Bird species turnover is related to changing predation risk along a vegetation gradient

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Abstract. Turnover in animal species along vegetation gradients is often assumed to reflect adaptive habitat preferences that are narrower than the full gradient. Specifically, animals may decline in abundance where their reproductive success is low, and these poor-quality locations differ among species. Yet habitat use does not always appear adaptive. The crucial tests of how abundances and demographic costs of animals vary along experimentally manipulated vegetation gradients are lacking. We examined habitat use and nest predation rates for 16 bird species that exhibited turnover with shifts in deciduous and coniferous vegetation. For most bird species, decreasing abundance was associated with increasing predation rates along both natural and experimentally modified vegetation gradients. This landscape-scale approach strongly supports the idea that vegetation-mediated effects of predation are associated with animal distributions and species turnover.

Key words: abundance; community ecology; density; distribution; forest bird species; habitat selection; landscape-scale experiment; population ecology; predation; species turnover; vegetation gradient; western Montana, USA.

Introduction

Classic and contemporary studies have documented turnover of animal species along environmental gradients (Kendeigh 1948, Odum 1950, Karr and Freemark 1983, Jankowski et al. 2009, Qian and Ricklefs 2012, Stegen et al. 2013). Yet specific mechanisms by which habitat differentially influences abundances of species and causes turnover remain unclear. Moreover, the ecological literature over the past 65 years has largely focused on potential causes of differences in overall biodiversity rather than the proximate causes of shifting abundances of individual species found along gradients (e.g., MacArthur and MacArthur 1961, Odum 1969, Karr and Roth 1971, Robinson and Terborgh 1997, Messmer et al. 2011).

Animal species should be less abundant in habitat conditions where the probabilities of survival and reproduction are low, assuming that abundance reflects adaptive habitat preferences (Fretwell and Lucas 1969, Martin 1998, Pulliam 2000). If locations of these poor-quality habitats along a gradient differ among species, then adaptive habitat use might explain species turnover. Correlations between habitat-specific fitness components and abundance of one or a few animal species have certainly been observed (Martin 1998, Morris and Davidson 2000, Martin 2001, Ries and Fagan 2003,

Pidgeon et al. 2006). However, data illustrating the way in which demographic parameters and abundance covary with habitat changes for a suite of species have not been published. Furthermore, habitat preferences are not always adaptive if cues used to make settlement decisions do not accurately reflect demographic consequences of settlement (Thompson et al. 1990, Arlt and Pärt 2007, Chalfoun and Schmidt 2012). Nonadaptive habitat use might be common for many species along vegetation gradients because broad differences in plant composition and structure provide animals with a multitude of habitat cues juxtaposed in space. If nonadaptive habitat use is common, then habitat-specific fitness probably will have little influence on species distributions.

A useful system in which to examine species turnover with habitat change is provided by bird species breeding along a gradient from aspen (*Populus* spp.) to mixed-conifer forest. Aspens are among the most widely distributed deciduous trees in the world, and rapid replacement of aspen forest by conifers is occurring across the northern hemisphere (Romme et al. 1995, Latva-Karjanmaa et al. 2007, Rehfeldt et al. 2009). This shift from aspens to conifers appears to facilitate an increase in conifer-dependent nest predators, which may increase nest predation rates (Tewksbury et al. 1998, Song and Hannon 1999, Goheen and Swihart 2005). Nest predation is the major source of reproductive failure for birds and can strongly influence avian populations and habitat preferences (Wilcove 1985, Martin 1992, Martin 1998, Lloyd et al. 2005).

PLATE 1. Photographs of study species taken at the Lewis and Clark site in western Montana, USA. From left to right: Lincoln's Sparrow in Engelmann spruce, red squirrel (a typical nest predator), and Dusky Flycatcher nesting in a mix of Rocky Mountain maple and willow. Photo credit: J. A. LaManna.

Vulnerability to risk may differ among bird species as a function of nest-site vegetation preferences. Habitat preferences differ among species, and increased abundance of preferred nest-site vegetation in a forest stand or nesting territory might impede the ability of predators to find the nest (Martin 1993, Martin 1998, Chalfoun and Martin 2009). For example, as conifers replace deciduous vegetation, nest predation might decrease for species that prefer coniferous nest sites while increasing for species that prefer deciduous nest sites. If birds choose habitats with respect to risk, then bird abundances might inversely track these vegetation-mediated changes in nest predation along the gradient (Fretwell and Lucas 1969, Fontaine and Martin 2006).

We used both observational and large-scale experimental approaches to test these hypotheses. We examined patterns in bird and nest-predator abundance as well as habitat use and nest predation rates of birds breeding along a deciduous (aspen) to conifer gradient (see Plate 1). We also experimentally tested the effect of vegetation structure and composition on bird abundances as mediated by nest predation with a replicated landscape-scale removal of conifers from mixed aspen–conifer forest stands. Observational analyses should provide inference on the effects of vegetation on bird species turnover because associated effects on nest predation were examined and nest predation is known to strongly affect bird populations (Wilcove 1985, Martin 1992, 1998, Lloyd et al. 2005). However, correlational analyses may not uncover causation because other factors change along the gradient. Our experiment addresses this issue by directly testing vegetation as the cause of changes in nest predation and bird abundances.

METHODS

This study was conducted from 16 May to 15 August for 2009–2013, on 19 forest stands that varied in relative composition of deciduous to coniferous vegetation across two sites in western Montana, USA (Appendix A). One site contained five stands and was located in the Mount Haggin Wildlife Management Area ~18 km southeast of Anaconda, Montana, at 1750 m elevation. A second site contained 14 stands and was located ~43 km northwest of White Sulphur Springs, Montana, on the Lewis and Clark National Forest and on adjacent private land at 1700–1850 m elevation. These two sites were 160 km apart but at the same elevation, both along north-facing slopes, and had similar vegetation communities. Within sites, forest stands were between 0.5 and 20 km apart. Stands varied in size (mean = 8.0 ha, SD = 4.1 ha), but stand size was not associated with changing vegetation characteristics (see *Results*). Dominant canopy trees at both sites were aspen, Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and Engelmann spruce (*Picea engelmannii*). The dominant understory woody species were saplings of canopy trees, common juniper (*Juniperus communis*), and a variety of deciduous shrubs such as Canada buffaloberry (*Shepherdia canadensis*), willow (*Salix* spp.), rocky mountain maple (*Acer glabrum*), and prickly rose (*Rosa acicularis*).

The gradient from deciduous to coniferous vegetation was surveyed with nested 11.3 m and 5 m radius plots placed systematically on a 35×35 m grid within each forest stand. All woody stems > 50 cm tall were classified to species and one of five size classes (Martin et al. 1997). Basal area of coniferous and deciduous trees (all shrubs and trees > 8 cm in diameter in the 11.3 m radius plot) and understory stems (all shrubs and small trees < 8 cm in diameter in the 5 m radius plot) were calculated for each systematic vegetation plot (Appendix A). These data were used in a principal components analysis (PCA) to determine the major axes of change in vegetation structure and composition. The first two principal components accounted for 68.6% of the total variation in basal area of deciduous (PC_{dec}) and coniferous (PC_{con}) trees and understory stems. These two PC axes were used in subsequent analyses.

We searched for nests of all breeding bird species in each forest stand. Data from 16 species (Appendix B) were sufficient to estimate nest predation rates. Vegetation plots centered at each nest (identical to the systematic vegetation plots) were used to quantify nest-site use, and these data were transformed on to

the PC axes. Territory habitat use was quantified by averaging across the nest-site vegetation plot and all available systematic plots within 50 m of the nest, approximating the mean radius of bird territories at our sites.

Bird and combined nest predator densities were estimated by spot-mapping territories in each forest stand (Svensson et al. 1970). Changes in densities of birds and nest predators along both PC axes were examined with linear models. Nest predation rates were determined by intensive nest monitoring following standard protocols (Martin and Geupel 1993). Every attempt was made to locate nests within all territories identified by spot-mapping. Changes in nest predation with both PC axes at stand, territory, and nest-site spatial scales were examined using logistic exposure models and data from 1067 nests (Shaffer 2004; Appendix C).

We examined the relationship between density and nest predation both among and within bird species. Among species, standardized effect sizes (standardized regression coefficients; Schielzeth 2010) describing the relative strength of vegetation's effect on density and nest predation were calculated for each species. We compared these effect sizes across species to assess if the relative strength of the vegetation's effect on nest predation and on density were inversely related. A negative relationship was expected because a given increase in nest predation should be associated with a relative decrease in density and vice versa. We next examined within-species relationships between density and nest predation across forest stands to determine if abundances decreased as risk increased, suggesting preferences for low-risk habitat.

We conducted a landscape-scale experimental removal of conifer trees and shrubs from mixed conifer–aspen forest stands to test vegetation as the cause of observed effects on bird abundances and nest predation rates. All conifer trees and most understory conifer shrubs were mechanically removed from within and 33 m around three forest stands at the Mount Haggin field site following the 2010 breeding season (see Appendix A for experimental stand details). Five other stands were selected a priori to serve as controls, allowing a before–after-control–impact (BACI) experimental design. Because this experimental treatment removed all coniferous vegetation, we also expected it to increase the abundance and density of smaller deciduous shrubs and trees that were early-successional species (willows and aspens). We therefore expected our landscape-scale habitat experiment to manipulate both PC axes and monitored effects of manipulation on those axes, densities and nest predation rates of birds, and nest predator densities (see Appendix D for detailed methods). All analyses were conducted with R version 3.0.3 and the lmtest, lme4, repeated, and lmerTest packages (Lindsey 2001, Zeileis and Hothorn 2002, Bates et al. 2014, Kuznetsova et al. 2014, R Core Team 2014).

RESULTS

Two principal component axes cumulatively described 68.6% of the overall variation in vegetation among 860 systematic vegetation plots. The first PC axis, PC_{con}, described increasing basal area of conifer trees (loading = 0.648) and understory conifer stems (loading = 0.595) that were moderately associated with an increase in understory deciduous stems (loading = 0.416) and a small decrease in deciduous trees (loading = −0.231). The second PC axis, PC_{dec}, described increasing basal area of deciduous trees (loading = 0.748) and understory deciduous stems (loading = 0.626) that were moderately associated with a decrease in understory conifer stems (loading = −0.212). Forest stand size was not associated with PC_{con} ($r = -0.20$, $P = 0.41$) or PC_{dec} ($r = -0.31$, $P = 0.20$). Centroids for systematic vegetation plots within each stand illustrated clear differences among forest stands along both PC axes (Fig. 1a). Vegetation characteristics in the patch surrounding nest sites and territories varied among bird species and illustrated differential use of the gradient (Fig. 1b, c). Most observed niche differentiation occurred along PC_{con} (Fig. 1b).

Densities of eight bird species declined as conifers increased along PC_{con}, and densities of four species increased along PC_{con} (Fig. 2a; see Appendix E). Densities increased with deciduous vegetation along PC_{dec} for six species (Fig. 2b). Densities of two species (American Robin and Lincoln's Sparrow) significantly declined along PC_{con} and significantly increased along PC_{dec} (Fig. 2a, b), indicating strong preferences for conifer-free deciduous stands. Density increased along both PC axes for one species (Dusky Flycatcher), but the effect of PC_{dec} was stronger and the weaker effect of PC_{con} was most likely due to the moderate increase in deciduous stems along this axis (Fig. 2a, b; Appendix E). Ultimately, the relative strength of association between bird density and vegetation varied substantially among bird species (Fig. 3a). Birds, of course, were not the only organisms to change density along the vegetation gradient. Density of nest predators increased with both PC axes (Fig. 2a, 2b) but was dominantly associated with PC_{con} (Appendix E).

Average daily nest predation rates ranged from 0.0013 for Red-naped Sapsuckers to 0.041 for Yellow Warblers (Appendix F). These daily nest predation rates represent a wide range in predation risk, equating to 5.5% of Red-naped Sapsucker nests and 63.4% of Yellow Warbler nests being depredated, assuming the observed average length of nest exposure (44 days for Red-naped Sapsucker and 23 days for Yellow Warbler). Changes in nest predation along the gradient were associated with differences in nest-site vegetation preferences among bird species. Nest predation rates decreased with increasing conifer vegetation along PC_{con} for two species (Chipping Sparrow and Ruby-crowned Kinglet; Fig. 3b) that predominantly nested in conifer-dominated sites (Fig. 1b). Nest predation rates increased along PC_{con} for
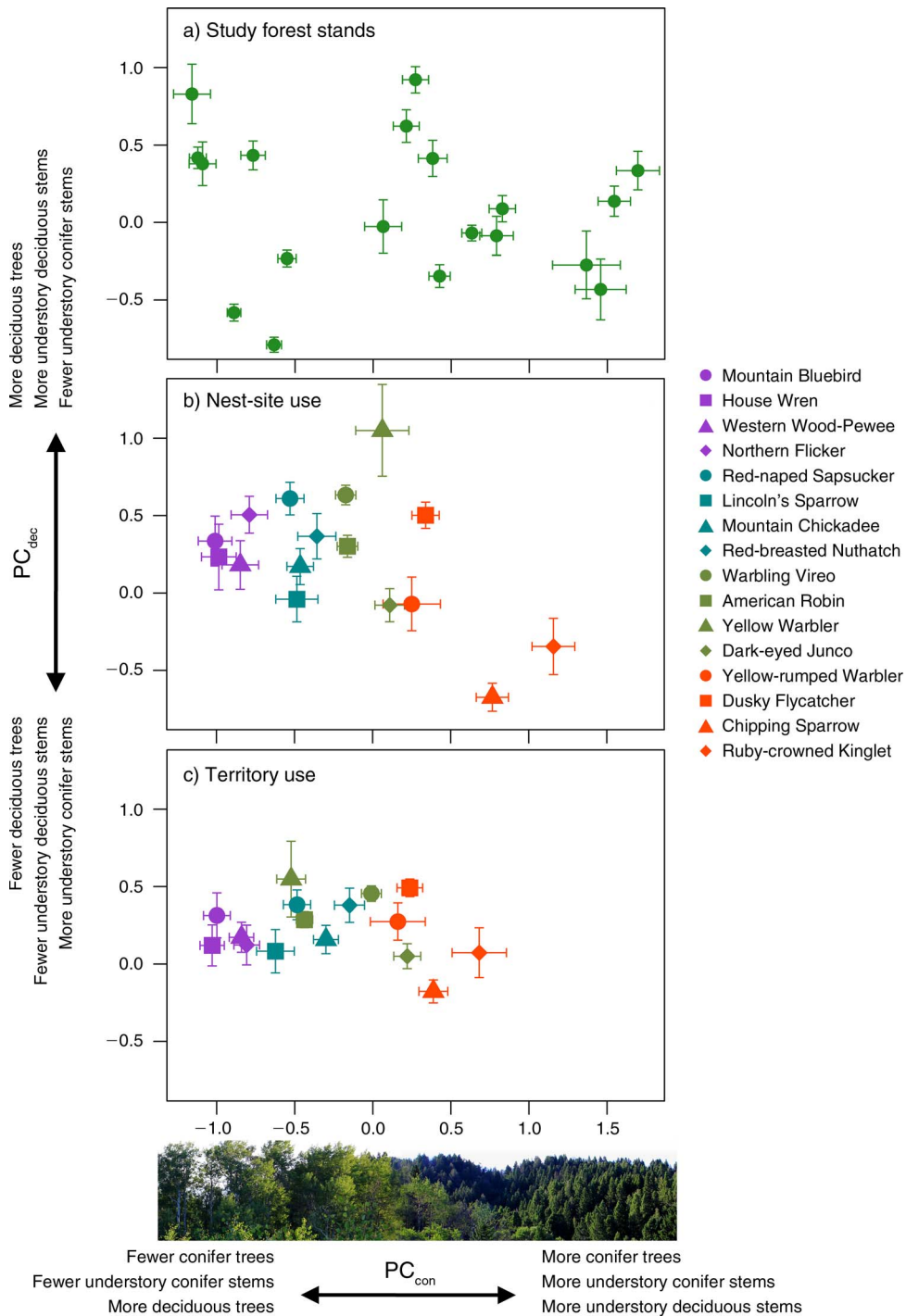
FIG. 1.   Characterization of vegetation composition and structure (centroids $\pm$ SE) along two PC axes for coniferous (PC_{con}) and deciduous (PC_{dec}) vegetation (a) within study forest stands, and (b) surrounding nest sites of 16 bird species and (c) within territories of those 16 species in western Montana, USA.

four species (Fig. 3b) that avoided nesting in conifer-dominated sites (Fig. 1b). Nest predation rates decreased with increasing deciduous vegetation along PC_{dec} for six species (Fig. 3b), and five of these species nested in sites dominated by deciduous vegetation (Fig.

1b). Nest predation for four remaining species appeared to increase (albeit nonsignificantly) along PC_{con} (Fig. 3b), but relatively low nest predation rates for these species probably reduced our power to detect significant increases in nest predation. Nest predation for almost all
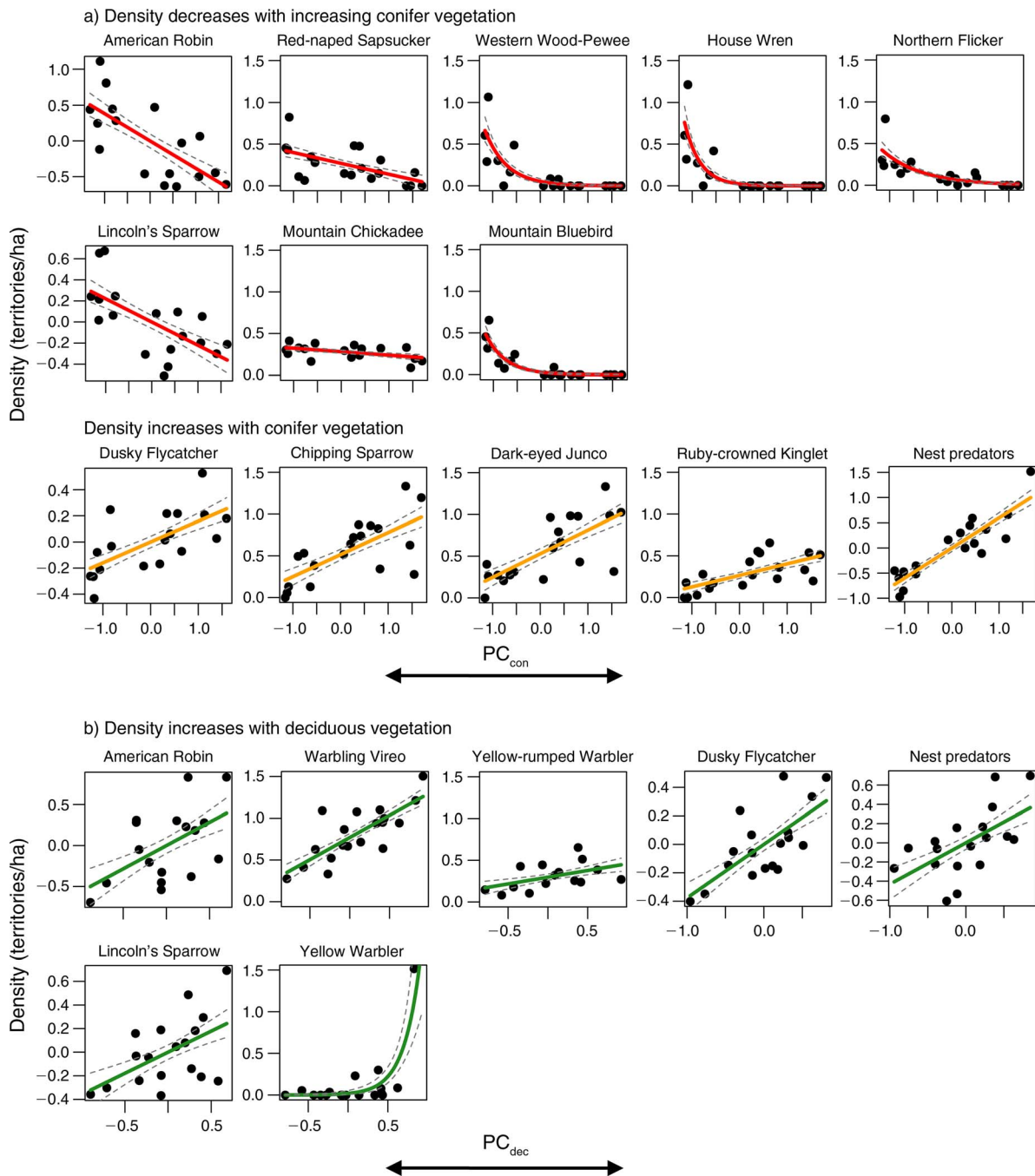
FIG. 2. Differences in population densities (territories/ha) of bird species and combined nest predators along two PC axes describing vegetation composition and structure in western Montana, USA: (a) conifer vegetation, PC_{con}, and (b) deciduous vegetation, PC_{dec}. Only significant relationships ($P < 0.05$) are shown (see Appendix E). Dashed gray lines represent error ($\pm SE$) around these relationships. Densities of three bird species (Dusky Flycatcher, American Robin, and Lincoln's Sparrow) and nest predators were significantly associated with both PC axes, and partial regression plots depicting relationships between density and one PC axis, while controlling for the other, are shown for these three species.

species showed stronger relationships with stand-scale vegetation than with territory- or nest-site-scale vegetation (Appendix F).

Among bird species, the relative change in density along a PC axis was strongly and negatively predicted by

the relative change in nest predation (Fig. 3c). This pattern was strong across species except for one outlier: Dark-eyed Junco. Within bird species, densities declined with increasing predation rates for 11 of 16 species (Fig. 4, Appendix G). Density decreased with nest predation,
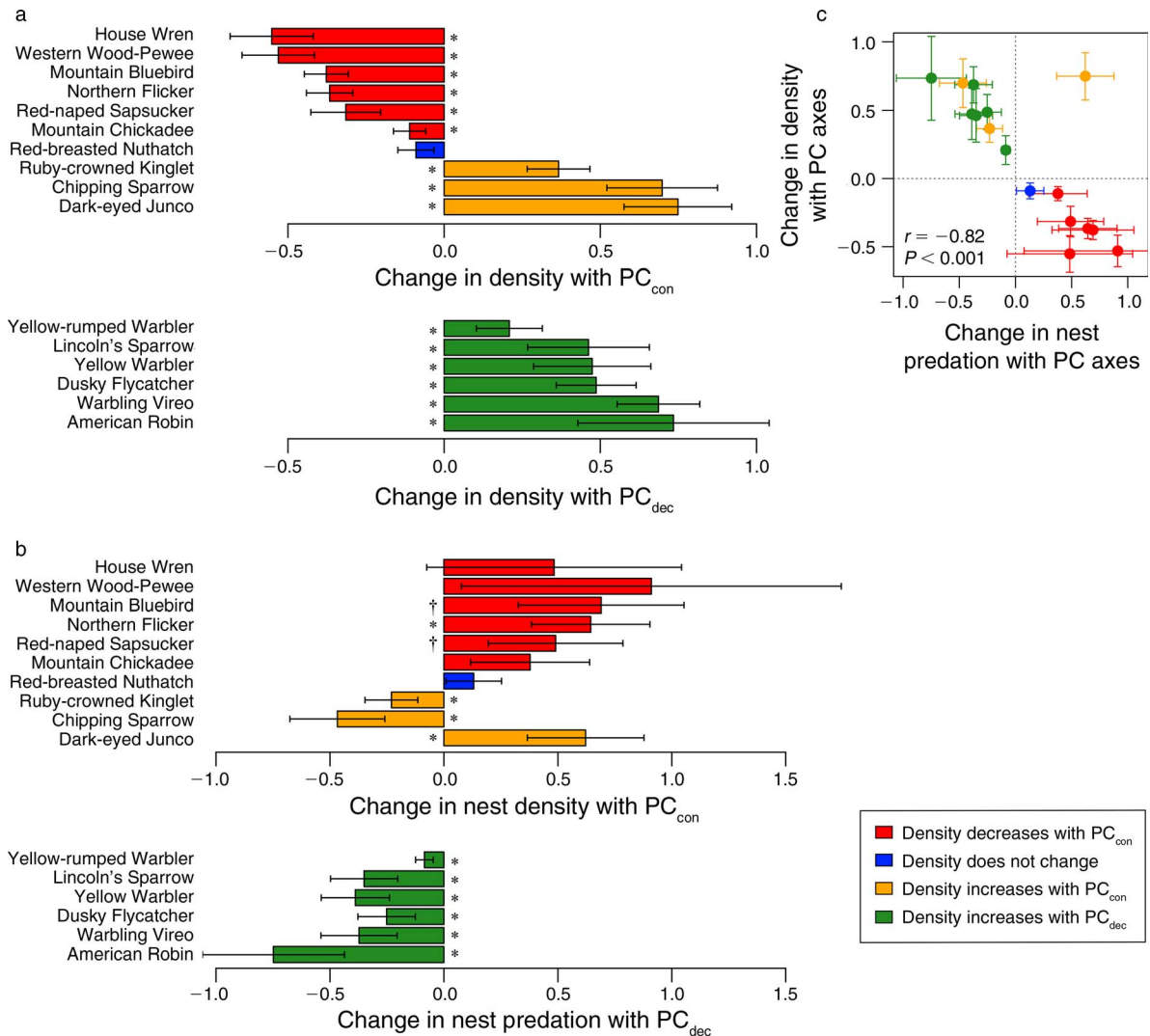
Fig. 3. Relative changes (standardized effect sizes ± SE) in (a) densities and (b) nest predation rates of bird species along two PC axes (conifer and deciduous vegetation) in western Montana, USA, with significance denoted as † $P < 0.10$; * $P < 0.05$. (c) The relationship between relative changes in nest predation (from panel b) and relative changes in density (from panel a) along PC axes (each point represents one species).

but nonsignificantly, for an additional three species (Mountain Bluebird, House Wren, and Western Wood-Pewee). Lack of statistical power might be responsible for the nonsignificance of these three relationships, given the relatively restricted distributions (Fig. 2a; see Appendix C) and generally low nest predation rates (Appendix F) for these species. Densities did not change with nest predation for the two remaining species (Dark-eyed Junco and Red-breasted Nuthatch) and, if anything, appeared to increase.

Landscape-scale experimental removal of conifers from forest stands reduced conifer vegetation (PC_{con}) and increased deciduous vegetation (PC_{dec}) in treatment stands relative to control stands as expected (Fig. 5a). Population densities for 11 bird species significantly changed following conifer removal (Fig. 5b, Appendix

H). Red-breasted Nuthatch density did not change along the vegetation gradient or following conifer removal, and we were unable to estimate a change in House Wren density with conifer removal because this species did not occur on treatment stands. Nest predator density substantially decreased with conifer removal, suggesting that the effect of conifer vegetation on nest predator density is greater than the effect of deciduous vegetation observed in earlier analyses (see Fig. 2). For the 15 bird species and combined nest predators in the conifer removal experiment, the relative change in each species' density following conifer removal was strongly predicted by the relative change in density along PC axes from observational analyses (Fig. 5c). The one exception to this pattern, again, was Dark-eyed Junco. Changes in nest predation following conifer removal (Fig. 5d; see
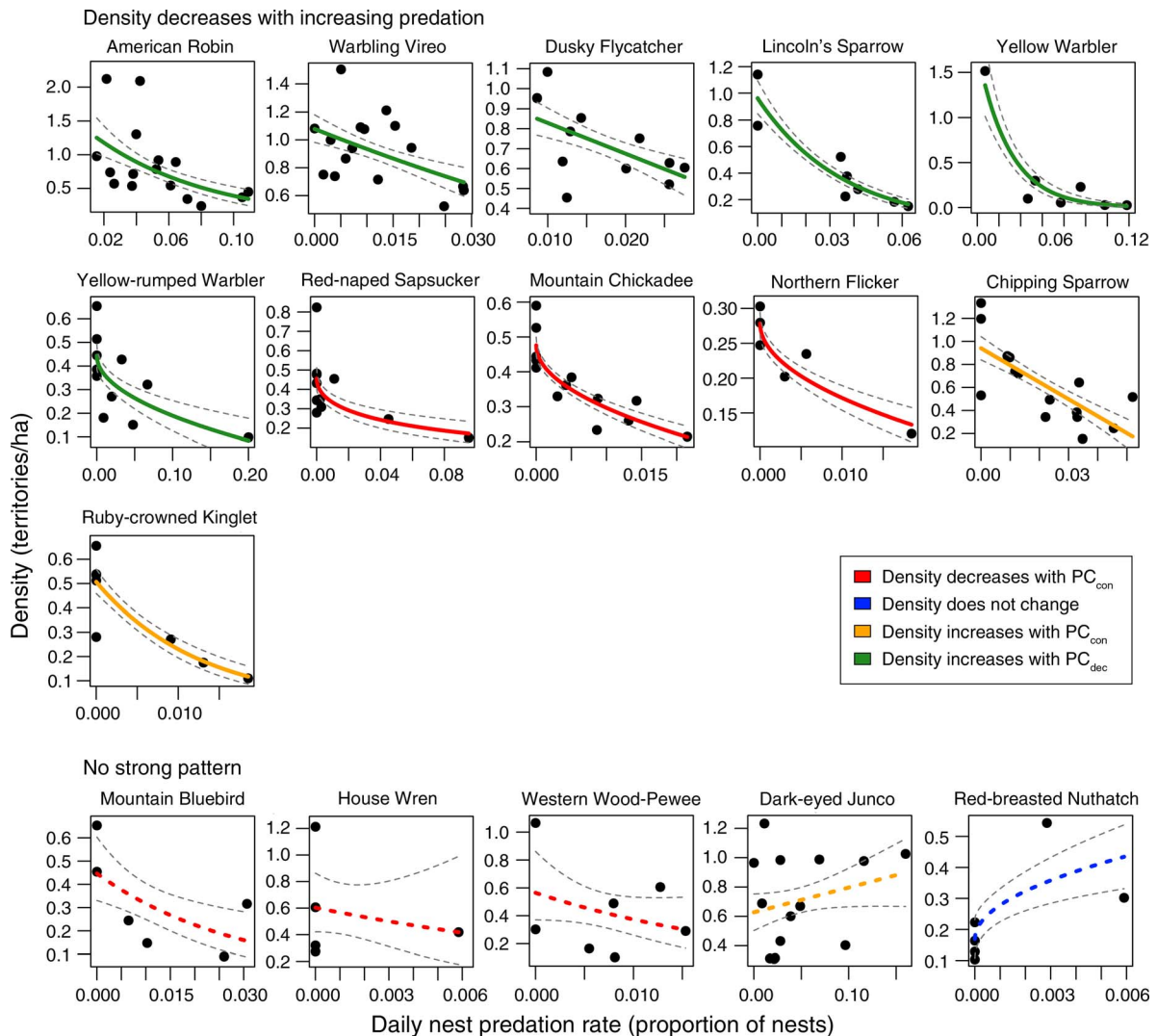
FIG. 4. Relationships between densities and nest predation rates (proportion of nests predated per day) for each bird species across forest stands in western Montana, USA. Solid curves indicate a significant relationship ($P < 0.05$), and dotted lines indicate weak responses. Dashed gray lines represent error ($\pm$SE) around relationships. Species are color-coded based on density responses along PC axes (see Fig. 3).

Appendix I) generally confirmed patterns observed along the vegetation gradient (Fig. 3b) for those species with sufficient sample sizes of nests for analysis. Sample sizes were too small either before or after conifer removal to estimate changes in nest predation for 10 bird species.

DISCUSSION

Our documentation of decreasing bird abundance with increasing predation rates along an existing natural gradient, and verification on an experimentally modified gradient, suggest that vegetation-mediated effects of predation can underlie animal distributions (Grinnell 1917, Hutchinson 1959, Leibold 1995, Soberón 2007). Other experimental studies have documented relationships between predation risk and habitat selection by

animals (Sih et al. 1985, Fontaine and Martin 2006, Forsman et al. 2013), but our study causally links changes in predation and abundances of multiple bird species to changes in vegetation. This result also provides a potential general explanation for bird species turnover along habitat gradients; turnover may generally reflect adaptive habitat preferences that are narrower than the full gradient. This hypothesis is parallel to theory that demographic costs should increase near the boundaries of geographic species distributions (Pulliam 2000), but it has received mixed support from empirical studies of range limits (Sexton et al. 2009). Here, we demonstrate increasing nest predation for most, but not all, species studied near their distributional limits as well as low predation risk near the center of distributions. Increasing predation rates near these
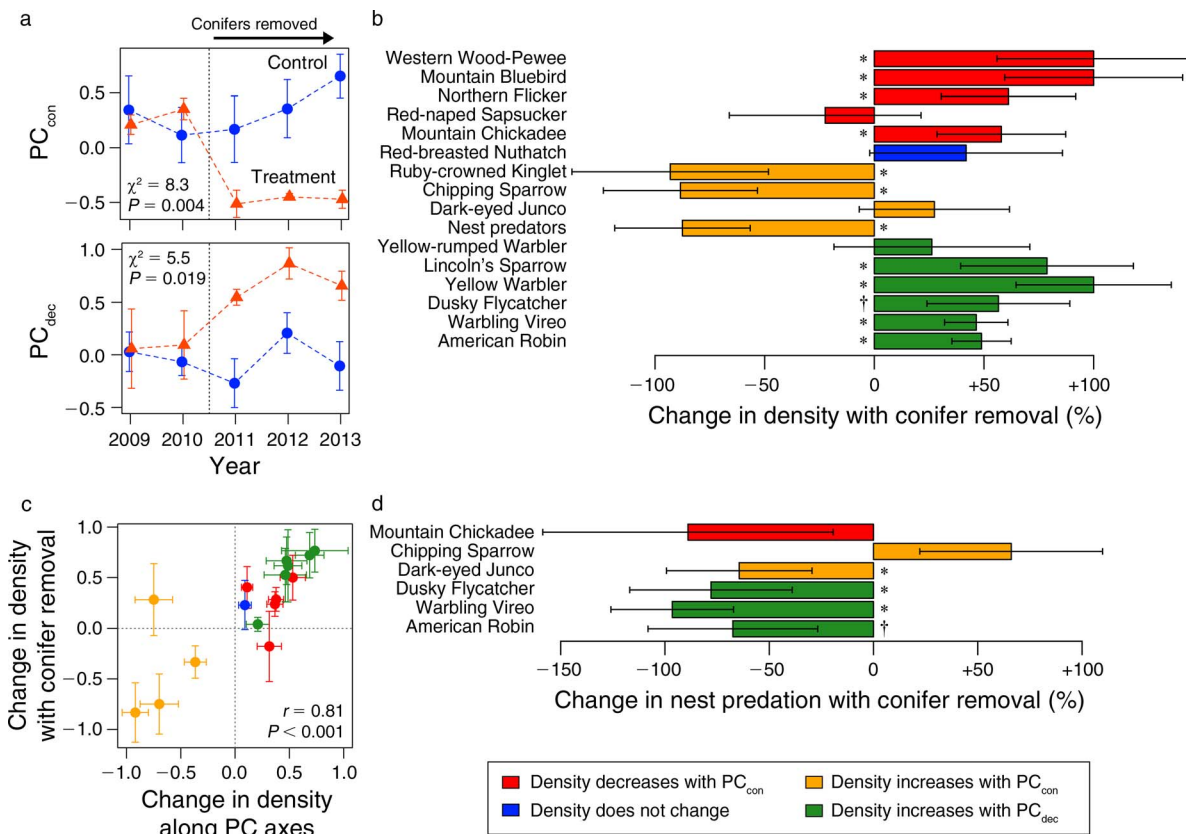
FIG. 5. Effects of experimental conifer removal (a) on PC axes (mean ± SE), and (b) bird densities as reflected by percentage change (±SE) in before–after comparisons. (c) Correlation between effect sizes on bird and nest predator densities from conifer removal and standardized effect sizes from observational analyses (one point represents one species; see Fig. 3a). (d) Effects of experimental conifer removal on nest predation rates for the few species with sufficient sample sizes for tests. For responses to conifer removal in (b) and (d), significance is indicated as: † $P < 0.10$; * $P < 0.05$. Bird species are color-coded based on density responses from observational analyses (see Fig. 3).

distributional limits probably mean decreasing fitness, given the strong influence of nest predation risk on avian population growth rates (Martin 1992, Lloyd et al. 2005, Zanette et al. 2011).

Our results provide strong observational and weaker experimental evidence that predation influences avian distributions. We experimentally manipulated vegetation structure and composition, and changes in nest predation appeared to be the proximate factor causing turnover. We did not, however, directly manipulate density or predation risk, and the reasons why birds occupied habitats with high predation rates may have been driven by other mechanisms, including competition associated with density-dependent habitat selection (Fretwell and Lucas 1969, Morris 1989). Yet some previous studies that directly manipulated predation risk independent of vegetation reported increased densities in low-risk treatments for multiple bird species (Duebbert and Kantrud 1974, Fontaine and Martin 2006). This result is not universal among predator reduction studies (reviewed in Côté and Sutherland 1997). Although nest predation explains a large portion of variation in

abundances of birds in our study, other biotic interactions such as adult survival or brood parasitism may explain the remaining variation in bird abundances.

Vulnerability to predation risk differed among bird species and, in some cases, appeared to be mediated by differences in nest-site vegetation preferences. Higher predation risk in conifers, which was observed for several bird species, probably was due to increased generalist predator density (i.e., Fig. 2). Higher predation rates with increased predator density have been observed previously (Johnson and Geupel 1996, Tewksbury et al. 1998, Dececco et al. 2000, Vucetich et al. 2011). However, predation rates decreased as generalist predator density increased for half of the bird species studied here. Increases in predator density were accompanied by increases in preferred nesting substrates that may ameliorate the impact of more predators (Martin and Maron 2012). For example, the predation risk of Chipping Sparrows decreased as both predators and coniferous vegetation increased, and Chipping Sparrows preferred conifers for nest sites. Greater availability of preferred nesting substrates may have better camou-

flaged nests or thwarted predators using a search image, thus offsetting the expected increase in predation risk from greater predator density (Martin 1993, 1998, Chalfoun and Martin 2009, Martin and Maron 2012). Therefore, although our study suggests that predation risk can increase with predator density for some species, variation among species in microhabitat use of the vegetation gradient determined differential vulnerabilities to predation risk despite substantial increases in predator density.

Predation risk appeared to underlie distributions for many species in our study. These results emphasize the importance of examining demographic consequences of habitat use when documenting species occurrence. Most current distributional models of species occurrence do not account for varying demography across distributions (Pulliam 2000, Soberón 2007). Unpublished data assuming constant juvenile and adult survival indicate that birds in our system occupied, albeit at lower densities, locations where habitat-specific population growth rates (λ) should not be self-sustaining (i.e., $\lambda <$ 1) due to excessive predation. These results suggest that habitat-specific sustainability or population growth ($\lambda \geq$ 1) might require a narrower subset of conditions than those over which a species occurs (Pulliam 2000). Although it is not surprising that subsets of populations occupy low-quality habitats (e.g., Lloyd et al. 2005), these considerations often are not taken into account when predicting impacts of habitat modifications or forecasting future distributions with climate-envelope models (e.g., Svenning and Skov 2004, Thomas et al. 2004). However, our results do suggest that abundance or density might be a reliable indicator of the demographic consequences of habitat use in natural systems for many species. We also caution that densities did not change with nest predation for all species in our study, and density is not always a reliable indicator of the demographic consequences of habitat use (reviewed in Chalfoun and Schmidt 2012).

We hypothesized that nonadaptive habitat use might be common for many species along vegetation gradients because broad differences in plant composition and structure provide animals with a multitude of habitat cues juxtaposed in space. This hypothesis was not supported by our results, as most bird species had preferences for low-risk habitat (Fretwell and Lucas 1969, Pulliam 2000). However, one species in particular, Dark-eyed Junco, did not decline in density despite significant increases in nest predation in both observational and experimental analyses. Although this pattern might indicate nonadaptive habitat use (Lloyd et al. 2005, Arlt and Pärt 2007, Betts et al. 2008), we did not measure all fitness components. It is possible that habitat use of Dark-eyed Juncos might appear adaptive once changes in adult and juvenile survival and brood parasitism rates are accounted for. Availability or quality of foraging sites might also increase in high-risk

habitats for this species, but these factors were not examined here.

Understanding how broad changes in vegetation affect demographic consequences for animals is essential because human influences such as land management and climate change are believed to have accelerated shifts in forest composition around the world (Latva-Karjanmaa et al. 2007, Anderegg et al. 2012). For example, gradual to severe aspen declines over the past 70 years have been noted in several regions across the northern hemisphere and are linked to conifer encroachment (Romme et al. 1995, Latva-Karjanmaa et al. 2007, Rehfeldt et al. 2009). Seven species (American Robin, Dark-eyed Junco, Mountain Chickadee, Northern Flicker, Western Wood-Pewee, Yellow Warbler, and Yellow-rumped Warbler) for which we document higher densities or lower nest predation in conifer-free aspen habitat are in regional decline (Sauer et al. 2012). These population trends associated with widespread aspen decline are consistent with the low nest predation and species' preference for deciduous habitat revealed by our study.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–I are available online: http://dx.doi.org/10.1890/14-1333.1.sm