Consequences of habitat change and resource selection specialization for population limitation in cavity-nesting birds

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Summary

1. Resource selection specialization may increase vulnerability of populations to environmental change. One environmental change that may negatively impact some populations is the broad decline of quaking aspen *Populus tremuloides*, a preferred nest tree of cavity-nesting organisms who are commonly limited by nest-site availability. However, the long-term consequences of this habitat change for cavity-nesting bird populations are poorly studied.

2. I counted densities of woody plants and eight cavity-nesting bird species over 29 years in 15 high-elevation riparian drainages in Arizona, USA. I also studied nest-tree use and specialization over time based on 4946 nests across species.

3. Aspen suffered a severe decline in availability over time, while understorey woody plants and canopy deciduous trees also declined. The decline of plants resulted from increased elk *Cervus canadensis* browsing linked to declining snowfall.

4. Woodpeckers exhibited very high specialization (>95% of nests) on aspen for nesting, and densities of all six species declined with aspen over time. Mountain chickadees *Poecile gambeli* and house wrens *Troglodytes aedon* exhibited increasingly less specialization on aspen. Chickadees strongly increased in density over time, despite a relatively high specialization on aspen. House wren densities declined moderately over time, but nest-box addition experiments demonstrated that nest-site availability was not limiting their population. House wren densities increased with understorey vegetation recovery in elk exclosures via increased generality of nest-site use, demonstrating that the decline in understorey vegetation on the broader landscape was the cause of their population decline.

5. Synthesis and applications. Management should target species that specialize in resource selection on a declining resource. Species with greater resource selection generalization can reduce population impacts of environmental change. Resource generalization can allow a species like the wren to take advantage of habitat refuges, such as those provided by the elk exclosures. Yet, resource generalization cannot offset the negative impacts of broad-scale declines in habitat quality on the landscape, as demonstrated by the general decline of wrens. Ultimately, aspen is an important habitat for biodiversity, and land management programmes that protect and aid recovery of aspen habitats may be critical.

Key-words: cavity-nesting, climate change, habitat change, habitat selection, nest-site limitation, *Paridae*, population limitation, *Troglodytes*, ungulate browsing, woodpeckers

Introduction

Identifying specific elements of habitats that directly influence populations is important to allow targeted management for conservation of populations and biodiversity (Martin 1992). The population impact of habitat change should vary among species depending on differential habitat requirements and habitat specialization; species with narrow, or specialized, habitat requirements are thought to be most vulnerable to population problems from habitat changes.

One habitat that appears to be broadly changing is the availability of quaking aspen *Populus tremuloides*. Area of aspen habitat has declined by as much as 75% in many places of the world, with climate and elk browsing being important contributors (Romme et al. 1995; White, Olmsted & Kay 1998; Anderegg et al. 2012; Brodie et al. 2012; Martin & Maron 2012), as well as forest management (Latva-Karjanmaa, Penttilä & Siitonen 2007). This decline is predicted to increase into the future (Rehfeldt, Ferguson & Crookston 2009) and is potentially critical because aspen forests are considered biodiversity hotspots (Tewsksbury, Hejl & Martin 1998; Hansen et al. 2000; Oaten & Larsen 2008).

One component of biodiversity that may be impacted by the loss of aspen is cavity-nesting organisms because aspen is often a preferred cavity-nesting tree (Harestad & Keisler 1989; Li & Martin 1991; Kalcounis & Brigham 1998). Cavity-nesting organisms are commonly, although not always, limited by availability of nesting cavities or substrates for creating cavities (e.g. von Haartman 1957; reviewed in Newton 1994). Given that (i) cavities or substrates commonly limit populations of cavity-nesting organisms, (ii) aspen often provides preferred cavity resources, and (iii) aspen is broadly declining, we might expect a strong negative consequence for populations of cavity-nesting species that prefer aspen for breeding sites. Moreover, the negative impact of declining aspen abundance might be expected to be greater for species that show greater specialization on aspen in their nest-site selection.

Cavity-nesting bird species in high-elevation snowmelt drainages in northern Arizona provide an interesting example and test for this theory. Aspen, along with understorey deciduous tree recruits, have been strongly declining in abundance in this system over the past quarter century due to increased browsing by elk as a result of reduced snowfall, which allows elk to remain overwinter on these high-elevation sites (Martin 2001; Martin & Maron 2012). Changes in the understorey may affect foraging habitat for understorey foragers (e.g. house wrens *Troglodytes aedon*) or habitat productivity, while loss of aspen might affect nest-site limits. Cavity-nesting birds in this system show a strong historical preference for nesting in aspen (Li & Martin 1991). Here, I test whether: (i) declining abundance of aspen was linked to population declines in cavity-nesting birds, (ii) declines in abundances of bird species were greater in species that showed stronger preferences for aspen, and (iii) environmental change other than nest trees limited populations. I report changes in aspen availability, nest-tree use, vegetation density and associated population sizes of eight cavity-nesting bird species across 29 study years. I also report experimental tests of the environmental limits of population sizes through two experiments: addition of nest boxes to test nest-site (cavity) limitation for one species (house wrens) and elk exclusion to allow understorey habitat recovery and its possible effects on populations of all eight species.

**Materials and methods**

**STUDY SITES AND SPECIES**

This study was conducted in 15 high-elevation (c. 2350 m above sea level) snow-melt drainages in Coconino National Forest of northern Arizona, and each drainage represented one study plot. The vegetation in these shallow drainages is characterized by a mix of deciduous and coniferous tree species (Martin 2001), including canyon maple *Acer grandidentatum*, quaking aspen *P. tremuloides*, New Mexican locust *Robinia neomexicana*, Gambel's oak *Quercus gambelii*, white fir *Abies concolor* and Douglas fir *Pseudotsuga menziesii*. These drainages are narrow (100–150 m wide) and contrast with the surrounding upland and drier forest dominated by ponderosa pine *Pinus ponderosa*.

Eight cavity-nesting bird species were relatively common on these sites. Six species were woodpeckers which usually excavate their own holes, although reuse of old holes varies among species (Martin 1993): red-shafted flicker *Colaptes auratus cafer*, red-naped sapsucker *Sphyrapicus nuchalis*, Williamson's sapsucker *Sphyrapicus thyroideus*, hairy woodpecker *Picoides villosus*, downy woodpecker *Picoides pubescens* and acorn woodpecker *Melanerpes formicivorus*. House wrens and mountain chickadees *Poecile gambeli* depend on existing holes created by woodpeckers or natural holes.

**BIRD POPULATION SIZES, NEST SEARCHING AND MONITORING**

I counted numbers of singing, calling or drumming birds throughout the length of these narrow habitats using the plot-mapping technique (Christman 1984; Martin 2007). Songbirds were censused from 1985, and woodpeckers were added to the survey in 1987. The same nine plots were censused from mid-May to mid-June each year from 1985 to 2013 for long-term bird population trends, and four more plots were added for an elk enclosure experiment from 2004 to 2013 (see Fig. S1, Supporting information). Censuses were not conducted in 1990 due to a lapse in funding. Censuses were checked against territory maps made by each nest searcher who visited the plots every other day (Martin 2001), and if I missed a breeding pair detected for the territory maps, I added that pair to my count, but this was rare. Most censused plots were about 10 ha in size, but two were 6 ha, and one was 4 ha. Bird abundance was standardized to numbers of pairs per 10 ha across all plots.

Nests were found using parental behaviour, vocal cues such as nest-leaving calls, and/or wood chips on the ground from excavation (Li & Martin 1991; Martin & Geupel 1993). Nests were found and monitored on 15 plots (Fig. S1, Supporting information) every 3–4 days until offspring fledged or were depredated. The tree species was identified for each nest.

**VEGETATION SAMPLING**

Densities of dominant woody plant species were measured in the understorey at stratified random sites in a 5-m radius on each
plot from 1987 to 2013, and larger trees were measured in 11.3-m-radius plots from 1995 to 2013 (Martin, 2001, 2007). A transect of five points spaced equidistant up the side of the drainage was established every 50 m on alternating sides for the length of the drainage, yielding 30–60 sampling points per plot (Martin, 2001, 2007). Vegetation sampling was not performed in 1997 because fire danger closed the forest. Sampling points were not permanently marked (except on exclosures and their control pairs – see later) causing differing points to be sampled every year. Understorey woody stems ≥20 cm tall were counted within the 5-m-radius plots by woody species (Martin, 2001, 2007). Canopy and subcanopy trees (>15 cm d.b.h.) were counted in the 11.3-m-radius plots by tree species. Snags with d.b.h. ≥ 20 cm were also counted in the 11.3-m-radius plots by species.

Canopy aspen have been dying and falling at a steady rate throughout this study with no recruitment for canopy replacement (Martin, 2007). I implemented sampling in 1995 to document the decline in aspen. We permanently tagged all aspen (dead or alive) and snags with d.b.h. ≥ 20 cm encountered within 25 m of the centre in each of the 15 drainages (878 total aspens; 897 other snags). Each year until 2011, field assistants resampled all marked trees to determine whether they remained standing or had fallen.

EXPERIMENTS

Tests of changing habitat structure due to elk browsing were conducted using exclosures. In autumn 2004, elk exclosures were erected around one drainage (10 ha) in each of three canyons (roughly 2–5 km apart, Fig. S1, Supporting information) and paired with adjacent control drainages (Martin & Maron, 2012). The exclosures yielded extensive recovery of the understorey vegetation (Martin & Maron, 2012) to allow a test of understorey habitat quality on cavity-nesting populations.

Nest boxes were erected on four unfenced plots in 2012 prior to nesting to examine whether nest sites limited house wren populations. Nest boxes were erected on a typical nest tree at 50-m intervals along the length of plot and near the bottom of each of the four drainages. House wren territories typically occupy about 100 m of the length of drainages (T. E. Martin, personal observation) such that the box density yielded two or three boxes per potential territory.

STATISTICAL ANALYSES

Habitat change

I first tested differences in relative rates of loss of aspen among three life classes (alive, partly alive, dead) characterized at the time that trees were tagged in 1995. I tested for differences in the relative rates of loss based on testing the interaction between life class and year using a general linear model. I used spss (ver. 22; IBM, Armonk, NY, USA) for all analyses, except when specified differently.

Habitat change was relatively consistent over time (see Martin, 2007; Martin & Maron, 2012). As a result, I tested differences between the two time endpoints (1995 and 2013) sampled with large radius plots (11.3 m radius) to characterize general habitat changes. I first tested changes in aspen and conifer (fire and pine species summed) snags between these two time periods using a general linear model. I next used multivariate general linear models to examine the change in density of tree species in the canopy (11.3-m-radius plots) and understory (5-m-radius plots) between the two time periods. I pooled the two pine species as total pine and pooled Douglas fir and white fir as total fir. Pillai’s Trace was used to test for significance of the multivariate test because it is the most robust to model assumptions (Quinn & Kcough, 2002).

Bird densities

Changes in densities (breeding pairs 10 ha−1) of the eight species were examined across years using generalized linear models of actual counts and plot size as a covariate.

I used a linear mixed model based on the Lme4 package in R v3.0.3 for Windows (R Development Core Team, Vienna, Austria) for a Before-After-Control-Impact (BACI) design to test for differences in bird densities between elk exclosures (n = 3) and control (n = 10) plots while accounting for repeated measures for woodpeckers and mountain chickadees. For house wrens, four of the 10 control plots served as box addition plots in the later years, so I used the other six control plots for the elk exclosure test across all years for wrens. Treatment (exclosure vs. control) and a before–after factor (2004 = before; 2005–2013 = after) served as fixed effects, year and plots as random factors (repeated measures). I used the same linear mixed model BACI approach to analyse the nest-box experiment, comparing house wren densities in nest-box addition (n = 4) to control (n = 6) plots in the 2 years before and the 2 years after nest boxes were added.

I examined potential habitat and competitor correlates of bird densities using generalized linear modes (GLMs). House wrens and mountain chickadees used natural cavities provided by cracks in maple as the primary alternative to aspen. I used GLMs to examine the trend in use of maple across years and relative to conspecific density in control and exclosure plots.

Results

TEMPORAL CHANGE IN ASPEN AND SNAG AVAILABILITY

The direct count of snags (standing dead trees) and aspen in 1995 yielded 1775 standing individuals, with nearly half (878 trees) being aspen, and fir snags represented the other most abundant category of potential nest trees (Fig. 1a). Of the aspen, about half (51.1%) were alive in 1995 and the rest divided between partly alive (22.5%), some dead branches) and dead trees (26.4%) (Fig. 1a). Aspen trees that were alive in 1995 fell at the slowest rate over time (h = −2.26 ± 0.43), with partly alive trees falling at a slightly faster rate (h = −2.93 ± 0.43), and trees that were dead in 1995 falling at the fastest rate (h = −4.39 ± 0.43) and leaving only 10.5% still standing by 2011 (Fig. 1b; GLM with no intercept; life class × year: $F_{2,45} = 12.7, P < 0.001$; life class: $F_{3,45} = 12.00, P < 0.001$; year: $F_{1,45} = 327.8, P < 0.001$). Out of all 878 aspen that were tagged in 1995, only 47.6% remained standing by 2011 (Fig. 1b). Of these remaining standing trees, 8.3% were still alive, 46.6% were partly alive, and 45.1% were dead. In other words, only 3.6% of
The densities of canopy and subcanopy tree species changed from 1995 to 2013 (Pillai’s Trace = 0.22, $F_{6,717} = 33.6, P < 0.001$), but changes were restricted to decreases in densities of aspen and maple, and increases in canopy locust and fir from 1995 to 2013 (Fig. 2a). The decrease in aspen was faster than maple, such that aspen made up 19.1% of the density of these two species in 1995, but made up only 2.8% of the density of these two canopy trees in 2013 (Fig. 2a).

The densities of woody recruits of canopy tree species declined dramatically from 1995 to 2013 (Pillai’s Trace = 0.38, $F_{6,717} = 57.7, P < 0.001$), with all species except pine decreasing in the understory from 1995 to 2013 (Fig. 2b). Overall, the density of deciduous woody stems declined dramatically in the understory due to elk browsing (Fig. 2b; also Martin & Maron 2012).

NEST-TREE USE

All woodpeckers used aspen for the majority of their nests across all years. Woodpeckers together used aspen for 96.3% of nests ($n = 2246$ nests) over all years, while mountain chickadees used them for 79.5% of nests overall ($n = 1136$ nests), and house wrens used them for 66.4% of nests overall ($n = 1564$ nests). Yet, proportional use of aspen declined over time for all bird species (Fig. 3) as
aspen declined (i.e. Fig. 1b). The three types of bird species differed in the rate of decline in use of aspen (GLM: bird species × year: $F_{2,72} = 23.8, P < 0.001$; bird species: $F_{2,72} = 23.3, P < 0.001$; year: $F_{1,72} = 91.2, P < 0.001$). House wrens showed the steepest decreases in use of aspen with time ($b = -1.63 \pm 0.163; r = -0.90, P < 0.001$). Mountain chickadees showed intermediate decreases over time ($b = -0.79 \pm 0.205; r = -0.62, P = 0.001$), and woodpeckers showed a very small decline ($b = -0.13 \pm 0.045; r = -0.51, P = 0.008$) in the use of aspen (Fig. 3).

Cavity nesters used alive and partly alive aspen as well as aspen snags for nests (Fig. 4). House wrens and mountain chickadees placed nearly half (46% and 44%, respectively) of the aspen nests in alive or partly alive trees (Fig. 4a,b). Nest holes in these trees were made by woodpeckers, and woodpecker species differed in their use of alive vs. dead aspen (Fig. 4c). Red-naped sapsucker and hairy woodpecker are strong excavators (Martin 1993), and they excavated holes in alive and partly alive aspen most frequently among the woodpecker species (Fig. 4c). Their congeners (Williamson’s sapsucker and downy woodpecker, respectively) are weaker excavators (Martin 1993) and depended extensively on dead aspen for nests (Fig. 4c). Although northern flickers show some use of alive and partly alive aspen (Fig. 4c), they do not excavate new holes in these life classes. Flickers are weak excavators that commonly reuse existing holes (nearly 60%, Martin 1993) and by enlarging holes originally created by red-naped sapsuckers or hairy woodpeckers in these life classes of aspen. They excavated new holes only in dead aspen. The same was true of acorn woodpeckers.

House wrens and mountain chickadees used holes created by woodpeckers in aspen, but also used maple as their secondary preference (Fig. 4a,b). Maple was the dominant canopy tree in this system, although it has been superseded by the combined abundance of Douglas fir and white fir in recent years (Fig. 2a). Nonetheless, maple remains abundant in the canopy (Fig. 2a) and it develops cracks and holes naturally while alive that are used by both house wrens and mountain chickadees during all life stages (Fig. 4a,b).

In all years, all cavity-nesting species chose aspen out of proportion to its availability. Woodpeckers do not excavate live trees of any tree species other than aspen in

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this system and instead depend on dead trees of other species. Conifer snags were more abundant than aspen snags (Fig. 1c), but conifer snags were used for a trivial percentage (<1%) of woodpecker nests. House wrens and mountain chickadees used aspen for more than half of their nests (Fig. 3) even though canopy maple, their secondary nest site (Fig. 4a,b), was substantially more abundant than aspen (Fig. 2a). Thus, aspen was clearly the preferred nest tree by all species.

BIRD POPULATION TRENDS

Each of the six woodpecker species showed significant population declines over the 27-year period of censuses (Fig. 5a). Total woodpecker density across all species exhibited a decline over time that was quite steep (Fig. 5b). Indeed, the low density in 2010 was only 37% of the peak (1992) recorded over 27 years (Fig. 5b). The decline in density of each woodpecker species was significantly correlated with the (log-transformed) decline in aspen density over the 18 years in which we sampled large radius vegetation plots ($r = 0.57–0.87$, $P = 0.013$ to <0.001 for the six species). The decline in total density of woodpeckers was strongly correlated with the log-transformed decline in aspen, indicating a faster rate of decline in woodpeckers as aspen became increasingly uncommon (Fig. 5c). In contrast, mountain chickadees increased strongly over the nearly three decades of censuses (Fig. 6a). House wren density declined moderately over the 29-year period of censuses, although the decline was not constant (Fig. 6b).

Possible correlates of annual changes in densities of mountain chickadees and house wrens were examined. Mountain chickadees foraged primarily in the canopy on the two fir species (T. E. Martin, personal observation),
as also observed in other mixed habitat (Franzreb 1978). I included densities of firs as foraging sites, house wren densities as competitors for holes, and log-transformed aspen density for nest-hole availability in a GLM. Aspen density alone was the best model, with some support (AAIC = 1.6) for an additional effect of fir density (Table S1, Supporting information). Yet, the relationship with aspen opposed expectations based on Aspen limiting nest-hole availability; chickadee density increased as aspen became more limited in availability ($b = -1.64 \pm 0.324$; $P < 0.001$). Woodpecker density, as possible hole creators, was not included because chickadees increased as woodpecker densities declined, which also was opposite to expectations based on nest-hole limitation. The increase in chickadees with declining aspen may reflect the decreasing density of deciduous trees in the canopy relative to the firs on which they forage, as possibly suggested by the second best model (Table S1, Supporting information). Indeed, chickadee density was strongly correlated with the log-transformed ratio of fir to aspen density across years (Fig. 7a), and this relationship provided the strongest model (AIC$_{c} = 24.924$; see Table S1, Supporting information).

For the decline in house wrens, I included total woodpecker density as nest-hole creators, density of mountain chickadees because they can compete for holes, and total density of deciduous woody stems in the understory because it influences foraging habitat. Only understory woody stem density was supported for explaining the decline in house wren density (Table S2, Supporting information; Fig. 7b). House wren density was not correlated with the decline in aspen over the 18 years that aspen density was measured ($r = 0.04, P = 0.9$).

### RESPONSES OF VEGETATION AND CAVITY-NESTING BIRDS TO ELK EXCLUSION EXPERIMENTS

Understorey vegetation recovered strongly in elk exclosures (Martin & Maron 2012). By 2013, densities of understory woody stems differed strongly between exclosure and control drainages ($n = 150$ plots × two treatments = 300 plots of 5 m radius) based on a multivariate GLM ( Pillai’s Trace = 0.217, $F_{6.293} = 13.6, P < 0.001$) that indicated that aspen, maple, locust and oak were all more abundant in exclosures (all $P < 0.001$), while small firs ($P = 0.54$) and pines ($P = 0.12$) did not differ between treatments. In contrast, none of the canopy and subcanopy trees (aspen, maple, locust, oak, fir and pine) differed in densities between the exclosure and control drainages ($n = 300$ plots of 11.3 m radius) in 2013 ( Pillai’s Trace = 0.029, $F_{6.293} = 1.4, P = 0.20$).

Elk exclosures did not affect densities of woodpeckers (Fig. 8a; treatment × Before–After: $t_{107} = 0.45, P = 0.58$; treatment: $t_{39} = 0.25, P = 0.80$; Before–After: $t_{103} = -1.18, P = 0.26$) or mountain chickadees (Fig. 8b; treatment × Before–After: $t_{107} = 1.12, P = 0.27$; treatment: $t_{103} = -0.52, P = 0.60$; Before–After: $t_{112} = 2.01, P = 0.047$). House wrens exhibited a strong density response to understory vegetation recovery in elk exclosures (Fig. 8c; treatment × Before–After: $t_{49.9} = 4.89, P < 0.001$; treatment: $t_{49.2} = -0.70, P = 0.49$; Before–After: $t_{10.4} = -0.54, P = 0.60$).

### DENSITY RESPONSES OF HOUSE WRENS TO EXPERIMENTAL INCREASES IN NEST HOLES

Nest boxes were added at a density of 13 boxes 10 ha$^{-1}$ for the last 2 years of study, when aspen was least available (Figs 1b,c and 2a), to test whether nest sites limited populations. Thirty-seven percentage of house wren pairs nested in boxes, which represented 27% of available boxes, on the four box-addition plots. House wrens also used most of the available nest boxes in nearby meadow habitat where natural cavities are largely unavailable, although this habitat type is not included in this study. Both sets of observations demonstrate that house wrens readily use the nest boxes. Densities of house wrens, however, did not respond to the nest-box additions (Fig. 8d; treatment × Before–After: $t_{26.0} = 0.88, P = 0.39$; treatment: $t_{10.1} = -1.67, P = 0.13$; Before–After: $t_{12.3} = -0.16, P = 0.89$). Only 3–4 house wrens nested per box-addition plot (Fig. 8d), leaving 9–10 boxes and large areas unoccupied per plot. These results indicate that availability of nest holes was not limiting house wren densities.

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Fig. 7. Population correlates of (a) mountain chickadees with the ratio of canopy firs to aspen tree densities and (b) house wrens with understory deciduous woody stem densities. Each point is 1 year.
House wrens decreased their use of aspen for nesting across years (Fig. 3), as aspen density declined over years (Figs 1b,c and 2a). The primary alternative nest site was natural cavities offered by cracks in maple (Fig. 4a). GLM results (Table S3, Supporting information) indicated that house wrens increased their proportional use of maple across years (Fig. 9a) and with increased house wren density (Fig. 9b) on control plots.

House wrens also increased their use of maple for nesting across years on exclosure plots (Fig. 9a). However, use of maple in exclosures substantially exceeded use of maple on control plots in the later years (Fig. 9a). The much greater use of maple in exclosures was correlated with the increased density (i.e. Fig. 8c) of house wrens in exclosures (Fig. 9c), while accounting for year effects ($b = 3.24 \pm 0.940$) that reflect the decline in aspen availability (i.e. Fig. 1b, see above).

Mountain chickadees also decreased their use of aspen across years, although to a lesser extent than house wrens (Fig. 3). Like house wrens, maple was the primary alternative nest site (Fig. 4b). GLM analyses that included year, chickadee density, house wren density and total woodpecker density (Table S4, Supporting information) yielded a best-fit model that only included year ($b = 0.786 \pm 0.197$, $P < 0.001$) for explaining use of trees other than aspen for nesting (as in Fig. 3).

**Discussion**

Aspen availability has declined dramatically in this system across the last three decades of study (Figs 1 and 2), as seen across North America and other parts of the world associated with climate change and climate-induced elk browsing, among other causes (Romme et al. 1995; White, Olmsted & Kay 1998; Latva-Karjanmaa, Penttilä & Siitonen 2007; Rehfeldt, Ferguson & Crookston 2009; Brodie et al. 2012; Martin & Maron 2012). The loss of aspen in this mixed forest system has had very different impacts on populations of cavity-nesting bird species.

The most negative impact was on woodpeckers (Fig. 5). All six woodpecker species showed very high specialization on aspen for nesting (>95% of nests, Fig. 3), and all showed significant population declines over time, correlated with the decline in aspen availability (Fig. 5). Total woodpecker density declined to nearly one-third of the peak density. The population decline became steeper relative to aspen availability as aspen availability became increasingly limited (Fig. 5c). Other aspects of the habitat, such as understory deciduous woody stem densities, also declined over time (Fig. 2, Martin & Maron 2012). Yet, this habitat change clearly did not contribute to the woodpecker decline given that recovery of the understory
in elk exclosures, when canopy trees like aspen did not change, had no effect on woodpecker densities (Fig. 8). Thus, loss of aspen in these high-elevation riparian systems that are embedded in a sea of pine upland has serious negative consequences for diverse woodpecker populations that exhibit high specialization on aspen for nest sites.

Mountain chickadees, on the other hand, increased strongly over time (Fig. 6a), despite their preferred nest tree (aspen) declining in availability over this time period (Figs 1 and 2). This increase may reflect an increase in the absolute (Fig. 2a) and relative (Fig. 7a) density of firs, their preferred foraging substrate. Reduced competition for nest holes because of declining house wren densities (i.e. Fig. 6b) might also have contributed to the population increase. Chickadee and wren densities were negatively correlated \( (r = -0.50, P = 0.007) \) across years. Yet, both species were sometimes observed nesting in different holes in the same aspen tree suggesting that competition for holes between them might be weak. The increase in chickadee densities over time demonstrated that nest-hole availability was not limiting their populations, likely facilitated by their decreased use of aspen (Fig. 3) and increased use of maple and other nest sites (Fig. 4).

The increased use of maple nest sites by house wrens across years (Fig. 9a) as aspen declined (Figs 1 and 2) and in years of higher population density (Fig. 9b) together indicated that aspen was increasingly limited in availability for nesting over time. This increased use of maple trees for nesting was not a result of increasing numbers of maple trees, as maple also declined over time (Fig. 2). Instead, wrens were clearly general in their nest-site use (Johnson 1998) and increased their use of maple as aspen became more limited in availability. Ultimately, plasticity in nest-site selection by house wrens prevented declining aspen from limiting populations, as demonstrated by the lack of population responses to nest-box additions (Fig. 8d).

Nest-site plasticity also allowed house wrens to take advantage of recovered habitat conditions created by elk exclusion. Populations strongly increased on exclosure plots (Fig. 8c) despite no increase in cavity availability; only young plants, which do not provide cavities, increased on exclosures (Figs 1d and 2; Martin & Maron 1998).
species can differ in their ability to discern and respond to portion of the population in high-quality habitat. Yet, impacts of environmental change by increasing the pro-

Such resource selectivity can reduce broader population quality habitat represented by unfenced plots (Fig. 8c). In short, their nest-site plasticity allowed increased population densities to take advantage of the presumably higher quality habitat in elk exclosures despite few aspen nest sites (Fig. 3), further verifying that resource selection generality prevented cavity availability from limiting populations.

These results demonstrate two points of importance for land managers. First, it is important to experimentally test environmental causes of population limits. It would have been easy to conclude that declining aspen was the cause of house wren declines, given that aspen was their preferred nest site and nest-site availability commonly limits populations of cavity-nesting organisms (see Newton 1994). As a result, the coarsely correlated decline of wrens with understorey foraging habitat (Fig. 7b) might have been overlooked. Yet, the elk exclosure and nest-box addition experiments demonstrated that understorey foraging habitat was the clear limit on populations. Nest-site selection plasticity ameliorated one potential population constraint arising from habitat change (i.e. reduced aspen cavities), but the population was still limited by broader habitat degradation associated with climate change and elk browsing. Thus, careful experiments that ascertain the environmental factors that limit populations can strongly benefit targeted management actions.

Secondly, the degree of resource selection specialization and spatial scale of habitat selection had important, but not universal, consequences for population responses to climate-induced habitat change. Woodpeckers in this system, with their very high specialization on aspen, showed very strong population declines with the decline in their preferred nest tree. Yet, specialization was not a perfect predictor of population trends. Mountain chickadees had intermediate, but still relatively high, specialization on aspen for nesting and their populations still increased despite the decrease in aspen. Mountain chickadees and house wrens, may be better able to withstand environmental changes. Yet, even strong resource use generality may be insufficient to offset the population impacts of large environmental degradation, such as the broad habitat change seen here, if suitable alternative habitat is not available. Understanding the mechanisms of population limitations and adaptability of species to environmental change needs to be a critical focus of future studies. More importantly, land management programmes that target protection and restoration of aspen habitats are critical given their importance to cavity-nesting organisms and biodiversity.

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Data accessibility

Data are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.zr25v (Martin 2014).