density, total tree density (including locust), and native tree density with increasing presence of an introduced plant (locust intensity index). Mean predicted values of each vegetation variable (solid lines) with 95% confidence intervals (dashed lines) are displayed. Shrub and tree densities (#stems/100 m^2) were calculated based on stem counts conducted within 50 m x 2 m belt transects placed perpendicular to the riparian corridor at sampling sites (n=125). Both measures of tree density (bottom panels) are based on combined counts of live trees, saplings, and snags. All relationships are statistically significant (p < 0.001) based on single covariate generalized linear models (Appendix 2.5).
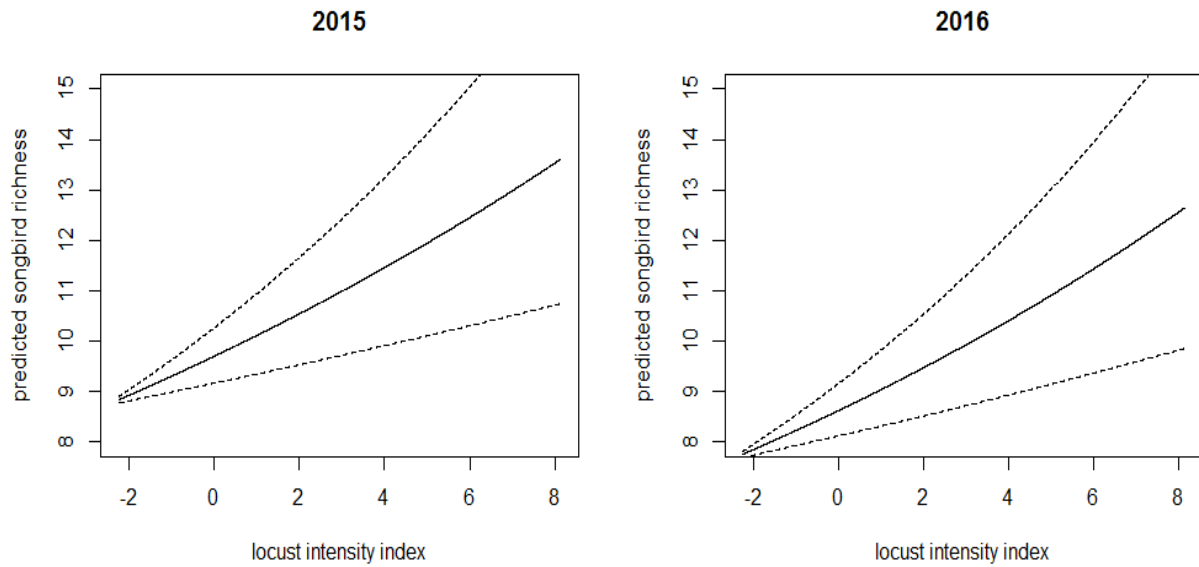
Figure 2.3. Mean predicted songbird species richness as a function of increasing intensity of locust, an introduced plant. Mean predicted richness (solid lines) with 95% confidence intervals (dashed lines) are displayed separately for each year based on detections within 100 m of sampling sites (n=125). In both years, the relationship was statistically significant (both p < 0.001) based on generalized linear model results (Appendix 2.6).
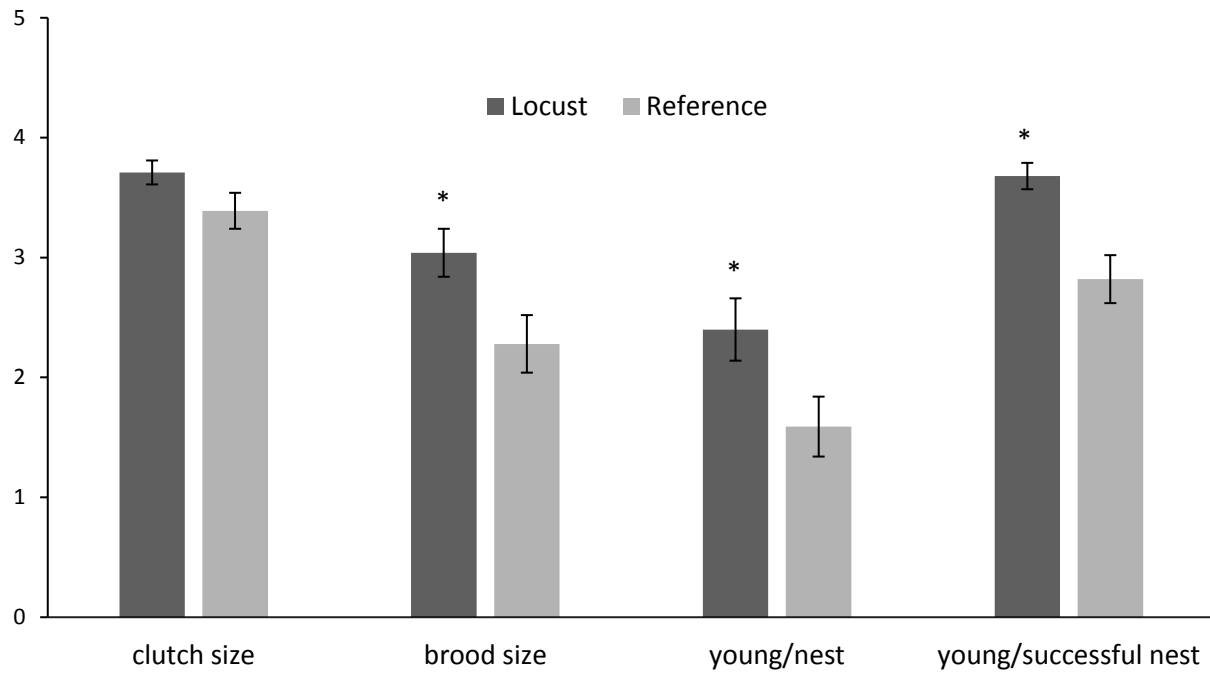
Figure 2.4. Comparison of productivity metrics (mean ± SE) between nests in sites with locust, an introduced plant (n=52), and nests in uninvaded reference sites (n=40). Clutch size, brood size, and young/nest were calculated based on all nests (both successful and failed, n=92), while young/successful nest was calculated based nests that fledged ≥ 1 nestling (n=57). Significant differences ($p < 0.05$, two-sample Wilcoxon tests) are indicated with *.

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CHAPTER THREE

AN INTRODUCED PLANT AFFECTS AQUATIC-DERIVED CARBON IN THE DIETS OF

RIPARIAN BIRDS[2]

INTRODUCTION

Invasive species impact ecosystem structure and function (Ehrenfeld, 2010) and lead to biotic homogenization of communities (Olden et al., 2004). Characteristics related to the life history, physiology, and chemistry of invasive plants can drive fundamental shifts in primary production, nutrient cycling, water usage, and decomposition (Ehrenfeld, 2010; Hladyz et al., 2011; Strong et al., 1984; Tallamy, 2004). Recent syntheses have attempted to identify patterns in the mechanisms and consequences of invasion across diverse ecosystems, taxa, and levels of ecological complexity (Pyšek et al., 2012; Schirmel et al., 2016; Vilà et al., 2011). However, few universal trends emerged from these assessments; rather, the effects of introduced plants appear to be highly context-specific, varying in direction and magnitude across ecosystems, taxa, and functional traits (Pyšek et al., 2012; Schirmel et al., 2016; Vilà et al., 2011). Equally apparent, studies tend to focus on a single ecosystem function and fail to address the interacting and potentially reinforcing mechanisms underlying invasion-driven ecosystem change (Levine et al., 2003). Resource subsidies, or fluxes of resources between ecosystems, can provide insight into the multiple ways invasive species alter biological communities (*e.g.*, Benjamin et al., 2011; Mineau et al., 2012).

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Riparian plant and animal communities are particularly susceptible to invasion, which can lead to impacts on ecosystem services and human well-being (Dudgeon et al., 2006; Tockner et al., 2010). New assemblages of taxa, driven by species invasions and climate change (Cardinale et al., 2012; Hellmann et al., 2008; Walther et al., 2009) can alter the timing, duration, and magnitude of aquatic and terrestrial insect subsidies, and these factors can interact to decouple cross-ecosystem subsidies (Larsen et al., 2016). Changes in the riparian forest canopy, for example, can affect aquatic insect communities by altering litter input quality and quantity, canopy openness, and algal communities (Hladyz et al., 2011; Kominoski et al., 2013). Furthermore, compared to native vegetation, non-native plants often support decreased terrestrial arthropod abundance, biomass, and richness (Litt et al., 2014; Simao et al., 2010). Changes in the relative availability of aquatic and terrestrial insects have potential to cascade through food webs, with bottom-up impacts on riparian insectivorous birds (Hladyz et al., 2011; Marczak et al., 2007).

Riparian bird assemblages are likely to be sensitive to invasion-mediated changes in resource subsidies because many insectivorous species consume aquatic prey. Aquatic insects can contribute substantially to avian insectivore diets, and some species are entirely dependent on aquatic food resources during certain times of year (Nakano and Murakami, 2001; Uesugi and Murakami, 2007). Differences in the diet composition *(i.e.,* proportion of aquatic vs. terrestrial prey) of birds using riparian habitats dominated by either native or introduced plants may reflect invasion-mediated diet shifts, with potential consequences for the health and persistence of diverse riparian bird communities (Murakami and Nakano, 2001). Yet, despite the susceptibility of riparian areas to invasive species (Richardson et al., 2007), few studies have addressed the potential effects of plant invasion on insect subsidies provided to avian consumers.

This study evaluates the contribution of aquatic-derived carbon to insectivorous songbird diets and how an introduced plant, New Mexico locust (*Robinia neomexicana*; family: Fabaceae), might alter the aquatic- and terrestrial-derived diet components of these riparian birds. New Mexico locust is native to the southwestern United States and extends into portions of southern Colorado (Little, 1976; Pavek, 1993). This species was introduced >100 years ago to an area north of its native range in the Clear Creek drainage of the Piceance Basin of northwestern Colorado, USA (Figure 3.1), where it has become well-established and dominant in some reaches of the watershed. Functional traits, such as rhizomatous growth and the ability to fix nitrogen, likely make New Mexico locust a successful pioneer species. Landowners have attempted to remove the plant, with no sustained success in limiting or reducing spread (C. Tysse, personal communication).

To determine whether plant invasion affected riparian consumers via altered resource subsidies, we compared the diets of insectivorous songbirds captured from reference sites and sites invaded by New Mexico locust using stable isotope analysis (SIA) of fecal samples. We predicted that aquatic insects would contribute to the diets of riparian songbirds, but that reliance on this resource subsidy would vary among species (Murakami and Nakano, 2001; Uesugi and Murakami, 2007; Yard et al., 2004). Specifically, we hypothesized that diets of strict insectivores would have higher proportions of aquatic-derived prey than more omnivorous species. Non-native vegetation often supports depauperate terrestrial arthropod communities compared to native plants (Litt et al., 2014; Simao et al., 2010), and songbirds often forage in proportion to prey availability (Busby and Sealy, 1979; Howe et al., 2000). Therefore, we predicted that bird fecal samples in invaded sites would have $\delta^{13}C$ more similar to aquatic-derived isotope signatures, indicating increased reliance on aquatic insects. In addition, non-native vegetation

invasions often disproportionately reduce higher trophic level arthropods compared to lower

trophic level taxa (Ballard et al., 2013; Simao et al., 2010). Thus, we hypothesized that fecal

samples of birds in invaded sites would be less enriched in $\delta^{15}N$ because of reduced populations

of predaceous or parasitic arthropods.

METHODS

Study Area

This study took place in the Clear Creek drainage of northwestern Colorado, USA

(39.5°N, 108.2°W), located in Garfield County ~60 km northeast of Grand Junction on privately

owned lands. The area has undergone oil and gas development, with oil pads and other

infrastructure near the riparian zone, including a gravel access road paralleling the main stem of

Clear Creek. The landscape is topographically diverse (1500-2700 m elevation) and is

characterized by high mesas and steep canyons surrounding the 1st and 2nd order streams of Clear

Creek and tributaries. The riparian corridor within the study area averaged 49 ± 8 m SE in width

and was dominated by native trees including boxelder (*Acer negundo)*, cottonwood (*Populus*

angustifolia), and Gambel oak (*Quercus gambelii*), as well as New Mexico locust in invaded

areas. The shrub layer consisted of Saskatoon serviceberry (*Amelanchier alnifolia*), big

sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus sp.*), snowberry (*Symphoricarpos*

sp.), chokecherry (*Prunus virginiana*), currant (*Ribes sp*.), and rose (*Rosa woodsii*).

Sampling Design

After reconnaissance mapping of stream reaches uninvaded and invaded by New Mexico

locust (hereafter, "reference" and "locust"), we established eight 180 m sampling sites within

reference and locust reaches, spaced >300 m apart and paired by elevation (Figure 3.1). Streams

within study reaches are relatively narrow (2.3 ± 1.1 m SE) and of moderate gradient (2.2 ± 1.7%

SE, measured from four GPS coordinate measurements), with fine silts and small gravel typical of the oil shale geology of the region.

Insect Sampling

Aquatic and terrestrial insects in reference and locust sites were sampled by deploying emergence and pan traps on the upstream, middle, and downstream transect of each sampling reach. We placed floating emergence nets (0.3 m^2) on the water surface to capture adult aquatic insects emerging from the stream channel (Cadmus et al., 2016). We placed pan traps (0.4 m^2) over the water surface to capture adult aquatic insects and terrestrial arthropods falling into the stream. The pan traps were filled 5 cm deep with stream water and approximately 5 mL of biodegradable surfactant was added to reduce surface tension (Wipfli, 1997). Both trap types were deployed simultaneously for 48 hr (2015: 21 – 22 July; 2016: 30 – 31 July) and collected insects were preserved in 70% ethanol.

We enumerated and identified all insects collected to family using taxonomic keys (Merritt et al., 1996; Triplehorn and Johnson, 2005). We selected dominant herbivorous terrestrial and aquatic insects based on mean percent of individuals in pan traps or emergence nets pooled across years. Dominant herbivorous terrestrial taxa included leafhoppers (Cicadellidae; 9.6%), caterpillars (Lepidopteran larvae; 5.8%), and aphids (Aphididae; 0.44%). Emergent aquatic insect richness averaged only 2 taxa per sample (a maximum of 6 taxa in one sample) throughout the study, so we considered all functional feeding groups except shredders as candidates for isotope analysis (*i.e.,* filter feeders, collector-gatherers, and algae grazers). Shredders were excluded because they feed on terrestrial leaf litter inputs, and thus would have similar δ^{13}C signatures to terrestrial-derived insects. Dominant aquatic taxa in emergence nets included midges (Chironomidae: 57.5%), black flies (Simuliidae: 7.7%, 2015), heptageniid

mayflies (7.5%, 2016), and baetid mayflies (6.1%). Heptageniid mayflies were substituted for black flies in 2016 because only one black fly occurred in all samples in 2016.

Songbird Fecal Sampling

Mist-netting of insectivorous songbirds to collect fecal samples for SIA was undertaken in late summer of each year (2015: 11 July–5 August; 2016: 17 July–6 August), corresponding with the time that insects were sampled. We sampled late in the songbird breeding season to minimize disturbance to nesting pairs, and allow capture of adults and fledged juveniles prior to migration. Within each of the eight sampling sites, we set up 4-7 mist nets (38-mm mesh, 6-12 m), placed along habitat edges and bisecting the riparian corridor. We opened nets for 2-4 days per site during the morning hours when weather conditions allowed safe capture and extraction of songbirds; nets were closed during times of rain or high wind. For each captured bird, we recorded the species, mass (g), fat score (0 to 3), and age class (hatch-year (HY) or after-hatch-year (AHY)). We used passive methods (placement in cloth bags) to collect fecal samples and stored samples in 70% alcohol. Bird feces contain insects ingested within a few hours before capture, making them ideal for examining diet changes over small spatial and short time scales (Salvarina et al., 2013). Using feces for dietary analysis is also a less invasive alternative to stomach lavage or tissue sampling (Painter et al., 2009; Podlesak et al., 2005; Salvarina et al., 2013).

Stable Isotope Processing

Naturally abundant isotopes of carbon (^{13}C) can be used to track time-integrated contributions of aquatic- and terrestrial-derived energy through food webs (Ben-David and Flaherty, 2012). Primary producers in aquatic and terrestrial ecosystems often have distinct δ^{13}C values because of variation in plant physiology and resource availability, and these tracers

exhibit little isotopic fractionation during trophic transfer (DeNiro and Epstein, 1978; Rounick and Winterbourn, 1986). Additionally, isotopes of nitrogen (^{15}N) can be used to track differences in food web structure because consumers typically become enriched in ^{15}N with increasing trophic position (DeNiro and Epstein, 1981; Vander Zanden et al., 1999).

Fecal and insect samples were dried at 60°C for 48 hr, homogenized, and weighed to a precision of 0.001 mg into 4 x 6 mm cylindrical tin capsules. Stable isotopes were measured at the Natural Resource Ecology Laboratory (Colorado State University) using a Carlo Erba NA 1500 (Milan, Italy) coupled with a VG Isochrom continuous flow isotope ratio mass spectrometer (Isoprime Inc., Manchester, UK) to simultaneously determine nitrogen and carbon isotope composition. Ratios of the heavy isotope to its common lighter counterpart *(i.e.,* $^{13}C/^{12}C$ and $^{15}N/^{14}N$) were expressed in standard δ-notation relative to international standards (Vienna Peedee Belemnite and atmospheric nitrogen, respectively) in parts per mil (‰). For instance, $\delta^{13}C_{sample} = [(^{13}C_{sample}/^{12}C_{sample})/(^{13}C_{standard}/^{12}C_{standard})-1] \times 1000$, and likewise for $\delta^{15}N$. Analytical precision from multiple in-house runs was 0.2 ‰ for $\delta^{13}C$ and 0.3 ‰ for $\delta^{15}N$ (Fry 2007).

Statistical Analyses

Aquatic-Derived Carbon in Songbird Diets. – To identify the relative contributions of aquatic- and terrestrial-derived prey in the diets of songbirds, we used $\delta^{13}C$ of fecal and insect samples in a single-isotope mixing formula (Fry 2007). SIA of insect samples provides context for $\delta^{13}C$ shifts in bird diets, and provides terms in the mixing formula used to calculate the proportions of aquatic and terrestrial diet components for each fecal sample. First, we tested for differences in $\delta^{13}C$ of insect samples to determine appropriate groupings for calculation of diet sources. $\delta^{13}C$ of insect samples were evaluated using two-way analysis of variance (ANOVA) by year with $\delta^{13}C$ as the dependent variable and site type (two levels, fixed effect), species (six

levels, fixed effect), and the interaction as independent factors in the model. ANOVA was conducted using SAS v9.3 (SAS Institute, Cary, North Carolina) PROC MIXED. For both 2015 and 2016, $\delta^{13}C$ isotopic signatures of insect samples were not statistically different between site types ($p > 0.15$), although there was significant species-specific variation ($p < 0.02$, Appendix 3.1). Therefore, $\delta^{13}C$ signatures of aquatic and terrestrial insects were determined as an average of the three dominant aquatic and terrestrial taxa, respectively, across all sites for each year.

Next, we used a mixing formula to identify the relative proportions of aquatic- and terrestrial-derived insects in songbird diets (Fry 2007):

$$p_1 = (\delta_{sample} - \delta_{source,2}) / (\delta_{source,1} - \delta_{source,2}) \text{ and}$$

$$p_2 = 1 - p_1$$

where δ_{sample} is the $\delta^{13}C$ value of each fecal sample, p_i is the proportion of aquatic or terrestrial diet sources, and $\delta_{source,i}$ is the average $\delta^{13}C$ for each diet source (Fry 2007). In instances of a "mixing muddle" (*sensu* Fry, 2007), where the fecal sample occurred outside the range characterized by aquatic and terrestrial insect isotope signatures, we classified the sample as composed entirely of the diet source the sample most closely resembled.

Because we selected dominant insects feeding primarily on aquatic- and terrestrial-derived primary producers, our source samples did not reflect signatures of higher trophic level arthropods (*e.g.*, predaceous spiders, parasitic wasps). Additionally, inclusion of filter-feeding aquatic insects as candidates for SIA could bias the aquatic-derived signature towards $\delta^{15}N$ enrichment since this feeding guild incidentally ingests animal parts. Thus, we did not use $\delta^{15}N$ of insect samples to make inference about trophic position of songbird diets (Appendix 3.1).

Invasion-Mediated Diet Shifts. – We conducted species-specific multivariate analyses to examine invasion-mediated diet shifts, which we defined as differences in songbird diet isotope

signatures between reference and locust sites. We analyzed fecal samples from seven songbird species with sufficient sample sizes (n ≥ 2 samples per site type and year), including five strict insectivores and two omnivorous species whose diets are dominated by insects during the breeding season (Table 3.1). We considered the two species of flycatchers, Cordilleran flycatcher (*Empidonax occidentalis)* and dusky flycatcher (*Empidonax oberholseri)*, as a single unit (*Empidonax* flycatcher). Analyses were conducted separately for each year to account for known annual variation in arthropod communities (Riedl et al., *in prep*).

We tested for songbird diet shifts between reference and locust sites using one-way MANOVAs with δ^{13}C and δ^{15}N as dependent variables and site type as the independent variable. All MANOVAs were conducted with SAS PROC GLM. Isotope data were normally distributed, and Satterthwaite degrees of freedom were used to correct for unequal variance where necessary. F-values from MANOVAs are reported from Wilks' Lambda criteria. ANOVAs were considered to determine whether differences were driven by δ^{13}C (diet source) or δ^{15}N (diet position). We considered MANOVA or ANOVA model results statistically significant for $p < 0.05$.

We used songbird characteristics associated with the individual birds that provided each fecal sample, including mass, fat score, and age class, to assess potential correlations with diet shifts. For species with sufficient sample sizes (n ≥ 2 per site and year combination), we tested for differences in mean mass and fat scores between site types using two-tailed Welch's t-tests and non-parametric Wilcoxon rank sum tests, respectively. In addition, where there were significant differences in these body condition measures between site types ($p < 0.05$), we examined the age class composition of samples (HY: AHY ratio).

RESULTS

Aquatic-Derived Carbon in Songbird Diets

We collected and analyzed isotopic signatures of 133 fecal samples from seven species of insectivorous songbirds in reference and locust sites (Table 3.1). Overall, the songbird community consumed $34 \pm 3\%$ SE aquatic-derived carbon throughout the study, with no difference between years or site types (Figure 3.2; Appendix 3.2). The total contribution (across both years) of aquatic-derived carbon to insectivore diets varied among species, ranging from 18% for MacGillivray's warblers (*Geothlypis tolmiei*) to 64% for green-tailed towhees (*Pipilo chlorurus*) (Appendix 3.2).

Insects collected from aquatic systems were more enriched in $\delta^{13}C$ than their terrestrial counterparts *(i.e.,* less negative $\delta^{13}C$ isotopic signatures). While the overall contribution of aquatic-derived insects to the diet of the songbird assemblage was similar between years, species-specific values were frequently different (Figure 3.2; Appendix 3.2). For example, black-capped chickadees *(Poecile atricapillus)* consumed mostly aquatic carbon in 2015, and mostly terrestrial carbon in 2016, and these trends were opposite for MacGillivray's warblers. During both years, however, *Empidonax* flycatchers, warbling vireos (*Vireo gilvus*), and yellow warblers (*Setophaga petechia*) consumed more terrestrial carbon, and green-tailed towhees consumed more aquatic carbon.

Invasion-Mediated Diet Shifts

General diet shift patterns varied among songbird species and between years, but all significant diet shifts were driven by diet source ($\delta^{13}C$), which reflects differences in the relative reliance on aquatic- and terrestrial-derived prey resources in reference and locust sites. No differences in $\delta^{15}N$ signatures were detected for any species evaluated, indicating diet shifts were

not driven by trophic position or altered populations of predaceous or parasitic arthropods in locust sites. Of the seven species evaluated, Virginia's warblers (*Leiothlypis virginiae*) showed a significant diet shift towards aquatic-derived carbon in 2015 (p = 0.021, Appendix 3.3), and warbling vireos showed a significant diet shift towards aquatic-derived carbon in 2016 (p = 0.023, Figure 3.3; Appendix 3.3). In contrast, *Empidonax* flycatchers showed a significant diet shift that trended towards more terrestrially-derived carbon and less $\delta^{15}N$ enrichment in 2016 (p = 0.002, Figure 3.3; Appendix 3.3). However, it is unclear if this shift was driven by $\delta^{13}C$ or $\delta^{15}N$ because separate univariate analyses revealed no statistical differences in either signature individually (Appendix 3.3). One explanation for this is that multivariate approaches test for differences in the combined effects of dependent variables and, therefore, can detect differences too slight for univariate analyses. Yellow warblers and green-tailed towhees showed no diet shifts consistently across years, and MacGillivray's warblers and black-capped chickadees showed no diet shifts in the single years they were evaluated (Appendix 3.3).

Of the seven species for which we investigated body condition differences between reference and locust sites, there were no significant differences in fat scores, but body mass differed for two species (Appendix 3.4). Yellow warblers and *Empidonax* flycatchers in reference sites had lower body mass than birds using locust sites, but these patterns were only found in one year for each species (Welch's t-tests: 2015 YWAR, p=0.036; 2016 EMPI, p=0.030; Appendix 3.4). Examination of age class ratios uncovered that mist nets captured only hatch-year yellow warblers from reference sites in 2015 (6HY:0AHY), and only after-hatch-year *Empidonax* flycatchers from locust sites in 2016 (0HY:4AHY).

DISCUSSION

   Aquatic-derived prey contributed substantially to the diets of avian insectivores in our
study, yet reliance on this subsidy varied greatly among species. New Mexico locust invasion
was associated with diet shifts toward aquatic-derived insects for Virginia's warblers and
warbling vireos. Diet patterns varied among other species and for species with sufficient sample
sizes in both years, the invasion did not appear to have consistent effects across years. Thus, we
found mixed support for our hypothesis that insectivores using locust habitats would rely more
on aquatic resources and no evidence that birds using locust habitats would have fecal signatures
less enriched in δ^{15}N due to reduced abundances of predacious and parasitic arthropods.

   Our results suggest that the insectivorous bird assemblage in the Clear Creek drainage
relies on approximately one-third aquatic insects and two-thirds terrestrial insects during summer
months. This finding highlights the importance of maintaining aquatic ecosystem functioning for
sustaining terrestrial communities. Our estimate of the aquatic insect contribution to bird diets is
somewhat higher than other published estimates. Along the Colorado River in Arizona, the
insectivorous bird community consumed only 9% aquatic insects during summer months (range:
$1 - 16\%$, n=6 species, Yard et al. 2004). In riparian forests in Japan, aquatic prey consumed in
summer by a diverse bird assemblage averaged 6% (range: $0 - 29\%$, n=18 species), with
flycatchers and warblers consuming the highest percentages of aquatic arthropods (Uesugi and
Murakami, 2007). However, community-level estimates are strongly influenced by the species
composition and foraging habits of songbirds included in an assemblage.

   We found large variation in diet compositions among insectivorous bird species as well
as between years for individual species. However, in both years, green-tailed towhees consumed
more aquatic carbon than other species in our assemblage (Figure 3.2). This is surprising

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considering their ground foraging behavior and more omnivorous feeding habits compared to the other stricter insectivores (Dobbs et al., 2012). If green-tailed towhees were transitioning to a more omnivorous diet at the end of their breeding season, we likely did not include all potential food resources (*i.e.,* seeds and fruits) for isotopic analysis. Black-capped chickadee, the other species that transitions to an omnivorous diet after the breeding season, displayed higher aquatic prey consumption in 2015, but higher terrestrial prey consumption in 2016. Differences in timing of shifts to omnivory in late summer could help explain inter-annual variation in diet composition for this species. Similar to our findings, utilization of aquatic subsidies has been found to vary greatly among species in other studies (Nakano and Murakami 2001, Uesugi and Murakami, 2007; Yard et al., 2004). For example, yellow warbler diets examined by Yard et al. (2004) contained a higher mean percentage of aquatic arthropods (16%) than the other five insectivores examined, and reliance on different insect taxa among species suggested resource partitioning within the insectivore assemblage.

Significant shifts in Virginia's warbler and warbling vireo diets, driven by $\delta^{13}C$, support our hypothesis that birds would rely more on aquatic insects at locust sites (Figure 3.3; Appendix 3.3). These species are foliage gleaners that might be more impacted by the reductions in terrestrial insects often associated with invasion (DeGraaf et al., 1985; Litt et al., 2014; Simao et al., 2010, Riedl et al., *in prep*). We found a significant shift in *Empidonax* flycatcher diets that trended towards more terrestrial-derived and lower trophic level prey; however, analysis of $\delta^{13}C$ and $\delta^{15}N$ independently could not account for this difference. Regardless, diet shifts for this feeding guild are consistent with previous research. In a meta-analysis evaluating the effects of subsidy alteration on riparian birds, Marczak et al. (2007) found aerial insectivores displayed the largest mean effect sizes compared to other foraging guilds (*e.g.*, foliage and ground

insectivores). Although we detected no significant diet shifts associated with trophic position (*i.e.*, driven by δ^{15}N) for all species evaluated, this is consistent with findings of Riedl et al. (*in prep*), which found no significant difference in the abundance of predaceous or parasitic arthropods between sites.

Our analysis of body condition showed evidence of higher body mass of yellow warblers and *Empidonax* flycatchers foraging in locust habitats (Appendix 3.4), suggesting that differences in diet do not necessarily translate into fitness consequences. However, age class compositions of songbirds sampled from reference and locust sites may provide some explanation for the body condition patterns found in our study. Additionally, differences in songbird reproductive success in reference and locust habitats might better indicate potential fitness effects of invasion (Stinson and Pejchar, *in prep*), but these metrics were beyond the scope of our study. Previous work comparing 12 measures of body condition in southwestern willow flycatchers (*Empidonax traillii extimus*) using native and non-native *Tamarisk* habitats similarly found little support for negative physiological effects associated with invasion (Owen et al., 2005). In general, few studies have rigorously addressed whether invasion-mediated diet shifts affect fitness and further research is warranted to better understand potential fitness consequences of invasion across different species and ecological contexts (Stinson and Pejchar, *in review*).

We assumed that insectivorous songbirds consume prey in proportion to what is available, exhibiting prey switching in response to reductions in preferred prey resources (Busby and Sealy, 1979; Howe et al., 2000; Uesugi and Murakami, 2007). Therefore, alterations to the availability of insects from different sources or trophic levels should translate into shifts in δ^{13}C or δ^{15}N, respectively. Because we did not detect differences in insect δ^{13}C or δ^{15}N signatures

between sites, diet shifts likely did not result from invasion-mediated changes to prey signatures. It is possible, however, that birds modify foraging strategies in response to altered resource subsidies (Yard et al., 2004). Studies evaluating food web impacts on other consumer taxa do not always reveal diet patterns parallel to subsidy alterations (*e.g.,* Roon et al., 2016; Saunders and Fausch, 2007). For example, Roon et al. (2016) found that compared to native deciduous trees, the invasive European bird cherry (*Prunus padus*) was associated with 4-6 times less terrestrial arthropod biomass on foliage and 2-3 times less biomass falling into streams. Despite the temporally consistent differences in resource availability reported, there was no difference in the proportion of terrestrial insects detected in the diets of juvenile coho salmon (*Oncorhynchus kisutch*).

Despite the diverse arthropod prey communities at our study sites, we are confident our selection of dominant low trophic level insects sufficiently describes source origin of diets. Multiple studies have reported that midges (or other Diptera), leafhoppers, and caterpillars comprise the majority of prey in insectivorous riparian bird diets, including for upper-canopy gleaners like yellow warblers (Busby & Sealy 1979; Durst et al. 2008; Yard et al. 2004). However, our inability to measure isotopic signatures of all available prey items limits interpretation of consumer isotope data in relation to prey items. Pan trap sampling may not have captured a representative sample of the prey items available to avian insectivores. Other studies have used Malaise traps to capture flying insects and sweep-nets or beat-sheets to sample at a variety of vegetative height classes (Uesugi and Murakami, 2007; Wiesenborn and Heydon, 2007; Yard et al., 2004), potentially providing a more accurate characterization of prey availability for assemblages with diverse foraging strategies. Additionally, because richness in pan trap samples averaged 18 taxa, there were more than three "dominant" herbivorous terrestrial

taxa. Our pan traps and emergence nets captured 139 and 23 different arthropod taxa, respectively (Riedl et al., *in prep*), and incorporating this level of isotopic resolution is rarely feasible. Furthermore, large isotopic variation of fecal samples may be indicative of more generalist foraging strategies (*i.e.,* feeding on a wide range of potentially unmeasured diet sources). Thus, our estimates of aquatic- and terrestrial-derived diet proportions should be considered to provide a general index rather than an exact proportion.

Our study system experienced differences in precipitation between years that may have contributed to inconsistencies in diet shifts. Higher spring and summer precipitation resulted in approximately 3 times faster stream discharge in 2016 compared to 2015, corresponding with more apparent invasion effects on arthropod resources in 2015 (Riedl et al., unpublished data). Likewise, Durst et al. (2008) detected invasion-mediated food web impacts only during the one drought year in their five year study. In addition, the timing of our sampling in the late summer likely influenced our findings (Uesugi and Murakami, 2007). Future work may find more pronounced invasion-mediated diet shifts in spring for systems invaded by plants with a later leaf-out phenology than native vegetation. In our system, delayed timing of New Mexico locust leaf-out likely provides less foliage to support arthropod production in late spring.

Future studies could employ SIA of blood or tissue samples, which incorporate diet components ingested over days to weeks (Podlesak et al., 2005; Wolf et al., 2009), and could be used in study systems with greater spatial separation between site types to eliminate random effects of the most recently ingested items. Unlike fecal SIA, blood/tissue SIA incorporates diet components assimilated into the consumers' tissues, which may better reflect utilized resources (Salvarina et al., 2013). Varying digestibility of diet components may also hinder the ability to detect diet shifts using fecal samples (Salvarina et al., 2013). Modern molecular genetic

techniques, such as non-invasive molecular scatology and DNA barcoding methods, can also be used to obtain more precise taxonomic identification of prey items (Carreon-Martinez and Heath, 2010; Wong et al., 2015).

Conclusions

Using isotopic signatures of insects and bird feces, we estimated the riparian bird community consumed 34% aquatic carbon, which highlights the importance of aquatic resource subsidies to terrestrial consumers. Diet shifts between reference and locust-invaded habitats were inconsistent among species and between years, but we found strong support that diet shifts towards aquatic-derived carbon were associated with plant invasion for two insectivorous bird species. These diet shifts occurred in a watershed near the introduced plant's native range, which suggests that species introduced from more geographically disparate areas could have even more pronounced impacts on riparian food webs. An increased focus on resource subsidies will provide a more mechanistic understanding of the consequences of anthropogenic change by examining interacting processes across ecosystems.

TABLES

Table 3.1. Number of fecal samples collected from songbird species at uninvaded (reference) and invaded (locust) sites in the Clear Creek drainage of northwestern Colorado, USA. Common names of songbird species are listed in taxonomic order. Cordilleran flycatchers and dusky flycatchers were analyzed together as *Empidonax* flycatchers. Black-capped chickadees and green-tailed towhees are omnivores that are insectivorous during the breeding season, while the other five species are strict insectivores year-round.

Songbird Species	Reference			Locust		
	2015	*2016*	*Total*	*2015*	*2016*	*Total*
Empidonax Flycatcher	6	4	10	12	4	16
Warbling Vireo	1	4	5	2	2	4
Black-capped Chickadee	0	8	8	8	4	12
MacGillivray's Warbler	3	2	5	8	1	9
Virginia's Warbler	2	1	3	7	0	7
Yellow Warbler	6	7	13	10	6	16
Green-tailed Towhee	2	7	9	11	5	16
All Species Combined	**20**	**33**	**53**	**58**	**22**	**80**

FIGURES
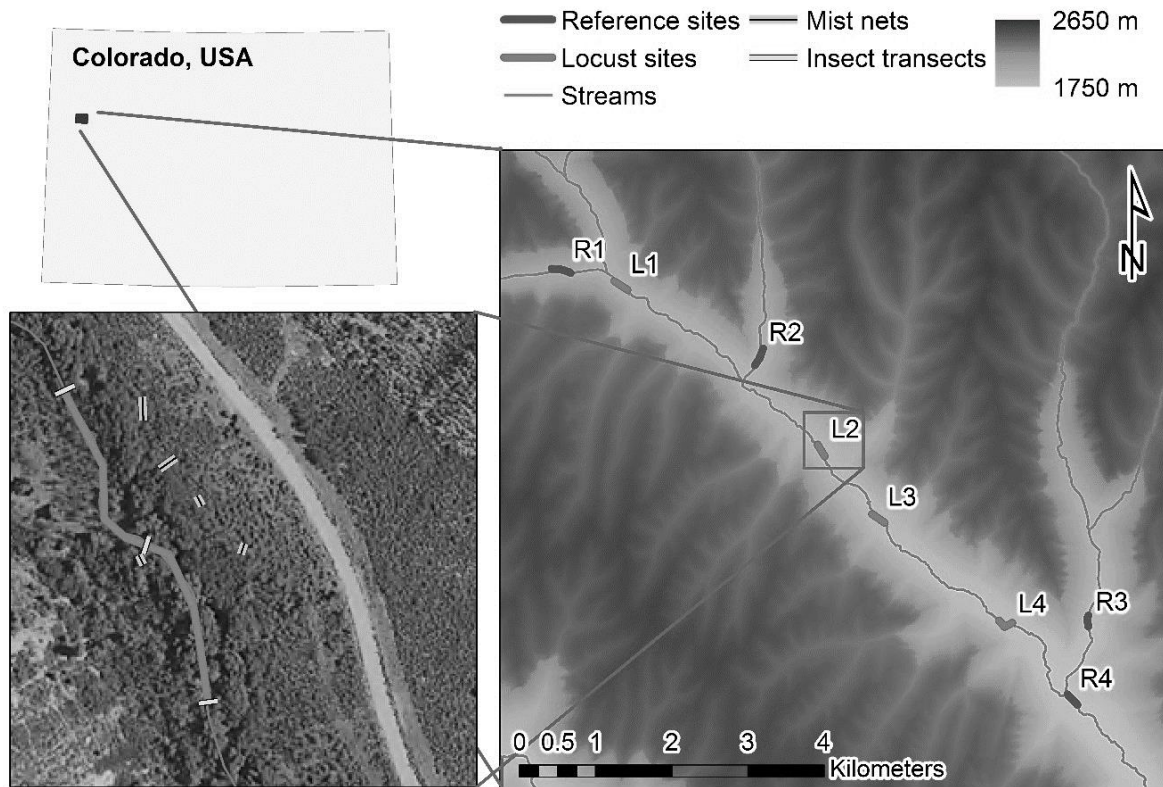
Figure 3.1. Insect and bird sampling sites along uninvaded (reference) and invaded (locust) stream reaches in the Clear Creek drainage of northwestern Colorado, USA. The lower left inset provides an example of mist net and insect transect locations at a single site, where fecal and insect samples were collected, respectively.
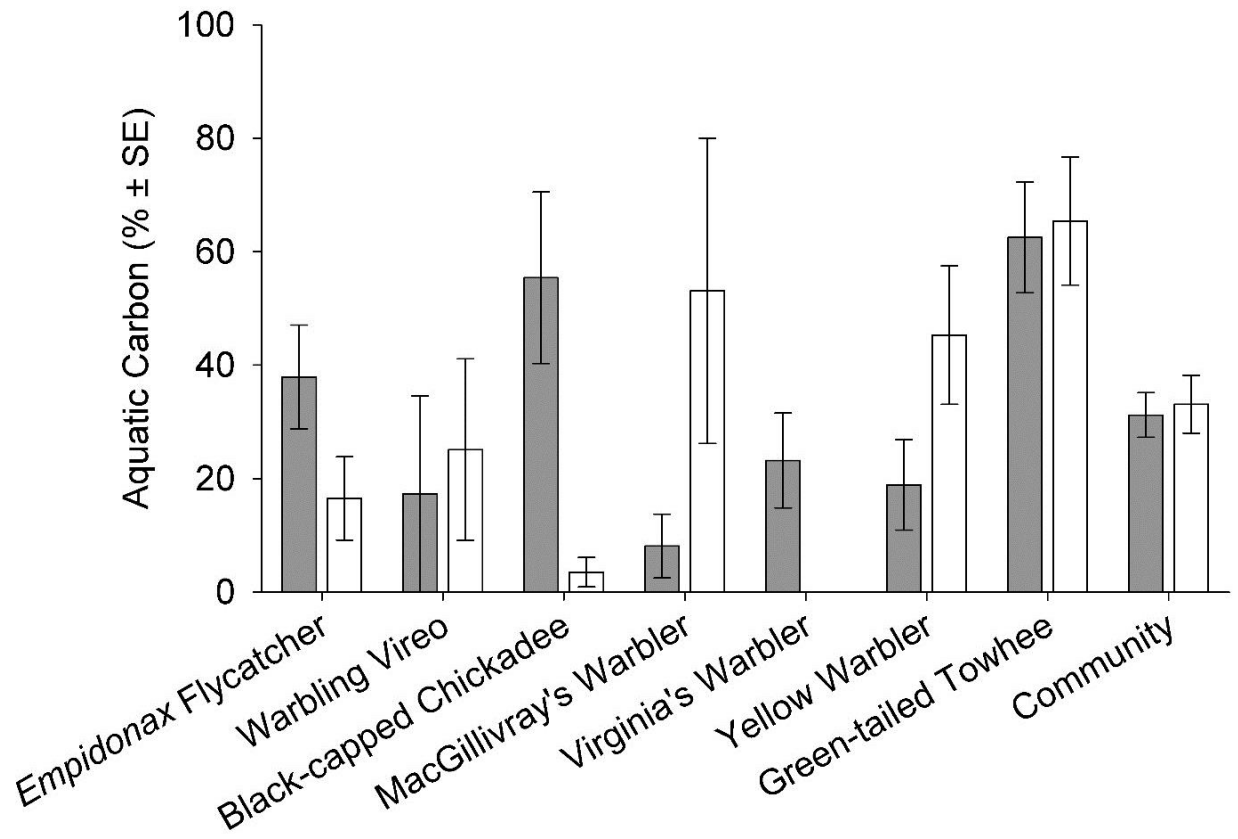
Figure 3.2. Contributions of aquatic-derived insect carbon (mean % ± SE) to the diets of songbird species, individually and overall (*i.e.,* "community"), for 2015 (grey) and 2016 (white). Results were determined using a single isotope mixing formula and $\delta^{13}C$ signatures of insect and fecal samples, pooled across reference and locust sites. There were insufficient sample sizes (n<2 per year) to calculate means for Virginia's warbler in 2016.
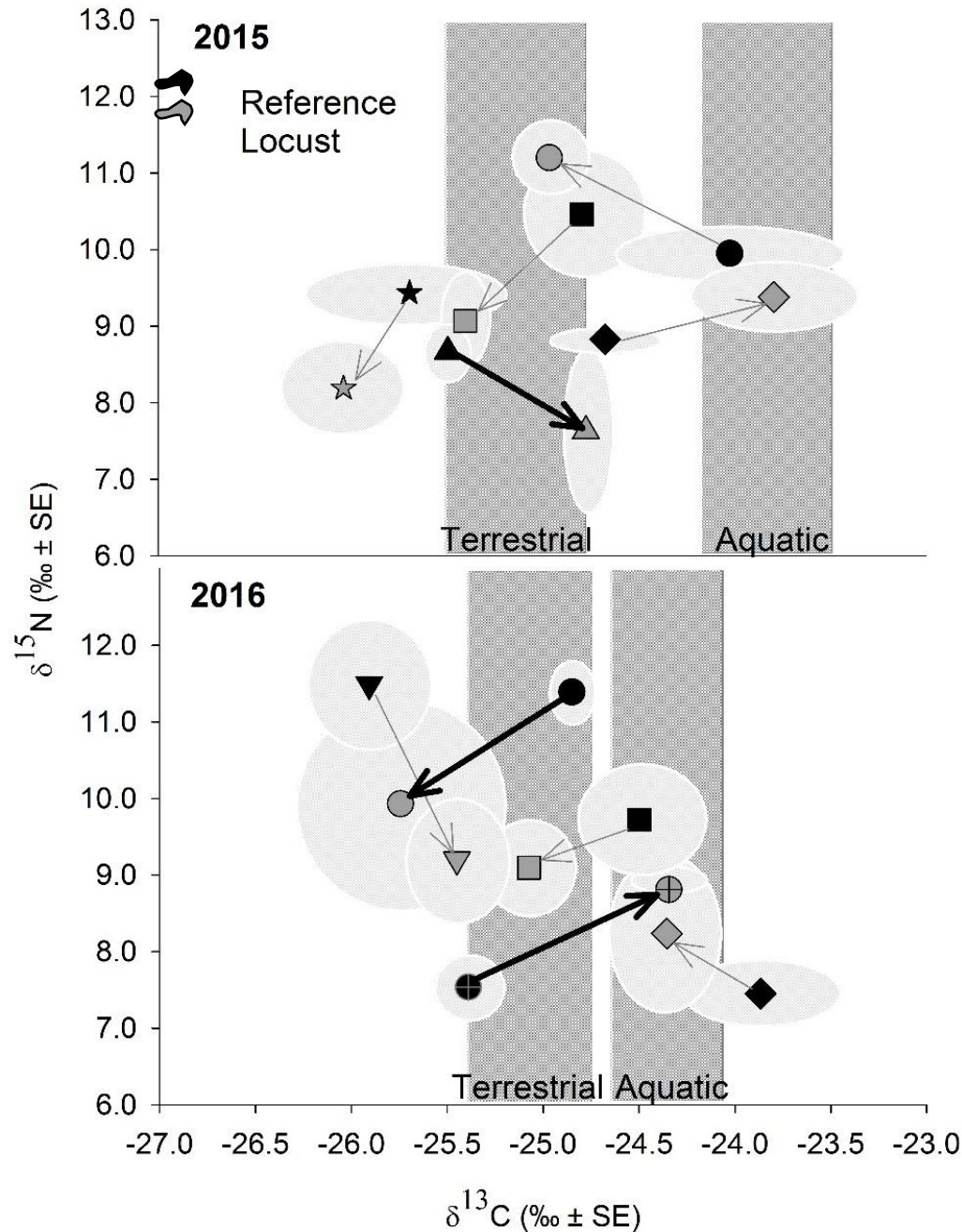
Figure 3.3. Biplots show $\delta^{13}C$ and $\delta^{15}N$ signatures of songbird fecal samples, illustrating 3 significant invasion-mediated diet shifts (bold arrows; see Appendix 3.3). Arrows connect reference to locust sites for each species sampled in the Clear Creek drainage of northwestern Colorado, USA. Dark gray shading shows the standard error of the $\delta^{13}C$ signatures of terrestrial and aquatic insect samples. Light gray ellipses represent the standard error encompassed by $\delta^{13}C$ and $\delta^{15}N$ signatures of songbird fecal samples. *Empidonax* flycatchers ($\bigcirc$), yellow warblers ($\square$), and green-tailed towhees ($\diamondsuit$) were evaluated in both years. MacGillivray's warblers ($\star$) and Virginia's warblers ($\triangle$) were only evaluated in 2015, and warbling vireos ($\oplus$) and black-capped chickadees ($\triangledown$) were only evaluated in 2016.

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APPENDICES

Appendix 1.1. Search terms used for the systematic review of songbird reproductive responses to non-native vegetation. Within each string, terms were combined with "OR" and topic searches of the three strings were combined with "AND" in the form TS=string 1 AND TS=string 2 AND TS=string 3 for a search across all years and geographic areas.

string 1 (all combinations)		string 2		string 3
non-native species	vegetation forms	reproductive measures		avian terms
exotic	*plant**	*"nest* success"*	*reproduction*	*avian*
alien	*shrub**	*"nest* survival"*	*productivity*	*avifauna**
introduced	*tree**	*"nest* predation"*	*fecundity*	**bird**
non-native	*grass**	*"nest* mortality"*	*clutch*	*passerine**
nonnative	*forb**	*"reproductive success"*	*brood*	*songbird**
	herb*	*"breeding success"*	*nestling*	
	vegetation	*"breeding biology"*	*fledg**	
	habitat*			
	forest			

Appendix 1.2. Search syntax used for the search of the Web of Science database for papers relevant to non-native plant effects on songbird reproduction. As of September 23, 2016, this search returned 132 records.

((TS=("invasive plant*" OR "invasive shrub*" OR "invasive tree*" OR "invasive *grass*" OR "invasive forb*" OR "invasive herb*" OR "invasive vegetation" OR "invasive habitat*" OR "invasive forest*" OR "exotic plant*" OR "exotic shrub*" OR "exotic tree*" OR "exotic *grass*" OR "exotic forb*" OR "exotic herb*" OR "exotic vegetation" OR "exotic habitat*" OR "exotic forest*" OR "alien plant*" OR "alien shrub*" OR "alien tree*" OR "alien *grass*" OR "alien forb*" OR "alien herb*"OR "alien vegetation" OR "alien habitat*" OR "alien forest*" OR "introduced plant*" OR "introduced shrub*" OR "introduced tree*" OR "introduced grass*" OR "introduced forb*" OR "introduced herb*" OR "introduced vegetation" OR "introduced habitat*" OR "introduced forest*" OR non-native plant*" OR "non-native shrub*" OR "non-native tree*" OR "non-native *grass*" OR "non-native forb*" OR "non-native herb*" OR "non-native vegetation" OR "non-native habitat* OR "non-native forest*" OR "nonnative plant*" OR "nonnative shrub*" OR "nonnative tree*" OR "nonnative *grass*" OR "nonnative forb*" OR "nonnative herb*" OR "nonnative vegetation" OR "nonnative habitat*" OR "nonnative forest*") AND TS=("nest* success" OR "nest* survival" OR "nest* predation" OR "nest* mortality" OR clutch OR brood OR nestling OR fledg* OR productivity OR fecundity OR reproduction OR "reproductive success" OR "breeding success" OR "breeding biology") AND TS=(avian OR *bird* OR avifauna* OR passerine* OR songbird*))) *AND* **LANGUAGE:** (English)
Refined by: [excluding] **DOCUMENT TYPES:** (REVIEW)
Indexes=SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, ESCI Timespan=All years

Appendix 1.3. Bibliography of articles (n=32) included in the systematic review of non-native plant effects on songbird reproductive success.

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Borgmann, K.L., Rodewald, A.D., 2004. Nest predation in an urbanizing landscape: The role of exotic shrubs. Ecological Applications 14, 1757–1765. doi:10.1890/03-5129

Cristinacce, A., Switzer, R.A., Cole, R.E., Jones, C.G., Bell, D.J., 2009. Increasing use of exotic forestry tree species as refuges from nest predation by the critically endangered Mauritius fody *Foudia rubra*. Oryx 43, 97–103. doi:10.1017/S0030605309001604

de la Hera, I., Arizaga, J., Galarza, A., 2013. Exotic tree plantations and avian conservation in northern Iberia: a view from a nest-box monitoring study. Animal Biodiversity and Conservation 36, 153–163.

Fisher, R.J., Davis, S.K., 2011. Post-fledging dispersal, habitat use, and survival of Sprague's pipits: Are planted grasslands a good substitute for native? Biological Conservation 144, 263–271. doi:10.1016/j.biocon.2010.08.024

Gleditsch, J., Carlo, T., 2014. Living with aliens: effects of invasive shrub honeysuckles on avian nesting. PLoS ONE 9, 1–9.

Grant, T.A., Madden, E.M., Shaffer, T.L., Pietz, P.J., Berkey, G.B., Kadrmas, N.J., 2006. Nest survival of clay-colored and vesper sparrows in relation to woodland edge in mixed-grass prairies. Journal of Wildlife Management 70, 691–701. doi:10.2193/0022-541X(2006)70[691:NSOCAV]2.0.CO;2

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Kennedy, P.L., DeBano, S.J., Bartuszevige, A.M., Lueders, A.S., 2009. Effects of native and non-native grassland plant communities on breeding passerine birds: Implications for restoration of northwest bunchgrass prairie. Restoration Ecology 17, 515–525. doi:10.1111/j.1526-100X.2008.00402.x

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Lituma, C.M., Morrison, M.L., Whiteside, J.D., 2012. Restoration of grasslands and nesting success of dickcissels (*Spiza americana*). Southwestern Naturalist 57, 138–143.

Lloyd, J.D., Martin, T.E., 2005. Reproductive success of chestnut-collared longspurs in native and exotic grassland. Condor 107, 363–374. doi:10.1650/7701

Ludlow, S.M., Brigham, R.M., Davis, S.K., 2015. Oil and natural gas development has mixed effects on the density and reproductive success of grassland songbirds. Condor 117, 64–75. doi:10.1650/CONDOR-14-79.1

Maddox, J.D., Wiedenmann, R.N., 2005. Nesting of birds in wetlands containing purple loosestrife (*Lythrum salicaria*) and cattail (*Typha spp.*). Nat. Areas J. 25, 369–373.

Mcchesney, H.M., Anderson, J.T., 2015. Reproductive success of field sparrows (*Spizella pusilla*) in response to invasive Morrow's honeysuckle: does Morrow's honeysuckle promote population sinks? Wilson Journal of Ornithology 127, 222–232.

Meyer, L.M., Schmidt, K.A., Robertson, B.A., 2015. Evaluating exotic plants as evolutionary traps for nesting veeries. Condor 117, 320–327. doi:10.1650/CONDOR-14-101.1

Miller, K.S., McCarthy, E.M., Woodin, M.C., Withers, K., 2013. Nest success and reproductive ecology of the Texas Botteri's sparrow (*Peucaea botterii texana*) in exotic and native grasses. Southeastern Naturalist 12, 387–398. doi:10.1656/058.012.0212

Nordby, J.C., Cohen, A.N., Beissinger, S.R., 2009. Effects of a habitat-altering invader on nesting sparrows: An ecological trap? Biological Invasions 11, 565–575. doi:10.1007/s10530-008-9271-9

Ortega, Y.K., McKelvey, K.S., Six, D.L., 2006. Invasion of an exotic forb impacts reproductive success and site fidelity of a migratory songbird. Oecologia 149, 340–351. doi:10.1007/s00442-006-0438-8

Pearson, S.F., Knapp, S.M., 2016. Considering spatial scale and reproductive consequences of habitat selection when managing grasslands for a threatened species. PLoS One 11, e0156330. doi:10.1371/journal.pone.0156330

Remes, V., 2003. Effects of exotic habitat on nesting success, territory density, and settlement patterns in the blackcap (*Sylvia atricapilla*). Conservation Biology 17, 1127–1133. doi:10.1046/j.1523-1739.2003.01611.x

Rodewald, A.D., Rohr, R.P., Fortuna, M.A., Bascompte, J., 2014. Community-level demographic consequences of urbanization: an ecological network approach. Journal of Animal Ecology 83, 1409–1417. doi:10.1111/1365-2656.12224

Rodewald, A.D., Shustack, D.P., Hitchcock, L.E., 2010. Exotic shrubs as ephemeral ecological traps for nesting birds. Biological Invasions 12, 33–39. doi:10.1007/s10530-009-9426-3

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Safford, R.J., 1997. Nesting success of the Mauritius fody *Foudia rubra* in relation to its use of exotic trees as nest sites. Ibis 139, 555–559.

Scheiman, D.M., Bollinger, E.K., Johnson, D.H., 2003. Effects of leafy spurge infestation on grassland birds. Journal of Wildlife Management 67, 115–121. doi:10.2307/3803067

Schlossberg, S., King, D.I., 2010. Effects of invasive woody plants on avian nest site selection and nesting success in shrublands. Animal Conservation 13, 286–293. doi:10.1111/j.1469-1795.2009.00338.x

Schmidt, K.A., Nelis, L.C., Briggs, N., Ostfeld, R.S., 2005. Invasive shrubs and songbird nesting success: Effects of climate variability and predator abundance. Ecological Applications 15, 258–265. doi:10.1890/03-5325

Schmidt, K.A., Whelan, C.J., 1999. Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. Conservation Biology 13, 1502–1506. doi:10.1046/j.1523-1739.1999.99050.x

Stoleson, S.H., Finch, D.M., 2001. Breeding bird use of and nesting success in exotic Russian olive in New Mexico. Wilson Bulletin 113, 452–455. doi:10.1676/0043-5643(2001)113[0452:BBUOAN]2.0.CO;2

Vander Haegen, W.M., Schroeder, M.A., Chang, W.-Y., Knapp, S.M., 2015. Avian abundance and reproductive success in the Intermountain West: local-scale response to the Conservation Reserve Program. Wildlife Society Bulletin 39, 276–291. doi:10.1002/wsb.523

Appendix 1.4. Covariates, coefficient estimates, standard errors (SE) and p-values from mixed effects logistic regression models fit to data for songbird responses to non-native vegetation (n=136), with significant negative responses coded as 1 and all other responses coded as 0. Responses were modeled as a function of a) habitat type and b) vegetation form. The reference category for habitat type is forest and the reference category for vegetation form is forb. We fit a random intercept for article (n=31) in both models.

a)

Habitat Covariate	Coefficient Estimate	SE	p-value
(Intercept)	-2.423	0.802	0.003
Grassland	-0.490	0.885	0.580
Wetland	0.919	1.814	0.612

b)

Form Covariate	Coefficient Estimate	SE	p-value
(Intercept)	-1.937	1.233	0.116
Grass	-0.858	1.399	0.540
Shrub	-0.888	1.439	0.537
Tree	-0.645	1.711	0.706

Appendix 1.5. Covariates, coefficient estimates, standard errors (SE) and p-values from mixed effects logistic regression models fit to data for songbird responses to non-native vegetation (n=136), with negative responses (either significant or trend) coded as 1 and all other responses coded as 0. Responses were modeled as a function of a) habitat type, b) vegetation form, and c) habitat type + vegetation form. The reference category for habitat type is forest and the reference category for vegetation form is forb. We fit a random intercept for article (n=31) in all models.

a)

Habitat Covariate	Coefficient Estimate	SE	p-value
(Intercept)	-1.086	0.542	0.045
Grassland	0.313	0.671	0.641
Wetland	2.489	1.670	0.136

b)

Form Covariate	Coefficient Estimate	SE	p-value
(Intercept)	-1.260	1.008	0.211
Grass	0.477	1.116	0.669
Shrub	0.906	1.120	0.419
Tree	-0.555	1.405	0.693

c)

Habitat+Form Covariate	Coefficient Estimate	SE	p-value
(Intercept)	-3.853	1.711	0.024
Grassland	1.919	1.232	0.120
Wetland[a]	**4.772**	**2.149**	**0.026**
Grass	1.021	1.170	0.383
Shrub[a]	**3.114**	**1.579**	**0.049**
Tree	2.159	1.866	0.247

[a] Significant effect at the $\alpha = 0.05$ level.

Appendix 1.6. Covariates, coefficient estimates, standard errors (SE) and p-values from logistic regression models fit to the dataset of studies that assessed ecological traps or habitat sinks (n=16), with studies that found support coded as 1 and studies that did not find support coded as 0. Data were modeled as a function of a) habitat type and b) vegetation form. The reference category for habitat type is forest and the reference category for vegetation form is grass.

a)

Habitat Covariate	Coefficient Estimate	SE	p-value
(Intercept)	-0.693	0.707	0.327
Grassland	0.406	1.041	0.697

b)

Form Covariate	Coefficient Estimate	SE	p-value
(Intercept)	-0.406	0.913	0.657
Shrub	-0.288	1.155	0.803
Tree	0.406	1.683	0.810

Appendix 2.1. Species-specific incubation, nestling and nesting periods used in determination of the fate of nests monitored during the breeding seasons of 2015 and 2016 within the Clear Creek drainage of northwestern Colorado, USA. Species-specific period durations were determined from Baicich and Harrison, 2005 and accounts from the Birds of North America Online database (P.G. Rodewald, Editor).

Species Code	Species Common Name	Incubation Period (days)	Nestling Period (days)	Total Nesting Period (days)
AMRO	American Robin	13	13	26
BGGN	Blue-gray Gnatcatcher	13	12	25
CHSP	Chipping Sparrow	11	10	21
DUFL	Dusky Flycatcher	15	16	31
GTTO	Green-tailed Towhee	12	10	22
HETH	Hermit Thrush	12	12	24
LAZB	Lazuli Bunting	12	10	22
MGWA	MacGillivray's Warbler	12	9	21
PLVI	Plumbeous Vireo	14	13	27
SOSP	Song Sparrow	13	10	23
SPTO	Spotted Towhee	12	9	21
YWAR	Yellow Warbler	11	10	21

Appendix 2.2. Environmental covariates associated with passerine nests (n=92) monitored during the breeding seasons in 2015 and 2016 within the Clear Creek drainage of northwestern Colorado, USA. A total of 12 species of songbirds were represented, with n=52 nests found in locust and n=40 nest found in non-invaded reference sites.

Species Common Name	Nest ID	Year	Habitat Type	Substrate Type	Substrate ID	Nest Height (cm)	Substrate Height (m)	Elevation (m)
	2015-MGWA-N6-loc	2015	locust	low shrub/forb	locust	15	0.9	1851
	2015-MGWA-N13-loc	2015	locust	low shrub/forb	locust	15	8.0	1980
	2015-MGWA-N15-loc	2015	locust	low shrub/forb	locust	61	1.1	1990
	2015-MGWA-N37-loc	2015	locust	low shrub/forb	locust	48	2.7	1911
	2015-MGWA-N35-ref	2015	reference	low shrub/forb	other	30	0.9	1940
	2015-MGWA-N41-ref	2015	reference	low shrub/forb	other	91	1.8	1996
	2016-MGWA-N1-loc	2016	locust	low shrub/forb	locust	41	1.4	1982
	2016-MGWA-N2-loc	2016	locust	low shrub/forb	other	61	1.1	2097
	2016-MGWA-N3-loc	2016	locust	low shrub/forb	locust	30	1.4	2083
	2016-MGWA-N4-loc	2016	locust	low shrub/forb	locust	28	2.7	1985
MacGillivray's Warbler (n=27)	2016-MGWA-N5-ref	2016	reference	low shrub/forb	other	58	1.2	1891
	2016-MGWA-N6-ref	2016	reference	low shrub/forb	other	74	1.1	2053
	2016-MGWA-N7-loc	2016	locust	low shrub/forb	locust	51	1.7	1911
	2016-MGWA-N8-ref	2016	reference	low shrub/forb	other	51	0.7	1998
	2016-MGWA-N9-loc	2016	locust	low shrub/forb	locust	41	2.7	1902
	2016-MGWA-N10-ref	2016	reference	low shrub/forb	other	46	0.9	1961
	2016-MGWA-N11-loc	2016	locust	low shrub/forb	locust	38	1.2	1824
	2016-MGWA-N12-loc	2016	locust	low shrub/forb	locust	48	1.8	1888
	2016-MGWA-N13-ref	2016	reference	low shrub/forb	other	38	0.9	1860
	2016-MGWA-N14-ref	2016	reference	low shrub/forb	other	89	2.7	1999
	2016-MGWA-N15-loc	2016	locust	low shrub/forb	other	43	1.6	1902
	2016-MGWA-N16-loc	2016	locust	low shrub/forb	other	30	0.8	1818
	2016-MGWA-N17-ref	2016	reference	low shrub/forb	other	43	1.4	2028

	2016-MGWA-N18-loc	2016	locust	low shrub/forb	locust	43	1.2	1855
	2016-MGWA-N19-loc	2016	locust	low shrub/forb	locust	38	5.0	1909
	2016-MGWA-N20-ref	2016	reference	low shrub/forb	other	84	1.1	2014
	2016-MGWA-N21-loc	2016	locust	low shrub/forb	other	51	0.7	1974
Yellow Warbler (n=10)	2015-YWAR-N1-loc	2015	locust	tree/tall shrub	other	122	3.0	1985
	2015-YWAR-N4-ref	2015	reference	tree/tall shrub	other	198	2.7	1950
	2015-YWAR-N23-ref	2015	reference	low shrub/forb	other	23	1.8	2016
	2015-YWAR-N32-loc	2015	locust	low shrub/forb	other	61	2.0	1844
	2015-YWAR-N40-ref	2015	reference	tree/tall shrub	other	229	3.4	1999
	2016-YWAR-N1-loc	2016	locust	tree/tall shrub	locust	320	6.0	1845
	2016-YWAR-N2-ref	2016	reference	tree/tall shrub	other	183	2.4	1828
	2016-YWAR-N3-loc	2016	locust	tree/tall shrub	other	201	3.0	1882
	2016-YWAR-N4-ref	2016	reference	tree/tall shrub	other	180	2.7	1945
	2016-YWAR-N5-loc	2016	locust	tree/tall shrub	other	130	2.4	1900
	2016-YWAR-N6-loc	2016	locust	tree/tall shrub	other	191	2.5	1918
	2016-YWAR-N7-ref	2016	reference	tree/tall shrub	other	366	12.0	2013
	2016-YWAR-N8-loc	2016	locust	tree/tall shrub	other	249	4.0	1828
	2016-YWAR-N9-ref	2016	reference	tree/tall shrub	other	145	2.0	1883
	2016-YWAR-N10-ref	2016	reference	tree/tall shrub	other	201	2.7	1893
Green-tailed Towhee (n=11)	2016-GTTO-N1-loc	2015	locust	low shrub/forb	other	58	1.1	1907
	2015-GTTO-N3-ref	2015	reference	low shrub/forb	other	46	0.8	2092
	2015-GTTO-N7-loc	2015	locust	low shrub/forb	other	46	0.8	1845
	2015-GTTO-N25-ref	2015	reference	low shrub/forb	other	15	0.6	1939
	2015-GTTO-N27-ref	2015	reference	low shrub/forb	other	30	0.9	2024
	2015-GTTO-N29-ref	2015	reference	low shrub/forb	other	30	1.2	1944
	2015-GTTO-N33-loc	2015	locust	low shrub/forb	locust	30	2.7	1903
	2015-GTTO-N42-ref	2015	reference	low shrub/forb	other	15	0.9	1934
	2015-GTTO-N45-ref	2015	reference	low shrub/forb	other	30	0.8	1955
	2015-GTTO-N52-loc	2015	locust	low shrub/forb	locust	46	2.7	1838
	2016-GTTO-N2-ref	2016	reference	low shrub/forb	other	38	0.8	2017

Species	Nest ID	Year	Treatment	Habitat	Type			
Hermit Thrush (n=10)	2015-HETH-N26-loc	2015	locust	tree/tall shrub	locust	183	6.0	1915
	2015-HETH-N39-ref	2015	reference	tree/tall shrub	other	152	2.1	2079
	2015-HETH-N47-loc	2015	locust	tree/tall shrub	locust	229	6.5	1953
	2015-HETH-N48-ref	2015	reference	tree/tall shrub	other	152	4.9	2012
	2015-HETH-N53-loc	2015	locust	tree/tall shrub	other	183	2.4	2043
	2016-HETH-N1-ref	2016	reference	tree/tall shrub	other	122	3.4	2015
	2016-HETH-N2-ref	2016	reference	tree/tall shrub	other	185	4.0	2047
	2016-HETH-N3-ref	2016	reference	tree/tall shrub	other	160	3.0	1996
	2016-HETH-N5-ref	2016	reference	tree/tall shrub	other	244	5.0	2027
	2016-HETH-N4-loc	2016	locust	tree/tall shrub	other	249	8.0	1993
Empidonax Flycatcher (n=8)	2015-EMPI-N21-ref	2015	reference	low shrub/forb	other	76	1.7	1833
	2015-EMPI-N38-loc	2015	locust	low shrub/forb	other	91	2.0	1844
	2015-EMPI-N43-loc	2015	locust	low shrub/forb	other	61	0.9	1764
	2016-EMPI-N1-loc	2016	locust	tree/tall shrub	other	163	3.4	1917
	2016-EMPI-N2-loc	2016	locust	tree/tall shrub	other	137	2.4	1918
	2016-EMPI-N3-ref	2016	reference	tree/tall shrub	other	249	3.5	1875
	2016-EMPI-N4-loc	2016	locust	tree/tall shrub	locust	203	6.0	1981
	2016-EMPI-N5-loc	2016	locust	tree/tall shrub	other	193	3.7	1979
Song Sparrow (n=7)	2015-SOSP-N2-loc	2015	locust	low shrub/forb	other	122	1.4	1982
	2015-SOSP-N30-loc	2015	locust	low shrub/forb	locust	84	2.5	1838
	2015-SOSP-N54-loc	2015	locust	low shrub/forb	locust	76	5.5	1847
	2016-SOSP-N1-loc	2016	locust	low shrub/forb	locust	71	2.0	1840
	2016-SOSP-N3-loc	2016	locust	low shrub/forb	other	38	1.0	1759
	2016-SOSP-N2-ref	2016	reference	low shrub/forb	other	48	1.2	2183
	2016-SOSP-N4-loc	2016	locust	tree/tall shrub	locust	183	9.0	1843
Spotted Towhee (n=5)	2015-SPTO-N14-loc	2015	locust	ground	other	0	0.0	1995
	2015-SPTO-N46-ref	2015	reference	low shrub/forb	other	91	2.1	1864
	2015-SPTO-N51-ref	2015	reference	ground	other	0	0.0	1893
	2016-SPTO-N1-loc	2016	locust	ground	other	0	0.0	1843
	2016-SPTO-N2-ref	2016	reference	ground	other	0	0.0	1916

Chipping Sparrow (n=4)	2015-CHSP-N17-loc	2015	locust	low shrub/forb	other	107	1.5	1762
	2015-CHSP-N50-ref	2015	reference	low shrub/forb	other	122	1.8	1806
	2016-CHSP-N1-loc	2016	locust	tree/tall shrub	other	137	5.2	1981
	2016-CHSP-N3-loc	2016	locust	low shrub/forb	other	91	1.4	1755
Blue-gray Gnatcatcher (n=2)	2015-BGGN-N16-loc	2015	locust	low shrub/forb	other	107	2.0	1771
	2015-BGGN-N49-ref	2015	reference	low shrub/forb	other	107	1.7	1912
Lazuli Bunting (n=1)	2015-LAZB-N55-loc	2015	locust	low shrub/forb	other	91	1.4	1973
Plumbeous Vireo (n=1)	2015-PLVI-N20-loc	2015	locust	tree/tall shrub	other	213	3.4	2045
American Robin (n=1)	2016-AMRO-N1-ref	2016	reference	tree/tall shrub	other	226	3.5	2044

Appendix 2.3. Summary of bird species (near passerine and passerine orders only, n=50) encountered within the Clear Creek drainage of northwestern Colorado, USA during May-August of 2015 and 2016. Species richness, occupancy, and abundance modeling components were based on datasets of birds detected < 100 m from point count stations (n=125), excluding flyovers. Occupancy and abundance modeling was undertaken only for species with > 50 detections in each year (n=12) and nest monitoring was undertaken for select riparian songbird species (n=12).

Order	Family	Common Name	Species Code	Species Richness	Occupancy Modeling	Abundance Modeling	Nest Monitoring
near-passerine	Columbidae	Mourning Dove	MODO	x			
near-passerine	Apodidae	White-throated Swift	WTSW	x			
near-passerine	Trochilidae	Black-throated Hummingbird	BTLH	x			
near-passerine	Picidae	Hairy Woodpecker	HAWO	x			
near-passerine	Picidae	Northern Flicker	NOFL	x			
passerine	Tyrannidae	Western Wood Peewee	WEWP	x			
passerine	Tyrannidae	Gray Flycatcher	EMPI	x	x	x	x
passerine	Tyrannidae	Dusky Flycatcher	EMPI	x	x	x	x
passerine	Tyrannidae	Cordilleran Flycatcher	COFL	x	x	x	
passerine	Tyrannidae	Say's Phoebe	SAPH	x			
passerine	Tyrannidae	Ash-throated Flycatcher	ATFL	x			
passerine	Vireonidae	Plumbeous Vireo	PLVI	x			x
passerine	Vireonidae	Warbling Vireo	WAVI	x	x	x	
passerine	Corvidae	Black-billed Magpie	BBMA	x			
passerine	Corvidae	American Crow	AMCR	x			
passerine	Corvidae	Common Raven	CORA	x			
passerine	Hirundinidae	Violet-green Swallow	VGSW	x			
passerine	Hirundinidae	Northern Rough-winged Swallow	NRWS	x			
passerine	Paridae	Black-capped Chickadee	BCCH	x			
passerine	Paridae	Mountain Chickadee	MOCH	x			
passerine	Aegithalidae	Bushtit	BUSH	x			
passerine	Troglodytidae	House Wren	HOWR	x	x	x	
passerine	Polyoptilidae	Blue-gray Gnatcatcher	BGGN	x			x

Order	Family	Common Name	Species Code	Species Richness	Occupancy Modeling	Abundance Modeling	Nest Monitoring
passerine	Regulidae	Golden-crowned Kinglet	GCKI	x			
passerine	Regulidae	Ruby-crowned Kinglet	RCKI	x			
passerine	Turdidae	Mountain Bluebird	MOBL	x			
passerine	Turdidae	Hermit Thrush	HETH	x	x	x	x
passerine	Turdidae	American Robin	AMRO	x			x
passerine	Fringillidae	Cassin's Finch	CAFI	x			
passerine	Fringillidae	House Finch	HOFI	x			
passerine	Fringillidae	Pine Siskin	PISI	x			
passerine	Fringillidae	Lesser Goldfinch	LEGO	x			
passerine	Fringillidae	American Goldfinch	AMGO	x			
passerine	Parulidae	Virginia's Warbler	VIWA	x			
passerine	Parulidae	Orange-crowned Warbler	OCWA	x			
passerine	Parulidae	MacGillivray's Warbler	MGWA	x	x	x	x
passerine	Parulidae	Yellow Warbler	YWAR	x	x	x	x
passerine	Parulidae	Audubon's Yellow-rumped Warbler	AUWA	x			
passerine	Emberizidae	Green-tailed Towhee	GTTO	x	x	x	x
passerine	Emberizidae	Spotted Towhee	SPTO	x	x	x	x
passerine	Emberizidae	Chipping Sparrow	CHSP	x	x	x	x
passerine	Emberizidae	Brewer's Sparrow	BRSP	x			
passerine	Emberizidae	Song Sparrow	SOSP	x	x	x	x
passerine	Emberizidae	Dark-eyed Junco	DEJU	x			
passerine	Cardinalidae	Western Tanager	WETA	x			
passerine	Cardinalidae	Black-headed Grosbeak	BHGR	x			
passerine	Cardinalidae	Lazuli Bunting	LAZB	x	x	x	x
passerine	Icteridae	Western Meadowlark	WEME	x			
passerine	Icteridae	Brown-headed Cowbird	BHCO	x			
passerine	Icteridae	Bullock's Oriole	BUOR	x			
			Total	50	12	12	12

Appendix 2.4. Locust variables collected during bird point count and vegetation surveys within the Clear Creek drainage of northwestern Colorado, USA. Locust intensity index values are composite variables generated using principal components analysis of the 11 variables listed in the table. Variables are summarized within three locust intensity groups: none (n=42 sites), low (n=41 sites), and high (n=42 sites) (Figure 2.1).

scale of data collection	locust variable	locust intensity group		
		none	low	high
multiple	locust intensity index	-1.77	-1.13	2.88
10m circular radius	% locust crown cover	0	4.33	28.31
25m line transect	% locust cover ht class 1 (< 0.5 m)	0	0.10	2.10
	% locust cover ht class 2 (0.5 - 1 m)	0	0.29	4.67
	% locust cover ht class 3 (>1 - 2 m)	0	0.78	10.86
	% locust cover ht class 4 (>2 - 5 m)	0	1.07	31.71
	% locust cover ht class 5 (>5 -10 m)	0	0.20	14.38
	% locust cover ht class 6 (> 10 m)	0	0	1.52
50m x 2m belt transect	density of locust trees (# stems/100 m^2)	0	0.32	8.36
	density of locust saplings (# stems/100 m^2)	0	5.83	39.02
	density of locust snags (# stems/100 m^2)	0	0.02	2.02
continuous	distance to nearest locust stem (m)	1285	26	1

Appendix 2.5. Coefficient estimates, standard errors (SE), and p-values from generalized linear models fit to vegetation data as a function of locust intensity index. Separate models were fit for datasets of tree species richness, shrub species richness, shrub density, total tree density (including locust), and native tree density (excluding locust). Species richness and density data were obtained from stem count surveys conducted within 50 m x 2 m belt transects at each sampling site (n=125). Significant relationships with locust index are indicated in bold ($p < 0.05$).

Tree Species Richness
Model: glm (tree richness ~ locust index, family = poisson)

Covariate	Estimate	SE	p-value
intercept	0.755	0.061	<0.001
locust index	0.015	0.025	0.550

Shrub Species Richness
Model: glm (shrub richness ~ locust index, family = poisson)

Covariate			
intercept	1.674	0.039	<0.001
locust index	**-0.097**	**0.019**	**<0.001**

Shrub Density
Model: glm (shrub density ~ locust index, family = poisson)

Covariate			
intercept	4.625	0.010	<0.001
locust index	**-0.226**	**0.005**	**<0.001**

Total Tree Density
Model: glm (tree density ~ locust index, family = poisson)

Covariate			
intercept	3.979	0.012	<0.001
locust index	**0.077**	**0.005**	**<0.001**

Native Tree Density
Model: glm (native tree density ~ locust index, family = poisson)

Covariate	Estimate	SE	p-value
intercept	3.408	0.018	<0.001
locust index	**-0.276**	**0.010**	**<0.001**

Appendix 2.6. Coefficient estimates, standard errors (SE), and p-values from generalized linear models fit to bird species richness data as a function of locust intensity. Maximum number of passerine and near-passerine species at each site (n=125) was modeled separately for 2015 and 2016 datasets. Significant covariates influencing species richness are indicated in bold (p < 0.05).

2015 Bird Species Richness

Model: glm (2015 bird richness ~ locust index, family = poisson)

Covariate	Estimate	SE	p-value
intercept	2.272	0.029	<0.001
locust index	**0.042**	**0.011**	**<0.001**

2016 Bird Species Richness

Model: glm (2016 bird richness ~ locust index, family = poisson)

Covariate	Estimate	SE	p-value
intercept	2.154	0.031	<0.001
locust index	**0.047**	**0.012**	**<0.001**

Appendix 2.7. Mean predicted estimates of occupancy (psi ± SE) at sites with no locust (n=42), low intensity invasion (n=41), and high intensity invasion (n=42) for 12 songbird species surveyed in 2015 and 2016. Common names for species codes are defined in Appendix 2.3.

species code	2015 Mean psi ± SE				2016 Mean psi ± SE			
	no locust	*low intensity*	*high intensity*	*all sites*	*no locust*	*low intensity*	*high intensity*	*all sites*
EMPI	0.783 ± 0.060	0.903 ± 0.041	0.984 ± 0.023	0.890 ± 0.026	0.716 ± 0.029	0.614 ± 0.028	0.618 ± 0.023	0.649 ± 0.016
COFL	0.637 ± 0.050	0.771 ± 0.045	0.973 ± 0.018	0.794 ± 0.026	0.569 ± 0.060	0.890 ± 0.034	1 ± 0	0.819 ± 0.028
HOWR	0.757 ± 0.049	0.966 ± 0.014	1 ± 0	0.907 ± 0.020	0.809 ± 0.048	0.940 ± 0.028	0.997 ± 0.002	0.915 ± 0.020
HETH	0.768 ± 0.046	0.613 ± 0.055	0.506 ± 0.053	0.629 ± 0.031	0.590 ± 0.053	0.567 ± 0.058	0.509 ± 0.050	0.555 ± 0.031
WAVI	0.843 ± 0.021	0.809 ± 0.029	0.788 ± 0.031	0.813 ± 0.016	0.920 ± 0.022	0.889 ± 0.026	0.886 ± 0.030	0.898 ± 0.015
YWAR	0.910 ± 0.033	0.951 ± 0	0.999 ± 0	0.953 ± 0.011	0.873 ± 0.014	0.965 ± 0.006	1 ± 0	0.946 ± 0.007
MGWA	0.987 ± 0.019	0.897 ± 0.021	0.935 ± 0.024	0.940 ± 0.012	1 ± 0	0.927 ± 0.041	0.786 ± 0.063	0.904 ± 0.026
LAZB	0.180 ± 0.038	0.407 ± 0.056	0.677 ± 0.044	0.421 ± 0.033	0.143 ± 0.055	0.464 ± 0.079	0.928 ± 0.040	0.512 ± 0.045
GTTO	0.767 ± 0.022	0.697 ± 0.030	0.676 ± 0.026	0.714 ± 0.016	0.710 ± 0.027	0.682 ± 0.029	0.786 ± 0.022	0.726 ± 0.015
SPTO	0.650 ± 0.045	0.596 ± 0.046	0.636 ± 0.039	0.628 ± 0.025	0.595 ± 0.047	0.582 ± 0.051	0.518 ± 0.049	0.565 ± 0.028
CHSP	0.548 ± 0.078	0.829 ± 0.063	0.952 ± 0.033	0.776 ± 0.038	0.237 ± 0.041	0.454 ± 0.047	0.920 ± 0.023	0.538 ± 0.034
SOSP	0.228 ± 0.024	0.379 ± 0.039	0.619 ± 0.035	0.409 ± 0.024	0.225 ± 0.025	0.426 ± 0.038	0.737 ± 0.026	0.463 ± 0.026

Appendix 2.8. Mean estimates of abundance (N ± SE) at sites with no locust (n=42), low intensity invasion (n=41), and high intensity invasion (n=42) for 12 songbird species surveyed in 2015 and 2016. Abundance estimates were predicted across sites based on model results from N-mixture models. Common names for species codes are defined in Appendix 2.3.

Species Code	2015 Mean N ± SE				2016 Mean N ± SE			
	no locust	*low intensity*	*high intensity*	*all sites*	*no locust*	*low intensity*	*high intensity*	*all sites*
EMPI	5.910 ± 0.318	4.448 ± 0.219	4.106 ± 0.149	4.824 ± 0.154	1.419 ± 0.085	1.127 ± 0.067	1.029 ± 0.062	1.192 ± 0.044
COFL	1.233 ± 0.081	1.333 ± 0.085	1.431 ± 0.071	1.332 ± 0.046	2.641 ± 0.159	2.634 ± 0.158	2.546 ± 0.115	2.607 ± 0.083
HOWR	2.825 ± 0.158	3.821 ± 0.176	4.031 ± 0.141	3.557 ± 0.103	2.662 ± 0.190	4.064 ± 0.231	4.629 ± 0.193	3.783 ± 0.139
HETH	1.517 ± 0.163	1.177 ± 0.141	1.202 ± 0.098	1.300 ± 0.079	2.915 ± 0.489	2.701 ± 0.518	2.582 ± 0.360	2.733 ± 0.264
WAVI	2.747 ± 0.130	2.810 ± 0.120	3.113 ± 0.101	2.891 ± 0.069	2.380 ± 0.126	2.146 ± 0.100	2.338 ± 0.090	2.289 ± 0.062
YWAR	3.222 ± 0.103	3.424 ± 0.096	4.494 ± 0.117	3.716 ± 0.079	5.282 ± 0.175	4.926 ± 0.106	5.672 ± 0.130	5.296 ± 0.085
MGWA*	20.13 ± 1.022	14.68 ± 0.527	13.75 ± 0.467	16.20 ± 0.484	40.59 ± 2.445	27.93 ± 1.669	17.45 ± 0.826	28.66 ± 1.328
LAZB*	4.542 ± 1.092	15.33 ± 3.382	18.13 ± 2.817	12.65 ± 1.582	7.067 ± 1.416	18.58 ± 2.815	27.86 ± 3.210	17.83 ± 1.672
GTTO	2.662 ± 0.147	2.144 ± 0.135	1.414 ± 0.074	2.073 ± 0.084	2.830 ± 0.167	2.651 ± 0.177	2.025 ± 0.127	2.501 ± 0.096
SPTO	1.855 ± 0.189	1.776 ± 0.247	2.128 ± 0.168	1.921 ± 0.117	1.993 ± 0.222	2.754 ± 0.521	2.494 ± 0.274	2.411 ± 0.208
CHSP	1.588 ± 0.159	2.568 ± 0.183	2.772 ± 0.157	2.308 ± 0.106	1.926 ± 0.215	3.446 ± 0.252	7.005 ± 0.507	4.131 ± 0.278
SOSP	0.269 ± 0.029	0.560 ± 0.069	1.132 ± 0.101	0.654 ± 0.053	0.396 ± 0.033	0.683 ± 0.062	1.299 ± 0.092	0.794 ± 0.051

*species with very low estimates of detection probability (<0.03) resulted in poor model performance and unidentifiable abundance estimates

Appendix 2.9. Estimates and Discussion of Detection Probability

Estimates of detection probability (p ± SE) generated from occupancy and abundance models for 12 songbird species surveyed in 2015 and 2016. Detection estimates were modeled based on mean covariate values for each variable included in the models. Common names for species codes are defined in Appendix 2.3.

Species Code	p ± SE (occupancy models)		p ± SE (abundance models)	
	2015	*2016*	*2015*	*2016*
EMPI	0.334 ± 0.027	0.483 ± 0.044	0.072 ± 0.064	0.296 ± 0.063
COFL	0.399 ± 0.035	0.356 ± 0.033	0.265 ± 0.071	0.135 ± 0.058
HOWR	0.662 ± 0.030	0.687 ± 0.027	0.252 ± 0.063	0.268 ± 0.067
HETH	0.371 ± 0.050	0.343 ± 0.055	0.200 ± 0.071	0.085 ± 0.057
WAVI	0.599 ± 0.035	0.463 ± 0.037	0.214 ± 0.063	0.217 ± 0.064
YWAR	0.867 ± 0.019	0.880 ± 0.018	0.462 ± 0.051	0.354 ± 0.048
MGWA	0.366 ± 0.026	0.421 ± 0.028	0.026 ± 0.055	0.018 ± 0.008
LAZB	0.388 ± 0.057	0.239 ± 0.041	0.022 ± 0.020	0.010 ± 0.005
GTTO	0.591 ± 0.037	0.494 ± 0.047	0.290 ± 0.054	0.200 ± 0.053
SPTO	0.482 ± 0.045	0.460 ± 0.046	0.185 ± 0.063	0.128 ± 0.075
CHSP	0.203 ± 0.026	0.188 ± 0.040	0.085 ± 0.052	0.029 ± 0.041
SOSP	0.430 ± 0.065	0.393 ± 0.057	0.312 ± 0.069	0.237 ± 0.073

In addition to modeling the state processes of occupancy and abundance, we also investigated the effects of survey-level covariates, such as varying conditions and timing of surveys, on the observation process, detection probability (Appendix 2.10, Appendix 2.11). For both occupancy and abundance models, noise level had a significant negative influence on detection probability for most species, which makes sense given the temporal variability in stream flows across our sites, and the fact that most of our detections were auditory rather than visual. Although we accounted for temporal variability in part through design-based sampling considerations, survey date influenced detection of 9 species. Changes in detection over time could be explained by changes in observer skill level (*e.g.,* enhanced observer ability over time) or changes in bird behaviors, such as singing rates and nesting activities, over the course of the breeding season (Alldredge et al., 2007).

Detection probability estimates were overall much lower for abundance than occupancy models. This could be explained by violation of the closure assumption for the abundance process, such that not all individuals were available for detection at each replicate visit, resulting in strong variation in recorded abundances across replicate visits. It may also indicate existence of some influential detection parameter for abundance that we were unable to account for in modeling. Due to low detection probability estimates, we encountered difficulties modeling abundance using N-mixture models for some species, resulting in high uncertainty and unreliable abundance estimates. While N-mixture models can incorporate extrinsic heterogeneity in the observation process using environmental and temporal covariates on detection (Royle, 2004), they cannot control for intrinsic heterogeneity in detection probability arising from behavioral differences among individuals (Veech et al., 2016). For example, detection probability may vary based on differences in individual singing rates, activity and movements, levels of boldness/shyness, and whether individuals are detected in pairs, groups, or individually (Veech et al., 2016). When detection probability is low, performance (*i.e.,* accuracy and precision) of N-mixture models is reduced, sometimes producing unreliable abundance estimates. Recent work assessing N-mixture model performance using simulated count data suggests these models cannot reliably estimate abundance for $p < 0.15$ (Veech et al., 2016). However, as our objective was to examine effects of invasion and other site characteristics on habitat use, we are confident in our assessment of effect direction and magnitude despite considerable uncertainty in some of the model-derived abundance estimates. As model performance generally improves with increased survey effort, future studies that aim to robustly estimate abundance should employ simulations to quantify adequate sampling effort (# sites and # replicate visits) to help ensure accurate parameter estimation using N-mixture models (Royle and Kéry, 2008).

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Appendix 2.10. Covariate estimates, standard errors (SE), and p-values from single season occupancy models examining songbird use as a function of locust intensity and other environmental covariates. Occupancy was modeled as a function of additive effects of locust intensity index (locust index), elevation, width of the riparian corridor (riparian width), total density of all trees, saplings, and snags (tree density), and total density of shrubs (shrub density). Detection probability was modeled as a function of additive effects of stream noise (noise), % cloud cover (cloud), survey date (date), and survey time (time). Each species was modeled separately in 2015 and 2016. Significant effects (p < 0.05) on occupancy and detection are indicated in bold.

2015 *Empidonax* Flycatcher

Occupancy Covariate	Estimate	SE	p-value
intercept	15.542	8.568	0.070
locust index	-0.237	1.751	0.892
elevation	-12.284	6.691	0.066
riparian width	-3.056	2.094	0.144
tree density	3.510	2.939	0.232
shrub density	5.597	3.610	0.121
Detection Covariate	Estimate	SE	p-value
intercept	-0.692	0.121	<0.001
noise	0.024	0.135	0.856
cloud	0.059	0.135	0.661
wind	0.163	0.125	0.192
date	-0.027	0.142	0.851
time	**-0.289**	**0.126**	**0.021**

2016 *Empidonax* Flycatcher

Occupancy Covariate	Estimate	SE	p-value
intercept	0.765	0.345	0.026
locust index	-0.032	0.322	0.920
elevation	-0.679	0.365	0.063
riparian width	0.065	0.278	0.814
tree density	-0.070	0.310	0.822
shrub density	**1.104**	**0.529**	**0.037**
Detection Covariate	Estimate	SE	p-value
intercept	-0.067	0.176	0.705
noise	0.018	0.204	0.929
cloud	0.060	0.138	0.665
wind	-0.043	0.138	0.754
date	**-0.289**	**0.147**	**0.050**
time	-0.244	0.132	0.065

2015 Cordilleran Flycatcher

Occupancy Covariate	Estimate	SE	p-value
intercept	4.419	2.212	0.046
locust index	3.931	2.715	0.148
elevation	**2.049**	**0.822**	**0.013**
riparian width	-0.339	0.565	0.548
tree density	1.776	1.032	0.085

2016 Cordilleran Flycatcher

Occupancy Covariate	Estimate	SE	p-value
intercept	24.128	12.733	0.058
locust index	31.924	16.842	0.058
elevation	**4.408**	**2.143**	**0.040**
riparian width	-0.520	0.919	0.572
tree density	2.342	1.760	0.183

shrub density	**-2.202**	**0.859**	**0.010**
Detection Covariate	Estimate	SE	p-value
intercept	-0.408	0.146	0.005
noise	0.269	0.147	0.067
cloud	0.259	0.159	0.103
wind	-0.220	0.139	0.115
date	**1.100**	**0.173**	**<0.001**
time	0.130	0.136	0.340

shrub density	-2.669	1.426	0.061
Detection Covariate	Estimate	SE	p-value
intercept	-0.591	0.143	<0.001
noise	0.074	0.135	0.582
cloud	-0.151	0.149	0.311
wind	-0.137	0.191	0.472
date	**0.822**	**0.150**	**<0.001**
time	0.105	0.140	0.452

2015 House Wren

Occupancy Covariate	Estimate	SE	p-value
intercept	19.984	14.056	0.155
locust index	24.679	18.928	0.192
elevation	-1.370	0.880	0.120
riparian width	-1.440	0.933	0.123
tree density	1.078	0.886	0.224
shrub density	1.501	1.392	0.281
Detection Covariate	Estimate	SE	p-value
intercept	0.674	0.134	<0.001
noise	**-0.885**	**0.163**	**<0.001**
cloud	-0.001	0.143	0.997
wind	-0.128	0.136	0.348
date	**-0.419**	**0.151**	**0.005**
time	0.177	0.132	0.180

2016 House Wren

Occupancy Covariate	Estimate	SE	p-value
intercept	7.114	3.354	0.034
locust index	0.104	1.816	0.954
elevation	**-4.479**	**2.142**	**0.037**
riparian width	-0.752	0.767	0.327
tree density	1.883	1.117	0.092
shrub density	0.139	0.686	0.839
Detection Covariate	Estimate	SE	p-value
intercept	0.786	0.123	<0.001
noise	-0.247	0.136	0.069
cloud	-0.074	0.125	0.556
wind	-0.233	0.138	0.091
date	**-0.443**	**0.134**	**0.001**
time	-0.187	0.122	0.125

2015 Hermit Thrush

Occupancy Covariate	Estimate	SE	p-value
intercept	1.195	0.786	0.129
locust index	-0.190	0.419	0.650

2016 Hermit Thrush

Occupancy Covariate	Estimate	SE	p-value
intercept	0.514	0.691	0.457
locust index	-0.276	0.496	0.578

	Estimate	SE	p-value
elevation	**2.428**	**0.880**	**0.006**
riparian width	0.825	0.582	0.156
tree density	0.270	0.694	0.698
shrub density	-0.087	0.580	0.881
Detection Covariate	Estimate	SE	p-value
intercept	-0.529	0.213	0.013
noise	-0.357	0.213	0.093
cloud	0.125	0.172	0.465
wind	-0.276	0.160	0.083
date	0.306	0.175	0.081
time	-0.148	0.160	0.354

	Estimate	SE	p-value
elevation	**2.329**	**1.155**	**0.044**
riparian width	0.539	0.502	0.283
tree density	1.082	0.646	0.094
shrub density	**-1.545**	**0.678**	**0.023**
Detection Covariate	Estimate	SE	p-value
intercept	-0.648	0.242	0.007
noise	**-0.429**	**0.188**	**0.023**
cloud	0.082	0.169	0.626
wind	-0.129	0.210	0.539
date	0.101	0.168	0.548
time	**-0.395**	**0.172**	**0.022**

2015 Warbling Vireo

Occupancy Covariate	Estimate	SE	p-value
intercept	1.836	0.430	<0.001
locust index	-0.330	0.371	0.374
elevation	0.394	0.420	0.348
riparian width	1.007	0.594	0.090
tree density	0.240	0.435	0.581
shrub density	0.094	0.413	0.820
Detection Covariate	Estimate	SE	p-value
intercept	0.402	0.144	0.005
noise	0.309	0.216	0.153
cloud	-0.039	0.144	0.788
wind	-0.122	0.130	0.351
date	0.109	0.149	0.465
time	0.060	0.129	0.642

2016 Warbling Vireo

Occupancy Covariate	Estimate	SE	p-value
intercept	4.564	2.256	0.043
locust index	0.086	0.491	0.861
elevation	1.505	0.907	0.097
riparian width	3.365	1.921	0.080
tree density	-1.035	0.933	0.267
shrub density	0.837	1.181	0.478
Detection Covariate	Estimate	SE	p-value
intercept	-0.148	0.148	0.317
noise	**-0.362**	**0.133**	**0.006**
cloud	-0.023	0.129	0.859
wind	**-0.602**	**0.180**	**0.001**
date	0.017	0.129	0.894
time	0.049	0.121	0.687

2015 Yellow Warbler

Occupancy Covariate	Estimate	SE	p-value
intercept	5.692	2.489	0.022
locust index	4.133	3.706	0.265
elevation	0.345	0.595	0.563
riparian width	-0.681	0.481	0.157
tree density	1.186	0.771	0.124
shrub density	-0.323	0.533	0.545
Detection Covariate	Estimate	SE	p-value
intercept	1.876	0.166	<0.001
noise	-0.096	0.175	0.583
cloud	-0.141	0.180	0.433
wind	-0.125	0.154	0.415
date	**-0.520**	**0.187**	**0.005**
time	0.197	0.160	0.219

2016 Yellow Warbler

Occupancy Covariate	Estimate	SE	p-value
intercept	10.427	5.151	0.043
locust index	11.631	7.437	0.118
elevation	0.705	0.726	0.332
riparian width	0.446	0.717	0.534
tree density	0.408	0.640	0.524
shrub density	0.254	0.526	0.629
Detection Covariate	Estimate	SE	p-value
intercept	1.989	0.172	<0.001
noise	-0.294	0.178	0.098
cloud	**-0.359**	**0.157**	**0.022**
wind	-0.061	0.169	0.720
date	-0.284	0.172	0.099
time	0.166	0.167	0.319

2015 MacGillivray's Warbler

Occupancy Covariate	Estimate	SE	p-value
intercept	47.042	55.920	0.400
locust index	8.179	9.650	0.397
elevation	38.691	46.315	0.404
riparian width	6.492	8.625	0.452
tree density	-21.844	27.252	0.423
shrub density	-7.550	11.154	0.498
Detection Covariate	Estimate	SE	p-value
intercept	-0.551	0.113	<0.001
noise	0.106	0.121	0.381
cloud	0.073	0.130	0.573
wind	-0.033	0.117	0.778

2016 MacGillivray's Warbler

Occupancy Covariate	Estimate	SE	p-value
intercept	155.407	108.725	0.153
locust index	1.597	4.288	0.710
elevation	102.711	72.751	0.158
riparian width	51.085	36.495	0.162
tree density	-65.216	49.337	0.186
shrub density	24.197	17.552	0.168
Detection Covariate	Estimate	SE	p-value
intercept	-0.318	0.114	0.005
noise	**-0.240**	**0.117**	**0.040**
cloud	0.117	0.118	0.323
wind	0.006	0.120	0.958

	Estimate	SE	p-value			Estimate	SE	p-value
date	**0.332**	**0.132**	**0.012**	**date**	**0.493**	**0.124**	**<0.001**
time	0.013	0.120	0.916	time	-0.030	0.117	0.796

2015 Lazuli Bunting

Occupancy Covariate	Estimate	SE	p-value
intercept	-0.895	0.392	0.022
locust index	0.491	0.403	0.224
elevation	**-2.302**	**0.504**	**<0.001**
riparian width	0.066	0.330	0.842
tree density	-0.278	0.434	0.522
shrub density	-0.234	0.405	0.563

Detection Covariate	Estimate	SE	p-value
intercept	-0.455	0.240	0.058
noise	**-0.534**	**0.235**	**0.023**
cloud	-0.128	0.222	0.565
wind	-0.047	0.192	0.807
date	**0.785**	**0.227**	**0.001**
time	0.122	0.186	0.514

2016 Lazuli Bunting

Occupancy Covariate	Estimate	SE	p-value
intercept	97.895	125.609	0.436
locust index	238.688	417.448	0.567
elevation	-883.636	1322.023	0.504
riparian width	291.405	399.115	0.465
tree density	401.656	584.910	0.492
shrub density	-244.816	449.336	0.586

Detection Covariate	Estimate	SE	p-value
intercept	-1.160	0.227	<0.001
noise	**-0.449**	**0.199**	**0.024**
cloud	0.006	0.174	0.974
wind	-0.330	0.307	0.283
date	**0.563**	**0.184**	**0.002**
time	-0.021	0.165	0.900

2015 Green-tailed Towhee

Occupancy Covariate	Estimate	SE	p-value
intercept	1.107	0.280	<0.001
locust index	0.003	0.280	0.991
elevation	**-0.696**	**0.296**	**0.019**
riparian width	**-0.639**	**0.234**	**0.006**
tree density	0.114	0.274	0.677
shrub density	**0.820**	**0.371**	**0.027**

Detection Covariate	Estimate	SE	p-value
intercept	0.367	0.153	0.016

2016 Green-tailed Towhee

Occupancy Covariate	Estimate	SE	p-value
intercept	1.144	0.423	0.007
locust index	0.549	0.432	0.203
elevation	-0.525	0.333	0.115
riparian width	**-0.644**	**0.271**	**0.018**
tree density	-0.122	0.287	0.669
shrub density	0.616	0.502	0.220

Detection Covariate	Estimate	SE	p-value
intercept	-0.023	0.187	0.903

	Estimate	SE	p-value		Estimate	SE	p-value
noise	-0.149	0.172	0.387	noise	-0.215	0.162	0.184
cloud	0.195	0.160	0.222	cloud	0.113	0.135	0.402
wind	-0.159	0.141	0.258	wind	-0.191	0.138	0.164
date	**0.417**	**0.164**	**0.011**	**date**	**0.280**	**0.140**	**0.046**
time	-0.169	0.141	0.232	time	-0.199	0.130	0.128

2015 Spotted Towhee

Occupancy Covariate	Estimate	SE	p-value
intercept	0.761	0.373	0.041
locust index	-0.208	0.326	0.525
elevation	**-1.729**	**0.459**	**<0.001**
riparian width	0.047	0.268	0.861
tree density	0.056	0.355	0.874
shrub density	**1.440**	**0.519**	**0.006**
Detection Covariate	Estimate	SE	p-value
intercept	-0.072	0.181	0.690
noise	**-0.475**	**0.160**	**0.003**
cloud	0.040	0.168	0.814
wind	-0.049	0.156	0.756
date	0.030	0.172	0.861
time	-0.233	0.149	0.119

2016 Spotted Towhee

Occupancy Covariate	Estimate	SE	p-value
intercept	0.325	0.319	0.308
locust index	**-0.857**	**0.379**	**0.024**
elevation	**-2.148**	**0.518**	**<0.001**
riparian width	0.503	0.286	0.079
tree density	-0.099	0.333	0.766
shrub density	**1.309**	**0.447**	**0.003**
Detection Covariate	Estimate	SE	p-value
intercept	-0.161	0.184	0.383
noise	-0.133	0.180	0.462
cloud	**0.317**	**0.150**	**0.035**
wind	**-0.411**	**0.173**	**0.017**
date	**0.361**	**0.164**	**0.028**
time	-0.036	0.148	0.808

2015 Chipping Sparrow

Occupancy Covariate	Estimate	SE	p-value
intercept	111.395	2228.254	0.960
locust index	-5.605	6679.459	0.999
elevation	-124.338	5762.192	0.983
riparian width	17.863	622.254	0.977
tree density	-5.786	511.743	0.991

2016 Chipping Sparrow

Occupancy Covariate	Estimate	SE	p-value
intercept	0.754	0.900	0.402
locust index	**3.554**	**1.723**	**0.039**
elevation	-0.973	0.737	0.187
riparian width	-1.029	0.654	0.116
tree density	-1.085	0.790	0.170

	Estimate	SE	p-value		Estimate	SE	p-value
shrub density	-6.357	1507.344	0.997	shrub density	-0.062	0.635	0.922
Detection Covariate	Estimate	SE	p-value	**Detection Covariate**	Estimate	SE	p-value
intercept	-1.370	0.159	<0.001	intercept	-1.463	0.259	<0.001
noise	**-0.485**	**0.158**	**0.002**	**noise**	**-0.717**	**0.211**	**0.001**
cloud	-0.018	0.166	0.915	cloud	0.007	0.173	0.966
wind	0.032	0.150	0.829	wind	-0.272	0.239	0.256
date	-0.072	0.174	0.679	date	0.107	0.187	0.569
time	0.173	0.147	0.240	time	0.123	0.171	0.472

2015 Song Sparrow

2016 Song Sparrow

Occupancy Covariate	Estimate	SE	p-value	Occupancy Covariate	Estimate	SE	p-value
intercept	-0.529	0.293	0.071	intercept	-0.253	0.332	0.445
locust index	0.217	0.302	0.472	locust index	0.573	0.379	0.131
elevation	**-1.159**	**0.348**	**0.001**	**elevation**	**-1.002**	**0.360**	**0.005**
riparian width	0.600	0.341	0.078	riparian width	0.461	0.357	0.197
tree density	0.007	0.334	0.984	tree density	-0.291	0.366	0.426
shrub density	0.080	0.333	0.810	shrub density	-0.192	0.348	0.582
Detection Covariate	Estimate	SE	p-value	**Detection Covariate**	Estimate	SE	p-value
intercept	-0.282	0.264	0.285	intercept	-0.435	0.238	0.068
noise	**-0.791**	**0.278**	**0.004**	noise	-0.043	0.219	0.844
cloud	-0.403	0.220	0.067	cloud	0.071	0.177	0.690
wind	**-0.832**	**0.230**	**<0.001**	wind	-0.414	0.263	0.115
date	-0.207	0.237	0.382	date	0.225	0.188	0.232
time	0.138	0.196	0.481	**time**	**0.354**	**0.175**	**0.043**

Appendix 2.11. Covariate estimates, standard errors (SE), and p-values from N-mixture models examining songbird abundance as a function of locust intensity and other environmental covariates. Abundance was modeled as a function of additive effects of locust intensity index (locust index), elevation, width of the riparian corridor (riparian width), total density of all trees, saplings, and snags (tree density), and total density of shrubs (shrub density). Detection probability was modeled as a function of additive effects of stream noise (noise), % cloud cover (cloud), survey date (date), and survey time (time). Each species was modeled separately in 2015 and 2016. Significant effects ($p < 0.05$) on abundance and detection are indicated in bold.

2015 *Empidonax* Flycatcher

Abundance Covariate	Estimate	SE	p-value
intercept	1.520	0.874	0.082
locust index	0.095	0.121	0.431
elevation	0.011	0.131	0.933
riparian width	-0.116	0.105	0.269
tree density	-0.137	0.116	0.235
shrub density	**0.324**	**0.106**	**0.002**

Detection Covariate	Estimate	SE	p-value
intercept	-2.550	0.952	0.007
noise	-0.246	0.128	0.054
cloud	0.028	0.104	0.787
wind	0.077	0.102	0.451
date	-0.067	0.110	0.542
time	**-0.221**	**0.099**	**0.026**

2016 *Empidonax* Flycatcher

Abundance Covariate	Estimate	SE	p-value
intercept	0.101	0.210	0.631
locust index	0.024	0.145	0.869
elevation	-0.134	0.134	0.317
riparian width	0.062	0.108	0.566
tree density	**-0.286**	**0.144**	**0.046**
shrub density	**0.396**	**0.124**	**<0.001**

Detection Covariate	Estimate	SE	p-value
intercept	-0.867	0.304	0.004
noise	-0.124	0.185	0.503
cloud	0.021	0.117	0.856
wind	-0.122	0.111	0.272
date	**-0.329**	**0.128**	**0.010**
time	-0.215	0.111	0.052

2015 Cordilleran Flycatcher

Abundance Covariate	Estimate	SE	p-value
intercept	0.212	0.243	0.384
locust index	0.071	0.116	0.539
elevation	**0.377**	**0.134**	**0.005**
riparian width	0.119	0.105	0.256
tree density	0.035	0.110	0.753

2016 Cordilleran Flycatcher

Abundance Covariate	Estimate	SE	p-value
intercept	0.898	0.414	0.030
locust index	0.035	0.108	0.743
elevation	**0.374**	**0.128**	**0.004**
riparian width	0.073	0.098	0.456
tree density	0.025	0.102	0.803

shrub density	**-0.323**	**0.140**	**0.021**	shrub density	**-0.248**	**0.122**	**0.043**
Detection Covariate	Estimate	SE	p-value	Detection Covariate	Estimate	SE	p-value
intercept	-1.018	0.363	0.005	intercept	-1.858	0.499	<0.001
noise	-0.005	0.213	0.983	noise	-0.124	0.160	0.436
cloud	0.113	0.139	0.415	cloud	-0.196	0.114	0.086
wind	-0.168	0.132	0.201	wind	-0.184	0.147	0.212
date	**0.769**	**0.174**	**<0.001**	**date**	**0.462**	**0.119**	**<0.001**
time	0.093	0.120	0.435	time	-0.055	0.104	0.598

2015 House Wren

2016 House Wren

Abundance Covariate	Estimate	SE	p-value	Abundance Covariate	Estimate	SE	p-value
intercept	1.212	0.246	<0.001	intercept	1.234	0.246	<0.001
locust index	-0.050	0.078	0.521	locust index	-0.037	0.073	0.610
elevation	**-0.273**	**0.098**	**0.005**	**elevation**	**-0.293**	**0.085**	**<0.001**
riparian width	-0.035	0.069	0.611	riparian width	-0.018	0.066	0.789
tree density	0.003	0.087	0.970	tree density	0.031	0.082	0.702
shrub density	-0.154	0.091	0.091	**shrub density**	**-0.283**	**0.095**	**0.003**
Detection Covariate	Estimate	SE	p-value	Detection Covariate	Estimate	SE	p-value
intercept	-1.089	0.334	0.001	intercept	-1.005	0.340	0.003
noise	**-0.243**	**0.123**	**0.049**	noise	0.011	0.101	0.914
cloud	0.035	0.077	0.651	cloud	-0.009	0.068	0.896
wind	-0.073	0.079	0.356	wind	-0.072	0.089	0.418
date	-0.004	0.077	0.955	date	-0.079	0.071	0.268
time	0.048	0.068	0.486	**time**	**-0.132**	**0.063**	**0.038**

2015 Hermit Thrush

2016 Hermit Thrush

Abundance Covariate	Estimate	SE	p-value	Abundance Covariate	Estimate	SE	p-value
intercept	0.072	0.335	0.830	intercept	0.562	0.653	0.390
locust index	0.091	0.138	0.508	locust index	0.152	0.124	0.219

	Estimate	SE	p-value		Estimate	SE	p-value
elevation	**0.566**	**0.169**	**0.001**	**elevation**	**0.968**	**0.180**	**<0.001**
riparian width	0.197	0.120	0.100	riparian width	0.173	0.126	0.172
tree density	0.201	0.111	0.069	**tree density**	**0.268**	**0.106**	**0.012**
shrub density	-0.130	0.140	0.354	**shrub density**	**-0.547**	**0.175**	**0.002**
Detection Covariate	Estimate	SE	p-value	Detection Covariate	Estimate	SE	p-value
intercept	-1.384	0.440	0.002	intercept	-2.379	0.734	0.001
noise	-0.218	0.259	0.399	**noise**	**-0.503**	**0.196**	**0.010**
cloud	-0.054	0.146	0.715	cloud	0.003	0.124	0.980
wind	**-0.168**	**0.150**	**0.261**	wind	-0.149	0.174	0.391
date	0.173	0.158	0.273	date	0.073	0.131	0.575
time	-0.185	0.136	0.174	**time**	**-0.309**	**0.133**	**0.020**

2015 Warbling Vireo   2016 Warbling Vireo

Abundance Covariate	Estimate	SE	p-value	Abundance Covariate	Estimate	SE	p-value
intercept	1.029	0.288	<0.001	intercept	0.785	0.281	0.005
locust index	-0.009	0.097	0.926	locust index	0.031	0.100	0.754
elevation	0.102	0.105	0.336	elevation	0.215	0.114	0.059
riparian width	**0.186**	**0.075**	**0.013**	**riparian width**	**0.192**	**0.083**	**0.020**
tree density	0.108	0.083	0.194	tree density	0.068	0.092	0.464
shrub density	-0.105	0.097	0.279	shrub density	-0.043	0.104	0.680
Detection Covariate	Estimate	SE	p-value	Detection Covariate	Estimate	SE	p-value
intercept	-1.303	0.373	<0.001	intercept	-1.283	0.375	<0.001
noise	0.274	0.145	0.059	noise	-0.282	0.146	0.054
cloud	-0.105	0.096	0.276	cloud	0.038	0.097	0.694
wind	-0.090	0.091	0.323	**wind**	**-0.486**	**0.153**	**0.002**
date	-0.023	0.099	0.812	date	0.074	0.098	0.455
time	-0.049	0.082	0.550	time	0.035	0.090	0.693

2015 Yellow Warbler

Abundance Covariate	Estimate	SE	p-value
intercept	1.286	0.114	<0.001
locust index	0.076	0.063	0.229
elevation	-0.077	0.072	0.282
riparian width	**0.142**	**0.053**	**0.007**
tree density	0.073	0.061	0.236
shrub density	0.011	0.069	0.872

Detection Covariate	Estimate	SE	p-value
intercept	-0.151	0.203	0.458
noise	0.173	0.106	0.102
cloud	-0.133	0.073	0.070
wind	-0.046	0.067	0.498
date	**-0.174**	**0.073**	**0.018**
time	0.080	0.060	0.181

2016 Yellow Warbler

Abundance Covariate	Estimate	SE	p-value
intercept	1.652	0.137	<0.001
locust index	0.041	0.058	0.475
elevation	-0.039	0.065	0.547
riparian width	**0.114**	**0.048**	**0.018**
tree density	0.038	0.055	0.492
shrub density	0.106	0.060	0.079

Detection Covariate	Estimate	SE	p-value
intercept	-0.602	0.212	0.004
noise	**-0.240**	**0.093**	**0.010**
cloud	**-0.143**	**0.054**	**0.008**
wind	**-0.132**	**0.063**	**0.035**
date	-0.085	0.057	0.135
time	**0.123**	**0.051**	**0.016**

2015 MacGillivray's Warbler

Abundance Covariate	Estimate	SE	p-value
intercept	2.739	2.092	0.190
locust index	0.044	0.104	0.670
elevation	0.165	0.113	0.143
riparian width	0.059	0.085	0.486
tree density	-0.070	0.089	0.431
shrub density	**0.217**	**0.090**	**0.015**

Detection Covariate	Estimate	SE	p-value
intercept	-3.609	2.153	0.094
noise	-0.040	0.114	0.724
cloud	-0.063	0.100	0.532
wind	-0.031	0.085	0.717

2016 MacGillivray's Warbler

Abundance Covariate	Estimate	SE	p-value
intercept	3.236	0.440	<0.001
locust index	-0.126	0.101	0.214
elevation	**0.377**	**0.100**	**<0.001**
riparian width	0.002	0.078	0.978
tree density	-0.073	0.081	0.372
shrub density	0.089	0.082	0.275

Detection Covariate	Estimate	SE	p-value
intercept	-3.997	0.441	<0.001
noise	**-0.369**	**0.103**	**<0.001**
cloud	0.112	0.073	0.124
wind	-0.031	0.080	0.697

	Estimate	SE	p-value		Estimate	SE	p-value
date	**0.254**	**0.100**	**0.011**	**date**	**0.268**	**0.080**	**<0.001**
time	0.043	0.088	0.625	time	-0.061	0.074	0.409

2015 Lazuli Bunting

2016 Lazuli Bunting

Abundance Covariate	Estimate	SE	p-value	Abundance Covariate	Estimate	SE	p-value
intercept	1.294	0.930	0.164	intercept	2.195	0.543	<0.001
locust index	-0.039	0.121	0.746	locust index	0.029	0.121	0.810
elevation	**-1.820**	**0.221**	**<0.001**	**elevation**	**-1.008**	**0.190**	**<0.001**
riparian width	-0.069	0.125	0.583	riparian width	-0.116	0.132	0.379
tree density	-0.218	0.200	0.277	tree density	0.006	0.179	0.971
shrub density	-0.090	0.163	0.581	**shrub density**	**-0.544**	**0.230**	**0.018**
Detection Covariate	Estimate	SE	p-value	Detection Covariate	Estimate	SE	p-value
intercept	-3.794	0.912	<0.001	intercept	-4.635	0.495	<0.001
noise	0.104	0.137	0.445	**noise**	**-0.299**	**0.131**	**0.023**
cloud	-0.092	0.129	0.478	cloud	-0.064	0.128	0.618
wind	0.085	0.107	0.427	wind	-0.129	0.200	0.519
date	**0.356**	**0.119**	**0.003**	**date**	**0.360**	**0.126**	**0.004**
time	-0.025	0.104	0.811	time	-0.012	0.110	0.914

2015 Green-tailed Towhee

2016 Green-tailed Towhee

Abundance Covariate	Estimate	SE	p-value	Abundance Covariate	Estimate	SE	p-value
intercept	0.629	0.182	<0.001	intercept	0.816	0.255	0.001
locust index	-0.092	0.117	0.430	locust index	-0.033	0.109	0.764
elevation	-0.124	0.101	0.223	**elevation**	**-0.213**	**0.107**	**0.047**
riparian width	**-0.228**	**0.102**	**0.026**	**riparian width**	**-0.399**	**0.115**	**<0.001**
tree density	-0.188	0.106	0.075	tree density	-0.063	0.110	0.566
shrub density	**0.315**	**0.093**	**<0.001**	shrub density	0.193	0.101	0.055
Detection Covariate	Estimate	SE	p-value	Detection Covariate	Estimate	SE	p-value
intercept	-0.894	0.261	<0.001	intercept	-1.386	0.328	<0.001

	Estimate	SE	p-value
noise	-0.206	0.130	0.114
cloud	0.146	0.102	0.154
wind	-0.063	0.101	0.532
date	**0.319**	**0.107**	**0.003**
time	-0.072	0.093	0.441

	Estimate	SE	p-value
noise	**-0.240**	**0.120**	**0.046**
cloud	**0.214**	**0.088**	**0.015**
wind	**-0.235**	**0.103**	**0.022**
date	**0.216**	**0.095**	**0.022**
time	-0.106	0.084	0.208

2015 Spotted Towhee

Abundance Covariate	Estimate	SE	p-value
intercept	0.471	0.331	0.154
locust index	0.011	0.118	0.925
elevation	**-0.596**	**0.139**	**<0.001**
riparian width	0.099	0.097	0.307
tree density	0.126	0.115	0.272
shrub density	**0.481**	**0.107**	**<0.001**

Detection Covariate	Estimate	SE	p-value
intercept	-1.480	0.415	<0.001
noise	**-0.419**	**0.146**	**0.004**
cloud	-0.071	0.120	0.556
wind	-0.055	0.122	0.651
date	-0.102	0.127	0.422
time	-0.191	0.100	0.056

2016 Spotted Towhee

Abundance Covariate	Estimate	SE	p-value
intercept	0.521	0.569	0.359
locust index	-0.210	0.134	0.116
elevation	**-1.011**	**0.143**	**<0.001**
riparian width	0.125	0.101	0.217
tree density	0.046	0.130	0.723
shrub density	**0.493**	**0.107**	**<0.001**

Detection Covariate	Estimate	SE	p-value
intercept	-1.917	0.672	0.004
noise	0.036	0.145	0.804
cloud	**0.245**	**0.100**	**0.014**
wind	-0.225	0.155	0.145
date	**0.287**	**0.111**	**0.010**
time	-0.086	0.100	0.389

2015 Chipping Sparrow

Abundance Covariate	Estimate	SE	p-value
intercept	0.674	0.603	0.264
locust index	-0.014	0.147	0.921
elevation	-0.352	0.190	0.064
riparian width	-0.081	0.130	0.530
tree density	-0.144	0.190	0.448

2016 Chipping Sparrow

Abundance Covariate	Estimate	SE	p-value
intercept	1.103	1.431	0.441
locust index	**0.383**	**0.144**	**0.008**
elevation	-0.277	0.191	0.147
riparian width	-0.123	0.147	0.400
tree density	-0.214	0.214	0.317

	Estimate	SE	p-value
shrub density	-0.318	0.188	0.091

Detection Covariate	Estimate	SE	p-value
intercept	-2.371	0.660	<0.001
noise	**-0.338**	**0.164**	**0.040**
cloud	0.029	0.143	0.841
wind	-0.045	0.141	0.747
date	-0.048	0.140	0.731
time	0.150	0.125	0.229

	Estimate	SE	p-value
shrub density	-0.407	0.252	0.106

Detection Covariate	Estimate	SE	p-value
intercept	-3.519	1.481	0.018
noise	**-0.569**	**0.158**	**<0.001**
cloud	0.042	0.140	0.763
wind	-0.248	0.217	0.252
date	**0.299**	**0.146**	**0.041**
time	0.141	0.129	0.272

2015 Song Sparrow

Abundance Covariate	Estimate	SE	p-value
intercept	-0.853	0.255	<0.001
locust index	0.180	0.141	0.203
elevation	**-0.864**	**0.221**	**<0.001**
riparian width	0.223	0.128	0.081
tree density	0.014	0.196	0.942
shrub density	-0.002	0.194	0.990

Detection Covariate	Estimate	SE	p-value
intercept	-0.791	0.322	0.014
noise	-0.371	0.247	0.133
cloud	-0.247	0.177	0.163
wind	**-0.563**	**0.191**	**0.003**
date	-0.024	0.180	0.896
time	0.210	0.148	0.156

2016 Song Sparrow

Abundance Covariate	Estimate	SE	p-value
intercept	-0.497	0.315	0.115
locust index	0.217	0.150	0.146
elevation	**-0.602**	**0.203**	**0.003**
riparian width	0.174	0.128	0.173
tree density	-0.091	0.208	0.661
shrub density	-0.008	0.207	0.968

Detection Covariate	Estimate	SE	p-value
intercept	-1.172	0.406	0.004
noise	-0.131	0.213	0.540
cloud	-0.017	0.151	0.913
wind	-0.311	0.240	0.195
date	0.183	0.163	0.263
time	0.245	0.151	0.104

Appendix 2.12. Comparison of fates, nest characteristics, and productivity metrics between nests (n = 92) monitored in locust and reference sites within the Clear Creek drainage of northwestern Colorado, USA. Significant differences (p < 0.05, two-sample Wilcoxon tests) are shown in bold.

		Locust	*Reference*
fate	# successful nests (%)	34 (65%)	23 (58%)
	# failed nests (%)	18 (35%)	17 (42%)
nest characteristics	# nests in locust substrate (%)	23 (44%)	0 (0%)
	nest height (mean ± SE)	99 ± 11 cm	107 ± 13 cm
	substrate height (mean ± SE)	2.77 ± 0.29 m	2.16 ± 0.32 m
	elevation (mean ± SE)	**1906 ± 12 m**	**1967 ± 13 m**
productivity	clutch size (mean ± SE)	3.71 ± 0.10	3.39 ± 0.15
	brood size (mean ± SE)	**3.04 ± 0.20**	**2.28 ± 0.24**
	young fledged/nest (mean ± SE)	**2.40 ± 0.26**	**1.59 ± 0.25**
	young fledged/successful nest (mean ± SE)	**3.68 ± 0.11**	**2.82 ± 0.20**

Appendix 2.13. Top model parameter estimates (β), standard errors (SE), and 95% lower (LCL) and upper confidence limits (UCL) for daily nest survival analyses. Parameter estimates are presented on the logit scale for the top community, MacGillivray's warbler (MGWA), and yellow warbler (YWAR) model in each candidate set based on lowest AICc value. Significant covariates influencing nest survival are indicated in bold, based on 95% CI that do not overlap 0.

Community: S (site type + substrate ID + nest height + substrate height + elevation)

Covariate	β	SE	LCL	UCL
intercept	-4.115	4.518	-12.970	4.739
site type (locust=1)	0.266	0.396	-0.511	1.042
substrate ID (locust=1)	1.110	0.606	-0.078	2.298
nest height	**0.019**	**0.008**	**0.003**	**0.034**
substrate height	**-0.008**	**0.003**	**-0.014**	**-0.002**
elevation	0.001	0.001	0.000	0.003

MGWA: S (site type)

Covariate	β	SE	LCL	UCL
intercept	19.416	0.000	19.416	19.416
site type (locust =1)	2.147	1.170	-0.146	4.441

YWAR: S (.)

| Covariate	β	SE	LCL	UCL
intercept	3.841	0.506	2.850	4.832

Appendix 2.14. Model selection results for models estimating nest survival (S) for the songbird community (n = 92 nests; 12 species), and two riparian dependent species: MacGillivray's warbler (n=27 nests) and yellow warbler (n=15 nests). Models are based on nest monitoring data collected in 2015 and 2016 in locust and non-invaded reference sites. Covariates examined include site type (locust or reference), year, substrate ID (locust or other), substrate type (low shrub/forb, or tree/high shrub), nest height, substrate height, and elevation. All community models included site type and all combinations of select covariates, while single species models include only single covariate models constructed with select variables. K is the number of parameters in each model and candidate models in each set are ranked based on AICc, with the top model in each set having the lowest AICc value (ΔAICc=0).

Community Nest Survival Candidate Models	K	AICc	ΔAICc	AICc Wt	Deviance
S(site type + substrate ID + nest ht + substrate ht + elevation)	6	212.329	0.000	0.099	200.254
S(site type + substrate ID + nest ht + substrate ht)	5	213.046	0.717	0.069	202.992
S(site type)	2	213.176	0.847	0.065	209.165
S(site type + year)	3	213.609	1.281	0.052	207.588
S(site type + elevation)	3	213.728	1.400	0.049	207.707
S(site type + year + substrate ID + nest ht + substrate ht + elevation)	7	213.769	1.441	0.048	199.670
S(site type + nest ht + substrate ht + elevation)	5	214.011	1.683	0.043	203.958
S(site type + year + elevation)	4	214.212	1.883	0.038	206.176
S(site type + year + substrate ID + nest ht + substrate ht)	6	214.229	1.900	0.038	202.154
S(site type + nest ht + substrate ht)	4	214.354	2.025	0.036	206.318
S(site type + substrate ID)	3	214.456	2.127	0.034	208.434
S(site type + substrate ht)	3	214.640	2.312	0.031	208.619
S(site type + year + substrate ht)	4	214.716	2.388	0.030	206.681
S(site type + nest ht)	3	214.896	2.568	0.027	208.875
S(site type + year + substrate ID)	4	214.962	2.633	0.026	206.926
S(site type + substrate ht + elevation)	4	214.979	2.650	0.026	206.943
S(site type + substrate ID + elevation)	4	215.038	2.710	0.025	207.003
S(site type + year + substrate ht + elevation)	5	215.049	2.720	0.025	204.996
S(site type + year + nest ht + substrate ht + elevation)	6	215.188	2.859	0.024	203.113
S(site type + year + nest ht + substrate ht)	5	215.296	2.967	0.022	205.242
S(site type + nest ht + elevation)	4	215.408	3.079	0.021	207.372
S(site type + year + substrate ID + substrate ht)	5	215.547	3.219	0.020	205.494

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	K	AICc	ΔAICc	AICc Wt	Deviance
S(site type + year + nest ht)	4	215.571	3.242	0.020	207.535
S(site type + year + substrate ID + elevation)	5	215.600	3.272	0.019	205.547
S(site type + substrate ID + substrate ht)	4	215.610	3.282	0.019	207.575
S(site type + year + substrate ID + substrate ht + elevation)	6	215.782	3.454	0.018	203.708
S(site type + substrate ID + substrate ht + elevation)	5	215.879	3.550	0.017	205.825
S(site type + substrate ID + nest ht)	4	216.047	3.719	0.015	208.012
S(site type + year + nest ht + elevation)	5	216.168	3.839	0.014	206.114
S(site type + substrate ID + nest ht + elevation)	5	216.615	4.286	0.012	206.562
S(site type + year + substrate ID + nest ht)	5	216.873	4.545	0.010	206.820
S(site type + year + substrate ID + nest ht + elevation)	6	217.518	5.189	0.007	205.443

MacGillivray's Warbler Nest Survival Candidate Models	K	AICc	ΔAICc	AICc Wt	Deviance
S(site type)	2	25.740	0.000	0.472	21.695
S(year)	2	28.051	2.312	0.148	24.006
S(substrate ID)	2	28.176	2.437	0.139	24.132
S(.)	1	28.769	3.030	0.104	26.754
S(elevation)	2	30.190	4.451	0.051	26.146
S(nest ht)	2	30.334	4.595	0.047	26.289
S(substrate ht)	2	30.755	5.015	0.038	26.710

Yellow Warbler Nest Survival Candidate Models	K	AICc	ΔAICc	AICc Wt	Deviance
S(.)	1	28.046	0.000	0.229	26.024
S(elevation)	2	28.269	0.223	0.204	24.202
S(site type)	2	28.987	0.940	0.143	24.920
S(substrate type)	2	29.351	1.305	0.119	25.284
S(substrate ht)	2	29.396	1.350	0.116	25.329
S(year)	2	29.595	1.548	0.105	25.528
S(nest ht)	2	30.059	2.012	0.084	25.992
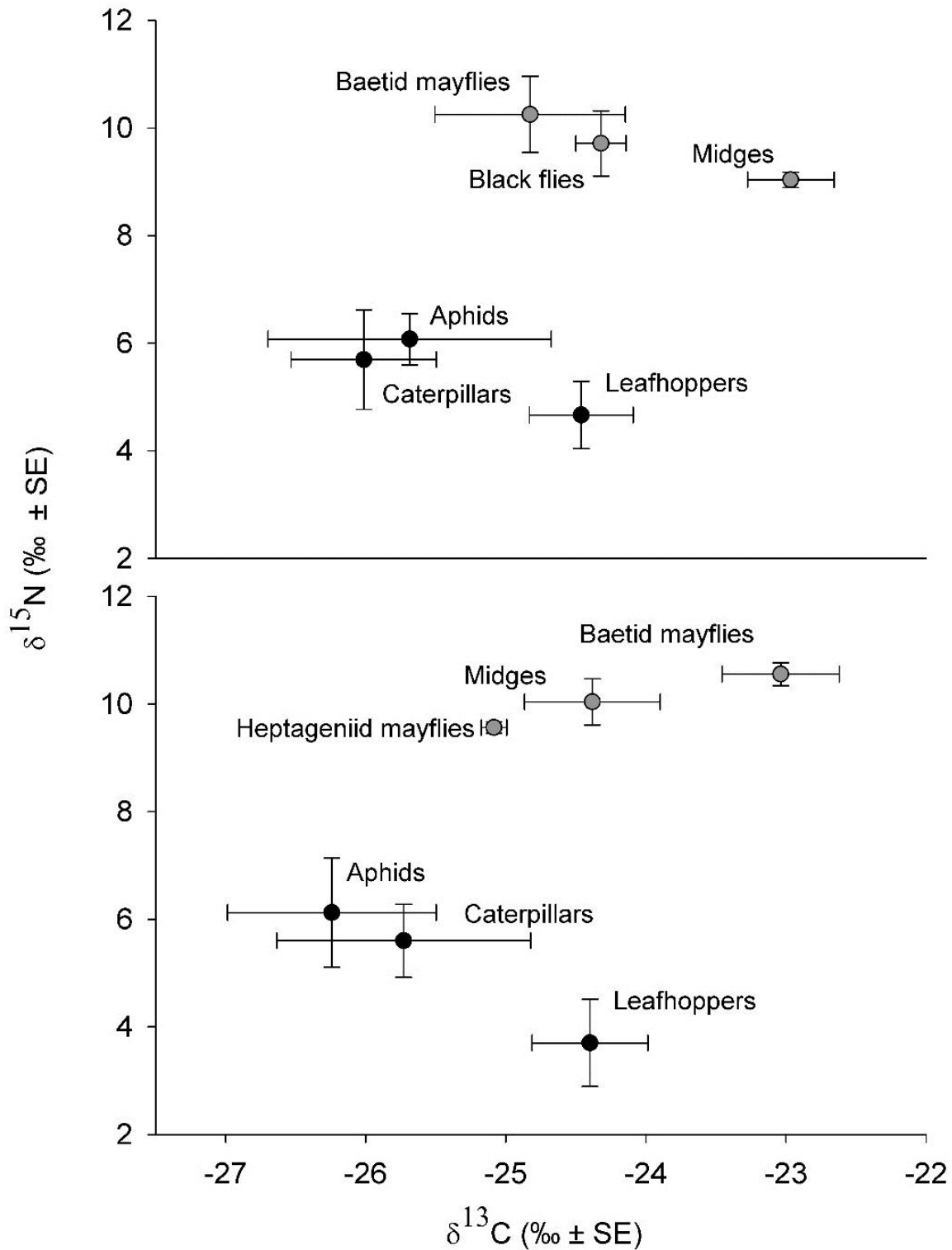
Appendix 3.1. Biplots showing $\delta^{13}C$ and $\delta^{15}N$ signatures of aquatic (gray) and terrestrial insect taxa (black) used as an index of songbird diet sources in 2015 (top) and 2016 (bottom). Common names of taxa are displayed near the mean.

Appendix 3.2. Comparison of aquatic carbon contributions to songbird diets across species and years, based on data pooled across reference and locust sites. Mean estimates of % aquatic carbon ± SE were calculated using a single isotope mixing formula and δ^{13}C signatures of insect and fecal samples. The terrestrial-derived diet component is the remaining percentage (1 − aquatic percentage).

Songbird Species	2015		2016		Total	
	n	*Mean % Aq.* ± SE	*n*	*Mean % Aq.* ± SE	*n*	*Mean % Aq.* ± SE
Empidonax Flycatcher	18	38 ± 9	8	17 ± 7	26	31 ± 7
Warbling Vireo	3	17 ± 17	6	25 ± 16	9	22 ± 12
Black-capped Chickadee	8	55 ± 15	12	3 ± 3	20	24 ± 8
MacGillivray's Warbler	11	8 ± 6	3	53 ± 27	14	18 ± 8
Virginia's Warbler	9	23 ± 8	1	-	10	24 ± 8
Yellow Warbler	16	19 ± 8	13	45 ± 12	29	31 ± 7
Green-tailed Towhee	13	62 ± 10	12	65 ± 11	25	64 ± 7
Community	**78**	**33 ± 4**	**55**	**34 ± 5**	**133**	**34 ± 3**

Appendix 3.3. One-way MANOVAs and ANOVAs by year, testing for differences in songbird diet $\delta^{13}C$ and $\delta^{15}N$ between reference and locust sites. Only species with multiple samples per site/year combination were evaluated (dashes in place otherwise). Significant differences (p < 0.05) are shown in bold. Figure 3.3 shows directionality of significant diet shifts with bold arrows.

	δ13C and δ15N (MANOVA)				δ13C (ANOVA)				δ15N (ANOVA)			
	2015		2016		2015		2016		2015		2016	
Songbird Species	F	p	F	p	F	p	F	p	F	p	F	p
Empidonax Flycatcher	1.28	0.32	**28.2**	**0.002**	0.81	0.38	2.52	0.16	2.13	0.17	1.08	0.34
Warbling Vireo	-		**19.4**	**0.019**	-		**13**	**0.023**	-		4.37	0.10
Black-capped Chickadee	-		1.43	0.29	-		0.8	0.38	-		2.9	0.12
MacGillivray's Warbler	0.64	0.55	-		0.31	0.59	-		1.41	0.27	-	
Virginia's Warbler	4.41	0.067	-		**8.79**	**0.021**	-		0.23	0.64	-	
Yellow Warbler	2.72	0.10	1.64	0.24	3.89	0.069	1.7	0.22	1.85	0.19	0.42	0.53
Green-tailed Towhee	0.38	0.70	0.54	0.60	0.51	0.49	0.79	0.40	0.24	0.63	0.61	0.45

Appendix 3.4. Summary of body condition measurements for songbird species with sufficient sample sizes (n ≥ 2 samples per site type and year; dashes in place otherwise). Sample sizes (n) and mean measurements of mass (g ± SE) and fat (score ± SE) are summarized by year and site type (reference and locust). Significant differences (p < 0.05) between site types are shown in bold.

Songbird Species	2015 Reference			2015 Locust			2016 Reference			2016 Locust		
	n	mass	fat	n	mass	fat	n	mass	fat	n	mass	fat
Empidonax Flycatcher	4	12.38 ± 0.94	0.50 ± 0.20	10	11.4 ± 0.49	0.50 ± 0.11	4	**10.88 ± 0.13**	0.75 ± 0.25	4	**11.38 ± 0.13**	0.75 ± 0.48
Warbling Vireo	1	-		2	-		4	12.00 ± 0.20	1.00 ± 0.00	2	11.50 ± 0.50	1.50 ± 0.50
Black-capped Chickadee	0	-		8	-		8	11.06 ± 0.20	0.75 ± 0.25	4	11.13 ± 0.66	1.00 ± 0.00
MacGillivray's Warbler	3	10.50 ± 0.29	0.00 ± 0.00	8	10.81 ± 0.28	0.25 ± 0.16	2	-		1	-	
Virginia's Warbler	2	8.25 ± 0.25	-	7	7.71 ± 0.26	-	0	-		1	-	
Yellow Warbler	6	**8.33 ± 0.38**	0.50 ± 0.18	10	**9.45 ± 0.25**	0.33 ± 0.22	7	9.14 ± 0.14	0.71 ± 0.29	6	8.75 ± 0.21	0.50 ± 0.22
Green-tailed Towhee	2	28.00 ± 2.00	1.00 ± 1.00	10	25.25 ± 0.55	1.60 ± 0.30	7	28.86 ± 0.96	1.29 ± 0.29	5	27.00 ± 1.64	0.80 ± 0.37