

## PERSPECTIVE

**Are declines in insects and insectivorous birds related?****Douglas W. Tallamy\*** and **W. Gregory Shriver**<sup>®</sup>

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**ABSTRACT**

A flurry of recently published studies indicates that both insects and birds have experienced wide-scale population declines in the last several decades. Curiously, whether insect and bird declines are causally linked has received little empirical attention. Here, we hypothesize that insect declines are an important factor contributing to the decline of insectivorous birds. We further suggest that insect populations essential to insectivorous birds decline whenever non-native lumber, ornamental, or invasive plant species replace native plant communities. We support our hypothesis by reviewing studies that show (1) due to host plant specialization, insect herbivores typically do poorly on non-native plants; (2) birds are often food limited; (3) populations of insectivorous bird species fluctuate with the supply of essential insect prey; (4) not all arthropod prey support bird reproduction equally well; and (5) terrestrial birds for which insects are an essential source of food have declined by 2.9 billion individuals over the last 50 years, while terrestrial birds that do not depend on insects during their life history have gained by 26.2 million individuals, a 111-fold difference. Understanding the consequences of insect declines, particularly as they affect charismatic animals like birds, may motivate land managers, homeowners, and restoration ecologists to take actions that reverse these declines by favoring the native plant species that support insect herbivores most productively.

*Keywords:* breeding bird, caterpillars, insect decline, Neotropical migrants, ornamental plants

**LAY SUMMARY**

- There may be a link between declining insect populations and bird population declines.
- Bird populations are often limited by the amount of insect food available to them.
- Most of the bird species that have declined in the last 50 years are those that depend on insects for food.
- One cause of insect declines is the widespread use of non-native plants in forestry and horticulture that do not support insects.
- The loss of insects, birds, and other forms of life is important because those are the species that run the ecosystems that support humans.
- One solution to this problem is to increase the populations of the insects that birds depend on by increasing our use of native plants in managed landscapes.

**Las disminuciones de insectos y aves insectívoras están relacionadas?****RESUMEN**

Una seguidilla de estudios recientemente publicados indica que tanto insectos como aves han experimentado disminuciones poblacionales a gran escala en las últimas décadas. Curiosamente, si las disminuciones de insectos y aves están relacionadas de modo causal ha recibido poca atención empírica. En este estudio hipotetizamos que las disminuciones de insectos son un factor importante que contribuye a la disminución de aves insectívoras. Sugerimos además que las poblaciones de insectos esenciales para las aves insectívoras disminuyen siempre que las especies de plantas leñosas no nativas, ornamentales o invasoras reemplazan a las comunidades de plantas nativas. Apoyamos nuestra hipótesis mediante la revisión de estudios que muestran que (1) debido a la especialización en las plantas huésped, los insectos herbívoros típicamente tienen un desempeño pobre en las plantas no nativas; (2) las aves están usualmente limitadas por el alimento; (3) las poblaciones de especies de aves insectívoras fluctúan con la provisión de presas esenciales de insectos; (4) no todas las presas de artrópodos sustentan la reproducción de las aves igualmente bien; y (5) las aves terrestres para las cuales los insectos son una fuente esencial de alimento han disminuido en 2.9 billones de individuos a lo largo de los últimos 50 años, mientras que las aves terrestres que no dependen de insectos durante su historia de vida han aumentado en 26.2 millones de individuos, una diferencia de 111 veces. Entender las consecuencias de las disminuciones de los insectos, particularmente al afectar a animales carismáticos como las aves,

puede motivar a los gestores de tierras, propietarios de casas y ecólogos de la restauración a emprender acciones que reviertan estas disminuciones a favor de especies de plantas nativas que sustentan insectos herbívoros de manera más productiva.

*Palabras clave:* ave reproductiva, disminución de insectos, migrantes neotropicales, orugas, plantas ornamentales

## INTRODUCTION

In 1987, Wilson made general but dire predictions about the ecological consequences of global insect declines that included the loss of flowering plants, terrestrial food web collapse, and its associated loss of animal diversity, as well as the end of rapid nutrient cycling (Wilson 1987). Although the biomass of some insect taxa may be locally stable (e.g., moths: Macgregor et al. 2019; aquatic insects: van Klink et al. 2020, reviewed by Montgomery et al. 2020), recent evidence from Germany (Hallmann et al. 2017), England (Conrad et al. 2006), Costa Rica (Janzen and Hallwachs 2019), the Netherlands (van Strien et al. 2019), North America (Cameron et al. 2011, Forister et al. 2019, Harris et al. 2019), as well as global assessments (Dirzo et al. 2014; reviewed by Cardoso et al. 2020, Wagner 2020) suggests that such declines are no longer simple predictions; they may be real. Understanding the impacts of insect declines, particularly as they affect both charismatic and ecologically critical species, may help motivate the changes in human culture and policy necessary to reverse them.

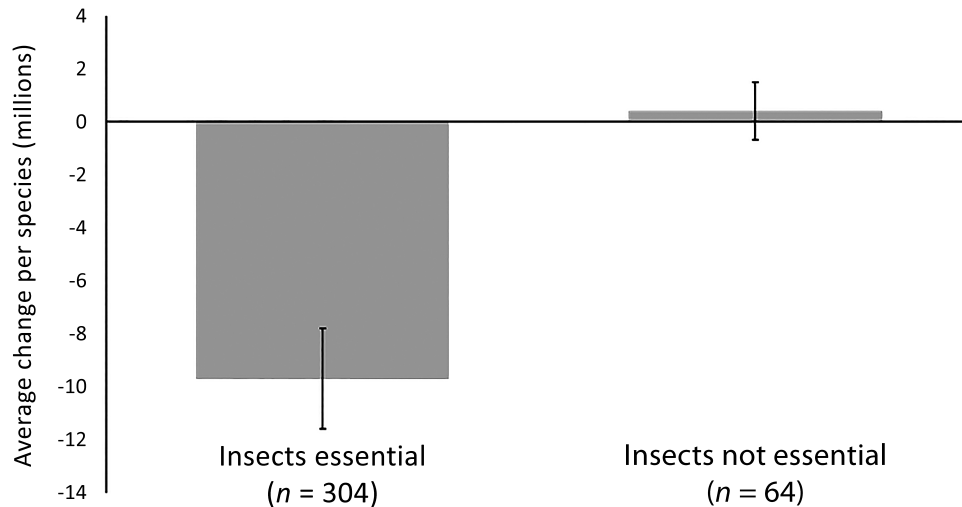
We suggest that species with life-history traits that evolved to capitalize on the food resources presented by large insect populations will suffer the most from a reduction in insect biomass. Perhaps the largest and historically most reliable pulse of insect biomass in any ecosystem is the explosion of insect herbivores that follows the seasonal flush of new leaves after winter senescence in the temperate zone. Both Neotropical–Nearctic migrants and temperate zone residents that rear young on insects have taken advantage of this resource bonanza for millennia.

Long-distance migration is physiologically and ecologically costly (Wiedenfled and Wiedenfled 1993, Faaborg 2002), and, to be adaptive, post-migration reproductive benefits must exceed costs from both natural- and human-induced risks, as well as the physiological stress associated with migration. There may be other advantages associated with obligate migration (Ricklefs 1976, Cardillo 2002), but in the absence of human perturbations, the abundance of spring insects in the temperate zone, particularly the protein and fat-laden Lepidoptera that are the largest component of nestling diets in hundreds of species of migrants (Martin et al. 1961, Kennedy 2019), has helped birds that migrate north produce more than enough young to offset the costs of migration (Lack 1954).

Similarly, most of the terrestrial resident birds rely on large numbers of insects during the breeding season. About 96% of North American terrestrial birds rear their young

in part or entirely on insects (derived from Peterson 1980, 1990), and in 16 of the 20 bird families for which there are data, caterpillars dominate nestling diet (Kennedy 2019). There is growing evidence that the abundance of caterpillars in bird diets does not simply reflect their abundance in the environment; rather, foraging birds often choose caterpillars over other prey options (Kennedy 2019). Such preference may reflect the relatively large size of caterpillars, their softness compared with many other insects, and/or their superior nutritional value. In particular, caterpillars contain significantly more essential carotenoids than Orthopteroids, spiders, Opilionids, or earthworms (Eeva et al. 2010, Kennedy 2019). Furthermore, studies suggest that a reduction in caterpillar availability during the breeding season can reduce nestling fitness. For example, Seress et al. (2018) found that urban Great Tits (*Parus major*) laid smaller clutches, experienced more frequent nestling mortality from starvation, reared fewer offspring to fledging age and at slower rates, and their fledglings had lower body mass when caterpillar biomass was low. Narango et al. (2017, 2018) had identical results with Carolina Chickadees (*Poecile carolinensis*).

Not only are caterpillars important components of nestling diets, but they are also required in great numbers. It requires many thousands of these insects to bring a clutch to independence; for example, Carolina Chickadees feed young 6,000–9,000 caterpillars before fledging, depending on the number of chicks in the nest, and continue to feed fledglings insects for weeks after they leave the nest (Brewer 1961). Similar data have been recorded for Wilson's Warblers (*Cardellina pusilla*, Stewart 1973), Bobolinks (*Dolichonyx oryzivorus*, Martin 1971), Downy (*Picoides pubescens*) and Hairy (*Leuconotopicus villosus*) woodpeckers (Lawrence 1967), and 10 species of European passerines (Bussman 1933). Martin (1987) reviewed the influence of food availability on all stages of breeding in birds (egg production, incubation, nestling period, and post-fledging stage) and costs to parents. For the brood size component of the nestling stage, multiple pieces of evidence confirm the relationship between nestling weight and food availability. Parents have the ability to modify food delivery rates with varying food availability. For example, females increase the foraging rate when males are removed and when the food supply is low. Increases in food through supplementation increase nestling weight and survival. Experimental increases in brood size, coupled with increases in food through supplementation, indicated that parents can compensate for extra energy demands of



**FIGURE 1.** The average change in population size over the last 50 years of terrestrial North American bird species for which insects are an essential part of the diet at some point in their life history and bird species that never rely on insects for food. Statistical intervals = standard deviations. Data from Rosenberg et al. (2019). Bird species in each category are listed in Supplementary Material Table S1.

increased brood size, but only when food is increased at the same time (Crossner 1977).

We recognize that bird breeding success depends on several interacting factors besides food abundance, including nest site availability, predation pressure, and weather (Sherry et al. 2015), but the numbers cited above, as well as numerous field studies, suggest that insectivorous bird species depend on large insect populations to breed successfully, regardless of whether they breed in the temperate zone after migration or after wintering in place. For example, Venier and Holmes (2010) found that forest bird community abundance increased at both local and regional scales in response to spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks in Northeastern North American forests. Holmes et al. (2009) reported a 5-fold increase in the total number of pairs of forest breeding birds compared with preoutbreak conditions. Cape May Warbler (*Setophaga tigrina*), Tennessee Warbler (*Leiothlypis peregrina*), and Bay-breasted Warbler (*Setophaga castanea*) are considered “budworm specialists” with some aspects of population regulation dependent on spruce budworm outbreaks (Morse 1989, Baltz and Latta 2020, Rimmer and McFarland 2020, Venier et al. 2020). Black-throated Blue Warbler (*Setophaga caerulescens*) population regulation has been studied extensively in New Hampshire, USA, with food availability identified as a major factor affecting breeding success (Holmes and Schultz 1988, Holmes et al. 1991, 2020 Nagy and Holmes 2005). Rodenhouse and Holmes (1992) experimentally manipulated Black-throated Blue Warbler food availability and found that annual productivity was greater when food was more abundant. Hallmann et al. (2014) showed that imidacloprid, a widely used

neonicotinoid insecticide, had a negative effect on insectivorous bird population trends in the Netherlands; in areas with higher concentrations of imidacloprid, bird populations declined by 3.5 % annually. This study clearly ties large-scale population declines of insectivorous breeding birds to declines in invertebrate biomass.

In recent decades, North American bird populations have declined by one-third, a total of over 3 billion birds (Rosenberg et al. 2019). Interestingly, these declines are not equally distributed across bird taxa; they are concentrated among terrestrial insectivores (Figure 1). In fact, terrestrial bird species that rely on insects during at least part of their annual life cycle (304 species) declined more than 2.9 billion individuals in the last 50 years, while terrestrial birds that do not rely on insects (64 species) gained 26.2 million individuals, more than a 111-fold difference (data from Rosenberg et al. 2019). Although the link between bird population declines and an insectivorous diet appears solid, it does not demonstrate cause and effect. Here, we hypothesize that insect declines do, in fact, contribute to population declines in insectivorous birds. Moreover, we suggest that declines in both taxa are reversible.

Habitat loss, climate change, industrial agriculture, light pollution, and pesticides have all been implicated in insect declines (reviewed by Forister et al. 2019, Montgomery et al. 2020, Wagner 2020), and policies aimed at mitigating these causes must be designed and implemented as soon as possible. We suggest, however, that an important and easily mitigated additional reason for insect declines in both managed and natural ecosystems is the widespread replacement of the native plant communities on which insect herbivores depend with non-native plants that do not

support robust insect populations. Although exceptions exist, non-native plants typically do not support the growth and reproduction of native insect herbivores (Tallamy and Shropshire 2009, Burghardt et al. 2010, Richard et al. 2019, reviewed by van Hengstum et al. 2014, Yoon and Read 2016, Tallamy et al. 2020). This is particularly true for the caterpillars that dominate the diets of terrestrial birds (Kennedy 2019). Unfortunately, after a century of landscaping primarily for aesthetics rather than ecological function, it is non-native ornamentals and lawn that dominate residential and corporate landscapes (Mckinney 2004, Dolan et al. 2011, Avolio et al. 2015, van Kleunen et al. 2015, Zeeman et al. 2017). Moreover, the displacement of native plant communities has not been confined to managed landscapes; more than 3,300 non-native plant species have become naturalized in North America, many of which are displacing native vegetation in ecosystems across North America (Qian and Ricklefs 2006) and Europe (Keller et al. 2011, Scalera et al. 2012, Pyšek et al. 2020).

Although many non-native ornamentals are not invasive (Sax and Gaines 2008, Thomas 2015), about 86% of the woody invasive plants in North America are escapees from our gardens (derived from Kaufman and Kaufman 2007). Invasive species such as *Phragmites australis* in eastern marshes; Bush honeysuckle (*Lonicera tatarica* and *L. maackii*) in Missouri, Kentucky, and Tennessee; privet (*Ligustrum* spp.) in Georgia; glossy buckthorn (*Frangula alnus*) from Michigan to Vermont; kudzu across the deep south of North America; burning bush (*Euonymus alatus*) in New England; cheatgrass (*Bromus tectorum*) across the western United States; and Himalayan blackberry (*Rubus armeniacus*) in the Pacific Northwest have converted diverse native plant communities to near monocultures in millions of hectares of the “natural” areas required by birds. Moreover, when purposely planted as ornamentals, non-natives effectively displace the natives that used to occupy the areas, even though the ornamentals are not invasive on their own. This is the case in millions of more hectares of managed landscapes across North America and Europe.

Finally, agroforestry, shade coffee plantations, and restoration efforts worldwide rely heavily on non-native tree species. The need for fast-growing colonizing trees in agroforestry and restoration (e.g., *Acacia* and *Albizia*) has increased the use of non-native species, many of which have escaped to dominate nearby native forests (Schroth et al. 2004). At least 25% of the world’s planted forests are now comprised of non-native tree species (Lombardero et al. 2012); one-fourth of Portugal’s forestland (900,000 ha), for example, is planted in *Eucalyptus* (Ames 2017). Dozens of studies suggest that this massive compositional shift in flora limits insect populations (reviewed by van Hengstum et al. 2014, Yoon and Read 2016, Tallamy et al. 2020) which, in turn, may be yet another important cause of avian population declines.

Why most of the insects do not thrive on non-native plant lineages has been attributed to plant evolutionary responses to reduce herbivory (Rosenthal and Berenbaum 2012). Plants are defended from insect herbivores by distasteful or toxic secondary metabolic compounds, tissue toughness, plant phenology, and limited plant apparency; thus, insects typically gain access to particular plant lineages through the evolution of specialized physiological, behavioral, and life-history counter-adaptations. The evolution of such host plant specialization is usually a slow process but has resulted in an estimated 90% of herbivorous insect species associating with one or a few plant lineages that share common phytochemical defenses (Bernays and Graham 1988; Janzen 1988, Forister et al. 2015). Not surprisingly, adaptation to non-native plant species by native insect species has been predictably slow (Tallamy 2004); even centuries after their introduction, non-native plants support on average 72% fewer insect species than do indigenous plants (Tallamy and Shropshire 2009).

The differences between productive native plants (those species contributing the most energy to local food webs) and introduced non-natives in terms of their ability to support insect herbivores are not trivial. In the mid-Atlantic region of North America, oaks (*Quercus* spp.) support 557 species of Lepidoptera, wild cherries (*Prunus* spp.) support 456 species, and native willows (*Salix* spp.) support 455 species. In contrast, less than 10 species of Lepidoptera in the mid-Atlantic states are recorded on Chinese privet (*Ligustrum vulgare* and *L. sinense*), Crape myrtle (*Lagerstroemia indica*), bush honeysuckle (*Lonicera tatarica* and *L. maackii*), buckthorn (*Rhamnus cathartica* and *Frangula alnus*), and burning bush (*Euonymus alatus*); only 3 species of Lepidoptera are recorded on Ginkgo (*Ginkgo biloba*) in North America (note, all 3 records are erroneous; there are no verified records of caterpillars herbivory on Ginkgo), only 2 native species have been found using Chinese tallow (*Triadica sebifera*), and no species are recorded on Dawn Redwood (*Metasequoia glyptostroboides*), Lebanon cedar (*Cedrus libani*), or English ivy (*Hedera helix*) (Tallamy and Shropshire 2009).

Because abundance is typically correlated with species richness (Beck et al. 2011, Choi and Miller 2013), replacing native plant communities with non-native vegetation can devastate native insect biomass. When plants that share an evolutionary history with insect herbivores are replaced by non-native lumber, ornamental, or invasive plant species, insect biomass per unit area can be reduced by up to 96% (Richard et al. 2019, Tallamy et al. 2020). Not surprisingly, there is increasing evidence that such reductions are correlated with insectivorous bird population declines (Burghardt et al. 2009, Narango et al. 2017, 2018). In the most comprehensive study of its kind, Narango et al. (2018) showed that Carolina Chickadee populations in suburban

habitats become unsustainable when non-native plants exceed 30% of total plant biomass.

Exacerbating the effects of non-native plants is the amount of area that has been landscaped for aesthetics rather than ecological function. Nonagricultural, managed landscapes total more than 242 million hectares or 31.5% of the conterminous US landscape (Theobald 2001, Ament et al. 2014, Conniff 2014, Bigelow 2017, Jacobs 2018). If the non-native plants in these landscapes reduce prey abundance for migrating and resident birds, this represents a substantial loss in viable stopover and/or breeding habitat for terrestrial birds that could be restored to productive sites if the abundance of their insect-rich plants was increased.

## RESEARCH DIRECTIONS FOR THE FUTURE

Although evidence is mounting that the heavy use of introduced plants depresses insect populations and thus the birds that depend on those insects (Burghardt et al. 2009, Narango et al. 2018), more research, particularly empirical manipulations, is required to clearly delineate cause and effect. Heleno et al. (2010), who found that the removal of non-native plants increased both insect and bird populations, provided an excellent model for such experiments. Future comparisons of insects and birds in areas in which native vegetation has been compromised by invasive species vs. areas where there have been no such invasions will be particularly informative. For example, studies within the Hubbard Brook Experimental Forest in New Hampshire, where there are no serious non-native plant invasions, have shown no bird population declines in recent decades, bucking national trends (Holmes 2011).

There is still much to learn. We need more thorough experiments quantifying the extent to which non-native plants have reduced insect populations in natural areas as well as in urban, suburban, and exurban landscapes. We also need to learn whether the relationships between plant community composition, insect populations, and bird populations vary with bioregion, longitude, and latitude; how bird and insect declines are spatially correlated; and why some (but not all) bird species have declined in boreal forests that are comprised entirely of native vegetation as well as the factors that have maintained the populations of some insectivorous birds such as vireos while most of the species have declined precipitously (Rosenberg et al. 2019).

Addressing these questions will help clarify the role that the large-scale displacement of native plant communities by non-native plants has had on insect and bird declines. Although not entirely delineated, the links between food availability and bird breeding success, as well as between insect population declines and non-native

plants, have already been well-enough established to encourage greater use of insect-producing native plant species in managed landscapes. We conclude that the use of native plants wherever possible could be an overlooked key to restoring insect densities, which, in turn, may help mitigate the declines in both migratory and nonmigratory insectivorous birds.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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