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A decade of emerald ash borer effects on regional woodpecker and nuthatch populations

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Abstract The emerald ash borer (EAB) *Agrilus planipennis*, first detected in 2002 in the vicinity of Detroit, Michigan, USA, has spread throughout much of eastern and midwestern North America as of 2016, resulting in widespread mortality of ash trees in the genus *Fraxinus*. We investigated the effects of this newly available, exotic food source on populations of six species of largely resident insectivorous birds, including five species of woodpeckers and white-breasted nuthatch (*Sitta canadensis*), using North American Breeding Bird Survey data for breeding season estimates and Audubon Christmas Bird Counts for winter season estimates. We found evidence for relatively modest and variable effects of EAB invasion on the populations of these birds during the breeding season, but highly significant numerical increases during the winter that in several cases appeared to be increasing as the EAB invasion has progressed. Our results confirm that the EAB invasion is resulting in

increased populations of several insectivorous birds, primarily during the winter. They also suggest that the numerical response of woodpeckers to EAB may be such that avian predation, which represents a significant, and possibly the largest, mortality factor affecting some EAB populations, may continue to increase and help control the EAB epidemic as the invasion continues.

Keywords *Agrilus planipennis* · Emerald ash borer · Forest pests · Invasive species

Introduction

The North American invasion of the emerald ash borer (EAB) *Agrilus planipennis*, continues to provide a particularly severe and well-documented example of an invasive forest pest with major ecological effects (Herns and McCullough 2014). First detected in the Detroit, Michigan area in 2002, this phloem-feeding Asian beetle had, by 2015, spread as far east as New Hampshire, as far west as Colorado, and as far south as Georgia (Fig. 1). With no effective means of control currently known, EAB threatens nearly all species of ash (genus *Fraxinus*) in North America and has already killed vast numbers of trees—an estimated 54 million alone through 2007 in Michigan, Ohio, and Indiana (Smith et al. 2009) causing billions of dollars in damage (Kovacs et al. 2010; Jennings et al. 2013). In regions where EAB has been established the

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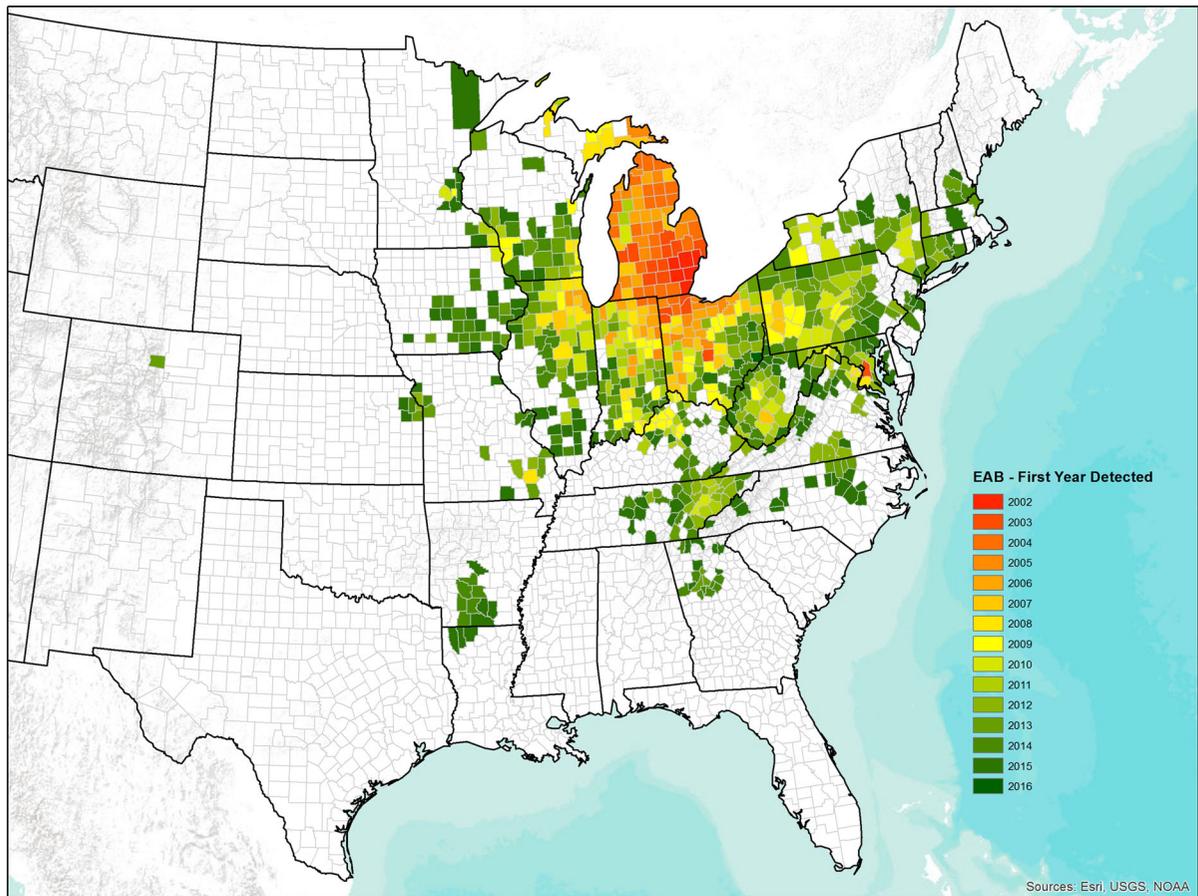


Fig. 1 Spread of emerald ash borers in the United States, 2002–2016

longest, it has eliminated the majority of host ash (Morin et al. 2017), potentially impacting forest communities in a variety of ways including nutrient cycling, succession, species composition, and facilitation of light-limited invasive plants (Gandhi and Herms 2010; Gandhi et al. 2014; Herms and McCullough 2014).

Natural enemies of EAB include several parasitoids (Cappaert and McCullough 2009; Bauer et al. 2015) and woodpeckers (family Picidae), the latter of which typically prey on late instars and prepupae in winter and early spring (Herms and McCullough 2014). Although the relative importance of these two sources of mortality vary considerably, woodpeckers have been reported to account for between 25 and 40% of EAB mortality in Asia (Wang et al. 2010; Duan et al. 2012) and has been identified as a major source of EAB mortality in several North American studies

(Cappaert et al. 2005b; Lindell et al. 2008; Duan et al. 2010; Jennings et al. 2013).

The ecological effects of an invasive organism is not limited to its negative effects on its hosts and/or prey, however. In the case of EAB, the tens of thousands of individuals that may develop from a single tree potentially provide a ‘trophic subsidy’ that may positively influence reproduction and survivorship of species that prey on them (Branch and Steffani 2004; Rodriguez 2006; McCullough and Siegert 2007). For EAB, this includes the woodpeckers and other bark-foraging species that depend on such insects for their food and that are potentially attracted to the large pulse of resources provided by an EAB infestation. In addition, woodpeckers are cavity-nesters, and thus the large number of dead trees left in the wake of an EAB invasion may facilitate nest building and further increase populations.

In a previous study, we investigated effects of EAB invasion on the abundance of four species of resident, insectivorous birds, including the downy woodpecker (*Picoides pubescens*), hairy woodpecker (*P. villosus*), and red-bellied woodpecker (*Melanerpes carolinus*), three species known to forage on ash trees infested by EAB (Lindell et al. 2008), and white-breasted nuthatch (*Sitta canadensis*), a common bark-gleaning species (Koenig et al. 2013). Using data from Project FeederWatch, a citizen science program based on observations of birds at backyard feeders during the winter (Bonter and Hochachka 2009), this earlier study was able to detect significant numerical increases in all four of the species, with two species immediately increasing and two increasing after a 2–3 year delay (Koenig et al. 2013).

With EAB having spread considerably farther and its ecological effects having several more years to play out, here we revisit the question of how EAB are affecting regional populations of woodpeckers and nuthatches. Instead of Project FeederWatch, which provides data only during the winter, we used two well-established sources of citizen science data to examine populations during both the breeding season (the North American Breeding Bird Survey; Bystrack 1981) and the winter (the Audubon Christmas Bird Count; Raynor 1975; Bock and Root 1981). Using these databases, we examined whether EAB have had significant effects on the populations of the four species examined earlier and two additional species, the pileated woodpecker (*Dryocopus pileatus*) and the red-headed woodpecker (*Melanerpes erythrocephalus*). All of these species are permanent residents, with the exception of the red-headed woodpecker, which is a partial seasonal migrant (Frei et al. 2015), but still resides primarily within the continental U.S. The continued persistence and spread of EAB populations within North America allows us to more fully investigate both the apparent numerical increases in avian abundance as well as how bird populations have apparently responded to EAB up to a decade since colonization.

Methods

Population data for downy woodpeckers, hairy woodpeckers, red-bellied woodpeckers, red-headed woodpeckers, pileated woodpeckers, and white-breasted

nuthatches were obtained from the North American Breeding Bird Surveys (BBS) and Audubon Christmas Bird Counts (CBC) within the current known range of EAB populations (Fig. 1). The BBS data consist of the sum counts of birds detected during 3-min censuses at series of 50 stops 0.8 km apart along road transects conducted during the main breeding season (usually May or June; Bystrack 1981), and were available from 1998 (4 years prior to the earliest records of EAB in North America) through 2015. The CBC data, representing population estimates during the nonbreeding season, consist of 1-day intensive surveys counted by a variable number of observers within a 2-week period around Christmas within a specific 24-km diameter circle. We used data for the years from 1998 through 2014.

As an index of relative abundance we \ln -transformed ($\ln[n + 1]$) the number of birds counted (BBS) and the number of birds per party hour (CBC), a procedure that helps normalize the variance of the data (Koenig 2003). In order to minimize the impact of measurement error on very low counts, previous analyses of population trends using these databases have generally restricted consideration to a subset of sites where abundance values are above a minimal threshold (Thomas and Martin 1996). Here we limited analyses to sites for which a particular species was recorded in more than 10% of years at a particular site.

Spread of EAB was documented by records of first discovery at the county level, made by the USDA Animal and Plant Health Inspection Service (APHIS) starting with the earliest records in 2002 and continuing on through 2016 (Fig. 1). We overlaid BBS routes and CBC plot locations with county boundaries to determine when EAB were first recorded in a particular county. For each route and survey, we then expressed the survey year relative to when EAB were first recorded (year 0), going as far back as year -5 prior to colonization and as far ahead as year 10 post-colonization. Subsequent analyses were thus standardized according to the time (in years) prior to or after the arrival of EAB to an area.

Analyses were conducted in R (R Development Core Team 2014) using the 'lme' mixed-effects model procedures in the package 'nlme' (Bates et al. 2015). In analyses of all species combined, total bird relative abundance was the dependent variable and years since EAB colonization the fixed factor. We included survey route (or site) within species as a random effect; in

analyses of individual species, the survey route or site was included as a random effect.

Because of long-term trends in some species independent of EAB, such as increases in red-bellied woodpeckers and decreases in red-headed woodpeckers (Koenig et al. 2017), we analyzed two sets of models. In the first, we used the (\ln -transformed) counts (birds per party hour in the case of the CBC data) as the dependent variable; these are referred to as 'raw' data. In the second set, we first regressed counts on year, but only included years up until EAB was first recorded at the site. We then calculated the residuals from this regression for all years of data—including subsequent to EAB invasion—and then standardized the residuals to a mean of 0 and standard deviation of 1. This procedure focused on differences in relative numbers of birds following EAB invasion in an area by controlling for long-term trends in numbers of birds detected prior to EAB presence. We refer to these as 'detrended' data.

In order to provide a baseline for comparison with populations subsequent to EAB invasion, raw and detrended values for the four years prior to EAB colonization through the year of colonization (years -4 to year 0) were averaged, and analyses were made for each year post-colonization for year 1 through year 10 relative to the averaged pre-colonization value (subsequently referred to as 'year 0'). Only routes and sites that provided data for at least three years prior to the EAB invasion and at least three years post-EAB invasion were included in the analyses.

In order to quantify the population-level effects of EAB invasion on species abundance, we performed linear regressions of the bird counts on year since EAB colonization using 'year 0' (the mean of years -4 to year 0) as the baseline. For the analyses of the raw data, we then predicted mean abundance at year 10 and divided the (back-transformed) change by the (back-transformed) baseline value in order to estimate the percent change over the decade since EAB invasion. For analyses using the detrended data, we predicted mean abundance at year 10 which, since values were standardized to a mean of 0 and standard deviation of 1, was equal to the mean change in standard deviations from the year of EAB colonization. Standard deviations were then converted to the percent change (per decade) assuming a normal distribution, and then, since values were again based on \ln -transformed values, back-transformed to yield an estimate of the percent change in numbers for the decade following EAB invasion.

Results

In mixed-effects models of all species combined, both absolute and detrended numbers of individuals exhibited significant increases after EAB colonization (Fig. 2). Based on back-transformed values, populations of the six species increased by 11.5–26.3% based on the BBS data and between 44.4 and 112.3% using the CBC data, depending on whether raw or detrended values are used (Table 1).

Results of mixed-effects models for the individual species are summarized in Fig. 3 (BBS) and Fig. 4 (CBC). During the breeding season, there was considerable variability in the apparent response to EAB among the species. Both hairy and downy woodpecker populations mostly fluctuated around baseline values, although downy woodpeckers were at above-baseline levels in year 7 and year 9. Pileated woodpecker numbers were significantly above baseline values almost immediately, remaining so until year 6 and

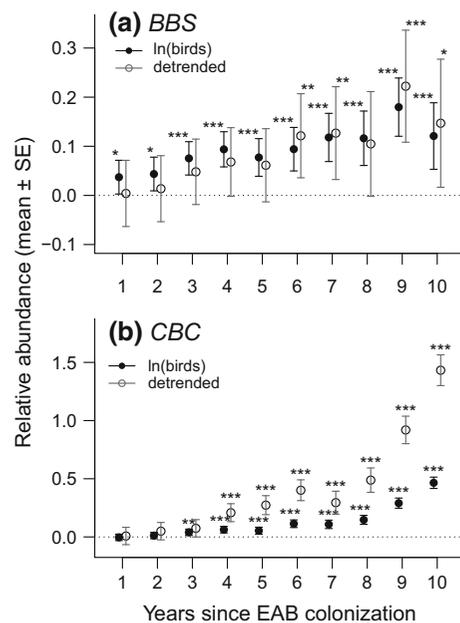


Fig. 2 Overall trends in relative populations of the six species of birds included in the analyses (all species combined) based on **a** the North American Breeding Bird Surveys and **b** Audubon Christmas Bird Counts. Data (mean \pm standard error of the effect size) are standardized by years since EAB colonization for each site, based on mixed-effects models in which 'survey' within 'species' was included as a random effect, and plotted relative to baseline values (the mean of years -4 to year 0). Values based on the raw (\ln -transformed) and detrended values are plotted. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; other $P > 0.05$

Table 1 Overall estimated percent change per decade in bird abundance relative to the year emerald ash borers were first detected in the area

Taxon	BBS counts (raw)	BBS (detrended)	CBC per party hour (raw)	CBC (detrended)
All species combined	26.3	11.5	112.3	44.4
Hairy woodpecker	31.8	14.3	200.4	40.8
Downy woodpecker	18.4	11.4	57.8	27.7
Pileated woodpecker	68.4	32.2	266.0	49.9
Red-headed woodpecker	12.9	21.3	907.2	48.5
Red-bellied woodpecker	45.3	-3.5	103.5	38.1
White-breasted nuthatch	8.0	-5.5	63.2	30.3

then returning to baseline values in years 7 and 8 after which they again increased, this time to relatively high levels. Red-headed woodpeckers showed no significant differences from baseline values in raw numbers, but the detrended values increased slowly and then fluctuated between being highly significantly above baseline (years 5, 7, 9, and 10) and being at baseline values (years 6 and 8). Red-bellied woodpeckers, in contrast, exhibited no pattern in the detrended values but had significant increases in raw numbers across the entire 10-year post-EAB period. White-breasted nuthatches exhibited a significant increase in raw numbers at year 4 and a significant decrease in detrended values at year 10 but otherwise were not significantly different than baseline. These latter two species were the only species to exhibit an overall decline based on the detrended values (Table 1).

In contrast to these variable patterns, values for all six species exhibited significant and in some cases dramatic increases during the winter (Fig. 4). Estimated decadal increases for the six species based on raw values ranged from a low of 57.8% for downy woodpeckers to a high of 907.2% (nearly an order of magnitude increase) for red-headed woodpeckers. Based on the detrended numbers, estimated decadal increases were more modest but still considerable (27.7–49.9%; Table 1).

Discussion

Our results confirm that the EAB invasion is significantly affecting populations of woodpeckers and other insectivorous resident bird species that are predators of EAB larvae. Because we analyzed data from both the breeding season (BBS) and winter

(CBC), we were able to show that increases in avian populations have been much more pronounced during the winter than during the breeding season, with increases detected using Christmas Bird Counts being several times greater than comparable values observed based on Breeding Bird Surveys. During the breeding season, overall estimated decadal increases were 26.3% using the raw data (ranging from 8.0% for white-breasted nuthatches to 68.4% for pileated woodpeckers) and 11.5% using the detrended data (ranging from -5.5% for white-breasted nuthatches to 32.3% for pileated woodpeckers). During the winter, estimated decadal increases for the six species combined more than doubled using raw data (ranging from 57.8% for downy woodpeckers to 907.2% for red-headed woodpeckers) and increased by 44.4% using detrended data (ranging from 27.7% for downy woodpeckers to 49.9% for pileated woodpeckers).

Whether raw or detrended values provide a more accurate representation of the effects of EAB on these populations may differ depending on the species, but in general depends on the temporal scale at which one is interested. Using the detrended data—values detrended based on trends prior to EAB presence—attempts to control for population trends that are independent of the EAB invasion. Although in some cases this makes little difference (for example, downy woodpeckers during the breeding season), it can potentially reverse trends, as is the case for red-bellied woodpeckers during the breeding season, which have been exhibiting population increases nationwide since well before EAB arrived in North America (Shackelford et al. 2000; Koenig et al. 2017). Controlling for such presumably unrelated population trends, our analyses indicated that populations of all six species exhibited increases due to EAB during the winter,

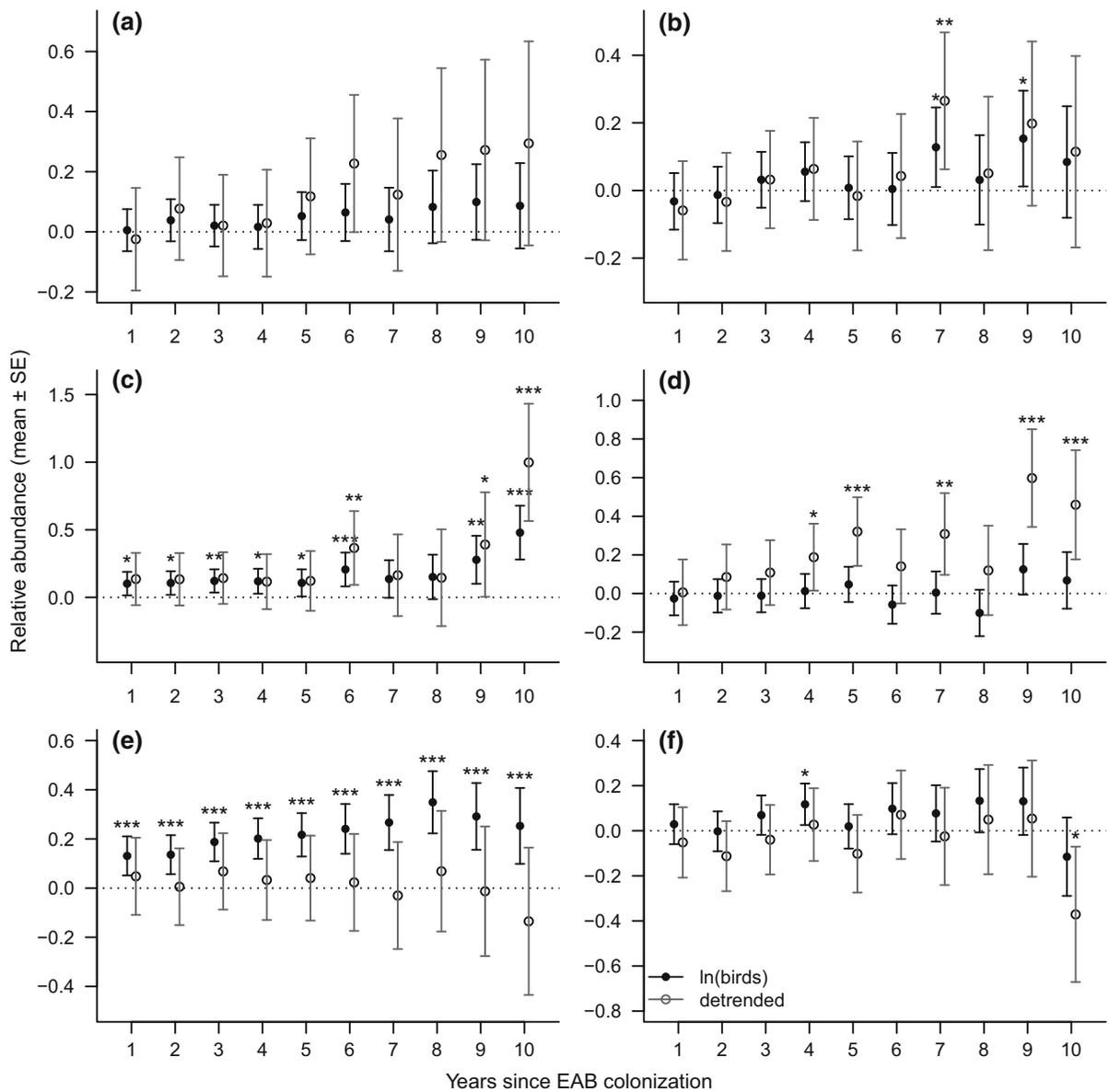


Fig. 3 Trends in relative populations of the six species of birds included in the analyses based on the North American Breeding Bird Surveys. Data (mean \pm standard error of the effect size) are standardized by years since EAB colonization, based on mixed-effects models in which ‘survey’ was included as a random effect, and plotted relative to baseline values (the mean

of years -4 to year 0). Values based on the raw (\ln -transformed) and detrended values are plotted. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; other $P > 0.05$. **a** Hairy woodpecker, **b** downy woodpecker, **c** pileated woodpecker, **d** red-headed woodpecker, **e** red-bellied woodpecker, **f** white-breasted nuthatch

while increases in breeding populations, although significant in several species, were smaller and more variable.

Of the six species considered, all but one is a permanent resident, and thus, except for the partially migratory red-headed woodpecker, territoriality is

unlikely to play a major role in the observed seasonal differences. More likely is that the enhanced food supply provided by EAB larvae during the winter has a significant positive effect on populations. EAB larvae enter dormancy by early November and pupate from their overwintering chambers between early April and

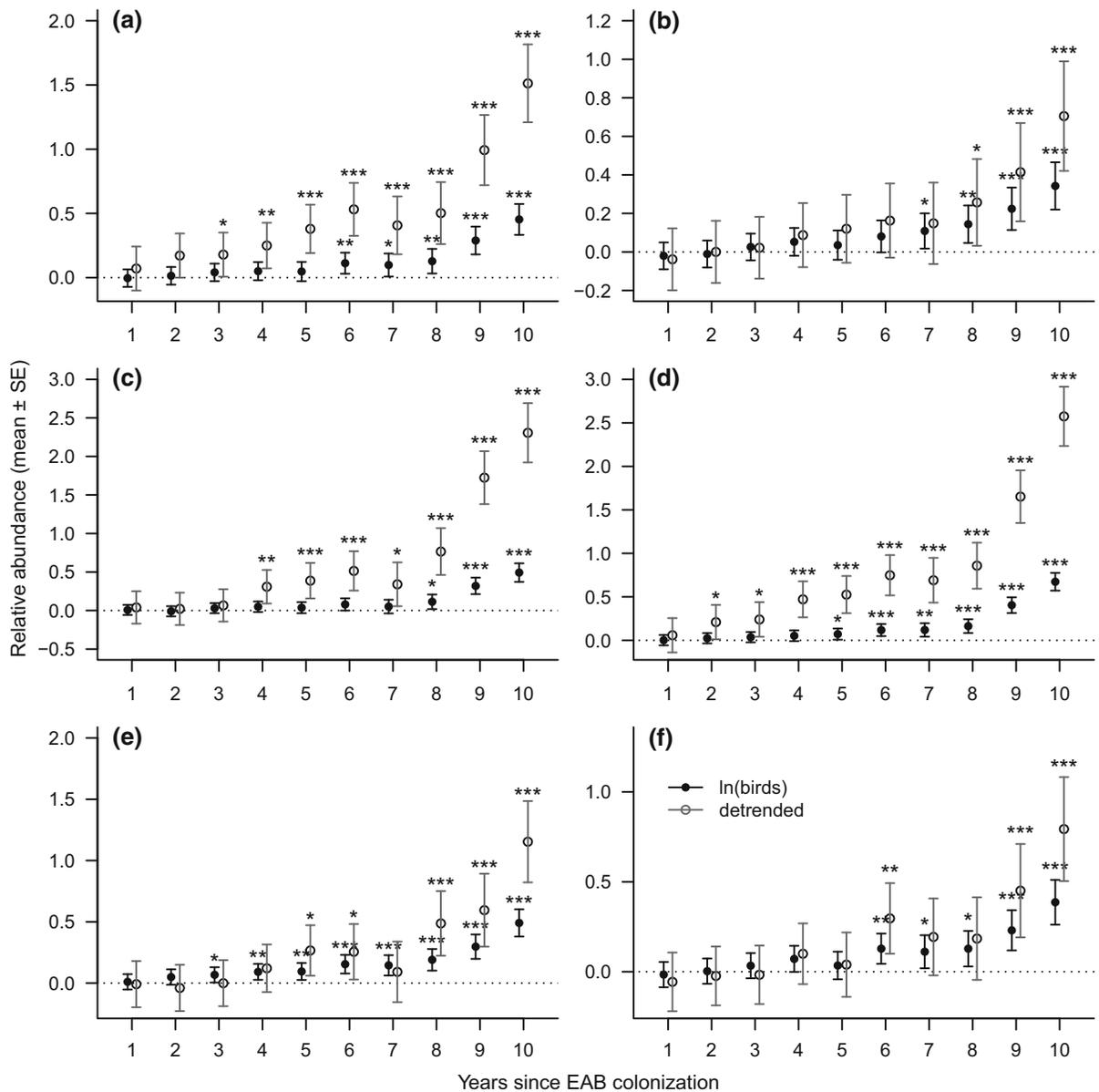


Fig. 4 Trends in relative populations of the six species of birds included in the analyses based on Audubon Christmas Bird Counts. Data (mean \pm standard error of the effect size) are standardized by years since EAB colonization, based on mixed-effects models in which ‘survey’ was included as a random effect, and plotted relative to baseline values (the mean of years

–4 to year 0). Values based on the raw (\ln -transformed) and detrended values are plotted. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; other $P > 0.05$. **a** Hairy woodpecker, **b** downy woodpecker, **c** pileated woodpecker, **d** red-headed woodpecker, **e** red-bellied woodpecker, **f** white-breasted nuthatch

mid-May the following spring; thus, winter is the primary season during which larval EAB are large and available to birds (Wang et al. 2010; Herms and McCullough 2014; Jennings et al. 2016). Why this apparent increase in population size fails to be

reflected in the breeding season surveys is unknown, but it could be due to birds dispersing away from relatively high density, EAB-infested sites to which they were attracted during the winter. Increases in bird populations during the breeding season, to the extent

they occurred, were potentially a consequence of enhanced survival during the winter rather than any direct response to EAB presence during the summer breeding season.

Although populations of woodpeckers are well known to respond numerically to increases in food abundance due to fire and regional insect outbreaks (Lindell et al. 2008; Koenig et al. 2013), we are aware of no prior study that has documented such dramatic increases in insectivorous bird populations following the large-scale eruption of an invasive insect species such as the emerald ash borer. It will continue to be of interest to follow how populations of these and other bird species respond as the EAB invasion peaks and eventually declines due to the depletion of host ash (Morin et al. 2017) and the impacts of introduced parasitoids and natural enemies (Duan et al. 2015). In the meantime, the current EAB invasion provides a “feast for woodpeckers” (Cappaert et al. 2005a) while changing the structure and composition of forests in its wake.

Woodpeckers have previously been identified as major predators of EAB in China, where they are native, as well as a significant source of EAB mortality in North America (Lindell et al. 2008; Wang et al. 2010; Duan et al. 2010, 2014). Of particular interest is the extent to which woodpeckers can potentially impact the population dynamics of EAB. Experimental work has shown that woodpeckers can be a major source of mortality on EAB larvae, but that woodpecker predation may reduce parasitism, thus counteracting at least some of their effects on EAB populations (Jennings et al. 2013). Whether the numerical response of woodpeckers and other insectivorous birds might be enough to overcome their effects on parasitoids and potentially control EAB numbers remains to be determined. Our results indicate, however, that this numerical response can be considerable, particularly in the winter, and will conceivably continue to be expressed as EAB spread and birds have more time to adapt to this newly available, abundant food source.

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