Diversified farms bolster forest-bird populations despite ongoing declines in tropical forests

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While some agricultural landscapes can support wildlife in the short term, it is uncertain how well they can truly sustain wildlife populations. To compare population trends in different production systems, we sampled birds along 48 transects in mature forests, diversified farms, and intensive farms across Costa Rica from 2000 to 2017. To assess how land use influenced population trends in the 349 resident and 80 migratory species with sufficient data, we developed population models. We found, first, that 23% of species were stable in all three land use types, with the rest almost evenly split between increasing and decreasing populations. Second, in forest habitats, a slightly higher fraction was declining: 62% of the 164 species undergoing long-term population changes; nearly half of these declines occurred in forest-affiliated invertivores. Third, in diversified farms, 49% of the 230 species with population changes were declining, with 60% of these declines occurring in agriculture-affiliated species. In contrast, 51% of the species with population changes on diversified farms showed increases, primarily in forest-affiliated invertivores and frugivores. In intensive farms, 153 species showed population changes, also with similar proportions of species increasing (50%) and decreasing (50%). Declines were concentrated in agriculture-affiliated invertivores and forest-affiliated frugivores; increases occurred in many large, omnivorous species. Our findings paint a complex picture but clearly indicate that diversified farming helps sustain populations of diverse, forest-affiliated species. Despite not fully offsetting losses in forest habitats, diversified farming practices help sustain wildlife in a critical time, before possible transformation to nature-positive policies and practices.

bird population trends | diversified farming | population declines | Costa Rica

With continuing destruction of forests across the world, particularly in the tropics, how can agricultural landscapes help to bolster wildlife populations outside of protected areas? Answering this question is urgent, as agricultural expansion and intensification are the greatest drivers of wildlife population declines globally (1), and food security is a growing concern (2). Protected areas are increasingly threatened by downgrading, downsizing, and degazettement (3), and, alone, are inadequate for protecting biodiversity and ecosystem services in over the long-term (4). At the same time, over 190 countries pledged to contribute to protecting "30 by 30" at COP15 of the Convention on Biodiversity. Under these contrasting pressures (5), it is important to understand how we can practice agriculture in ways that support both people and nature (6).

Over the short term, "working" farming and grazing landscapes with forest patches, riparian corridors, hedgerows, remnant trees, live fences, and agro-forestry and silvo-pasture practices have potential to support diverse wildlife (6–8). Little is known, however, about the long-term effects (>10 y) of alternative agricultural practices on wildlife populations, particularly in species-rich tropical regions (6, 7).

Recent studies suggest that populations of tropical birds are declining (9–13), even in large and undisturbed regions of tropical forest in the Amazon (14). Across studies, forest-affiliated (15), large-bodied (16), and insect-eating (9, 14) species tend to be particularly susceptible to population declines, though in a Panamanian forest, community-wide declines were found irrespective of species' traits (10).

In agricultural landscapes, diversified farming practices have been shown to help stabilize population dynamics (17) and reduce extirpation rates relative to intensive management practices (18, 19). For example, in a region of southwest India with >2,000 y of continuous agricultural production, traditional diversified farming systems contained 90% of the bird diversity found in regional forests (20). However, populations may persist for extended periods even if they are doomed to extirpation over the long-term (21). For example, small increases in forest cover on coffee farms reduce the magnitude of, but do not reverse, bird population declines over a 7-y period (9). As the threats to biodiversity continue to grow,

Significance

While diversified farms provide habitat for many species, it is unclear whether agricultural areas can support viable populations of species that are sensitive to environmental changes. We explored this question by tracking changes in bird populations in different farming systems over 18 y in Costa Rica. We found that diversified farming practices can support the long-term population growth of many sensitive forest-affiliated and insect-eating species over time. Unexpectedly, population declines in surrounding forest habitats outweigh the increases in diversified farms. Our findings suggest that the benefits of diversified farming practices for biodiversity can accrue through time and that such practices retain vital potential for future restoration.

can the wildlife benefits of diversified farming practices be sustained over multidecadal time scales?

In this study, we investigate the long-term effects of alternative agricultural practices on Neotropical bird populations. We conducted 18 y of replicated bird counts in 48 transects across large-scale intensive agricultural landscapes, small-holder diversified farms, and tropical forests to quantify population trends for 429 Neotropical species, out of which 349 are resident and 80 are Neotropical-Nearctic migrant species in Costa Rica.

Costa Rica provides a model system for this study, having experienced rapid deforestation for agricultural production during the mid-20th century, at one stage experiencing the highest rate of deforestation of any country (22). Deforestation in the country largely halted and forest cover began to increase around the year 2000 (23), and today nearly 60% of the country is forested (24).

Compared to intensive farms, diversified farms tended to contain more distinct farm plots of smaller size; a greater variety of crop species planted; a higher percentage of surrounding forest cover; larger and denser hedgerows beneficial for birds (25); and a higher number of vegetation strata (26). In contrast, intensive farms were approximately 20 times larger on average, with around five times fewer crop species compared to those in diversified farms.

We developed multispecies hierarchical models to estimate local changes in the population sizes of 429 species with sufficient data for the duration of the study, allowing us to quantify the impact that land use type has on population trends. We combine 1,287 estimates of annual local population changes with species-specific trait information to test three predictions related to 1) land use, with the prediction that magnitude of population declines relative to increases would be most pronounced in intensively managed agricultural systems (17–19, 21, 27); 2) forest affinity and body size, with the prediction that large, forest-affiliated birds would show the greatest declines across all habitats (15, 16); 3) trophic niche, with the prediction that insect-eating birds would show the greatest declines across all land-use types, but that the number of guilds showing disproportionate declines will increase with land-use intensity (14).

Results

Forest Affinity. We found a continuum in forest affinity and habitat use among the 506 species detected, 503 of which are native to Mesoamerica (Fig. 1). Approximately half of the species (262) were detected in both forest and agricultural habitats. The other half of the species (244) were found in either forest habitats (93) or agricultural habitats (151). Of the 151 species found in agricultural habitats, 20 were found only in diversified farms and 36 were found only in intensive farms.

Population Trends. In total, we found evidence that 547 or 43% (547/1,287), of the local populations monitored over the 18-y period showed long-term changes in size. Across land use types, the relative magnitude of population declines was greatest in forest landscapes (Fig. 2A), though no land use type showed community-wide population declines or growth (*SI Appendix*, Fig. S1). Sixty-two percent of species showing long-term population changes were declining in forest habitats, 49% in diversified farms, and 50% in intensive farms. Within forests, 62 (58 Resident, 4 Migratory) species showed long-term population growth, whereas 102 (92 Resident, 10 Migratory) species exhibited long-term population declines. Within diversified farms, 118 species (101 Resident, 17 Migratory) showed long-term population growth, and 112 (86 Resident, 26 Migratory) species exhibited long-term declines (Fig. 2B). In
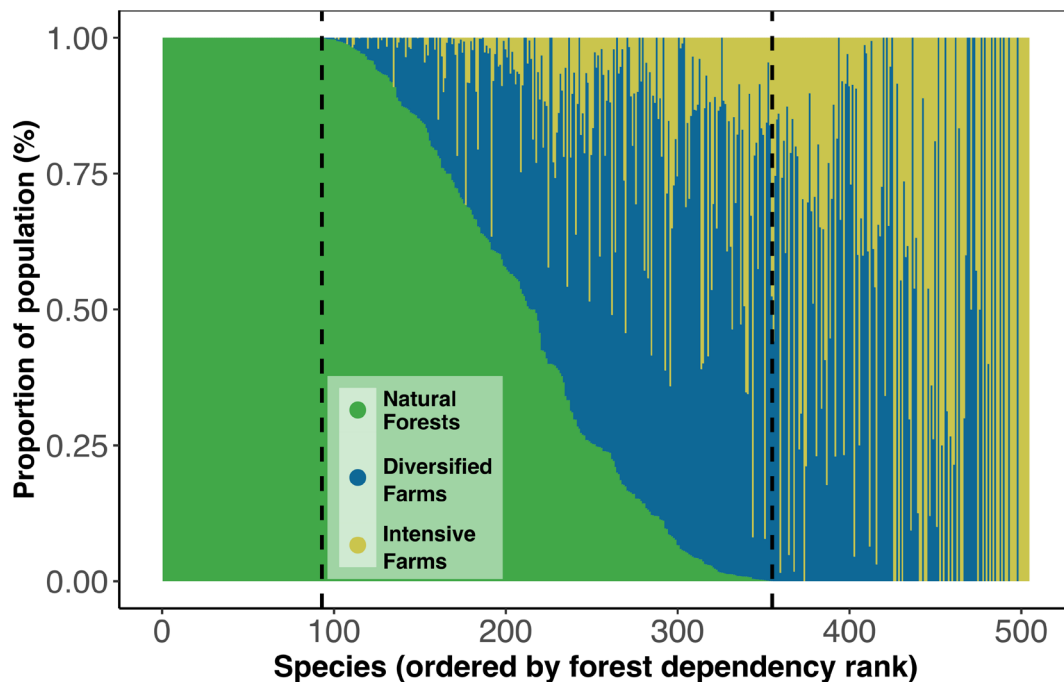
Fig. 1. Distribution of forest affinity and habitat use among 506 detected bird species. Proportion of population in forest (green), diversified farms (blue), and intensive farms (yellow) for the 506 Neotropical bird species detected from 2000 to 2017. Species are ordered by dependence on forest habitats, ranging from complete forest dependence (rank 1) to complete forest avoidance (rank 506). The dashed lines represent cutoff points between species only found in forest habitats (ranks 1 to 93), species found in both forest and agricultural habitats (ranks 94 to 356), and species found only in agricultural habitats (ranks 357 to 506). Histogram bars are filled with color matching the percentage of the detected population found within a given land use type, where green denotes natural forests, blue denotes diversified farms, and yellow denotes intensive farms. Data plotted show proportion of population in each land use type calculated using the raw bird detections for each of the 506 species found within the 48 transects from 2000 to 2017. Forest affinity values used in downstream analyses were derived from multispecies occupancy models and not raw proportions depicted.
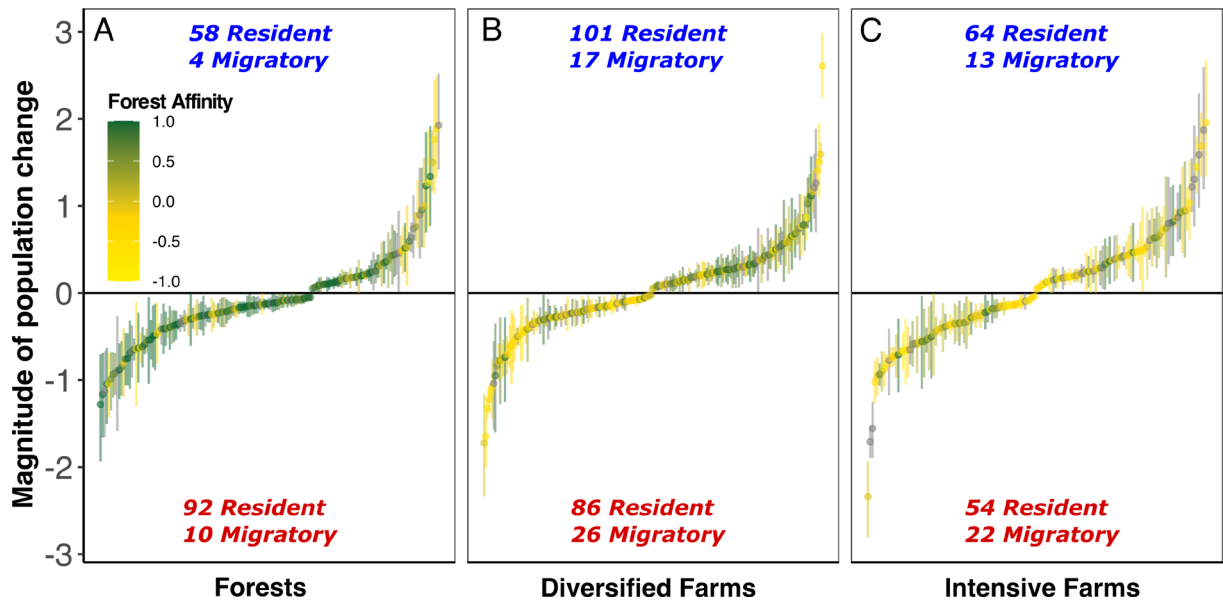
Fig. 2. Population declines are greatest in forest landscapes, while all land-use types contain both species undergoing population declines and others undergoing increases. (*A–C*) In each panel, points depict species-level estimates of annual rates of population change by local land use type from 2000 to 2017 that did not overlap with zero (i.e., high confidence that local population showed long-term change in size). Estimates were derived from regional multispecies trend models. Points depict mean estimates, with 95% Bayesian Credible Intervals. Species-specific estimates are shaded by forest affinity scores derived from multispecies occupancy models. Texts within each panel summarize the number of resident and migrant species showing population growth (blue text in upper panels) and population declines (red text in lower panels).

intensive agriculture, fewer species exhibited population changes (Fig. 2*C*), in part due to the generally smaller community size. In intensive farms, 77 species (64 Resident, 13 Migratory) showed long-term growth, and 76 species (54 Resident, 22 Migratory) exhibited long-term declines.

Of the 429 species included in this study, 172 species exhibited long-term population changes in more than one land use type. When comparing population trends in farming landscapes to forest habitats, 52 species showed significant population changes of the same sign (i.e., increase or decrease) in diversified farms and 28 species in intensive farms. Thirty-six species showed diverging population trends between forest and diversified farms, and 27 species between forest and intensive farms. Of the species, 102 species decreasing in forest, only 27 (26.5%) and 17 (16.7%) of the same species grew in population size in diversified and intensive farms, respectively.
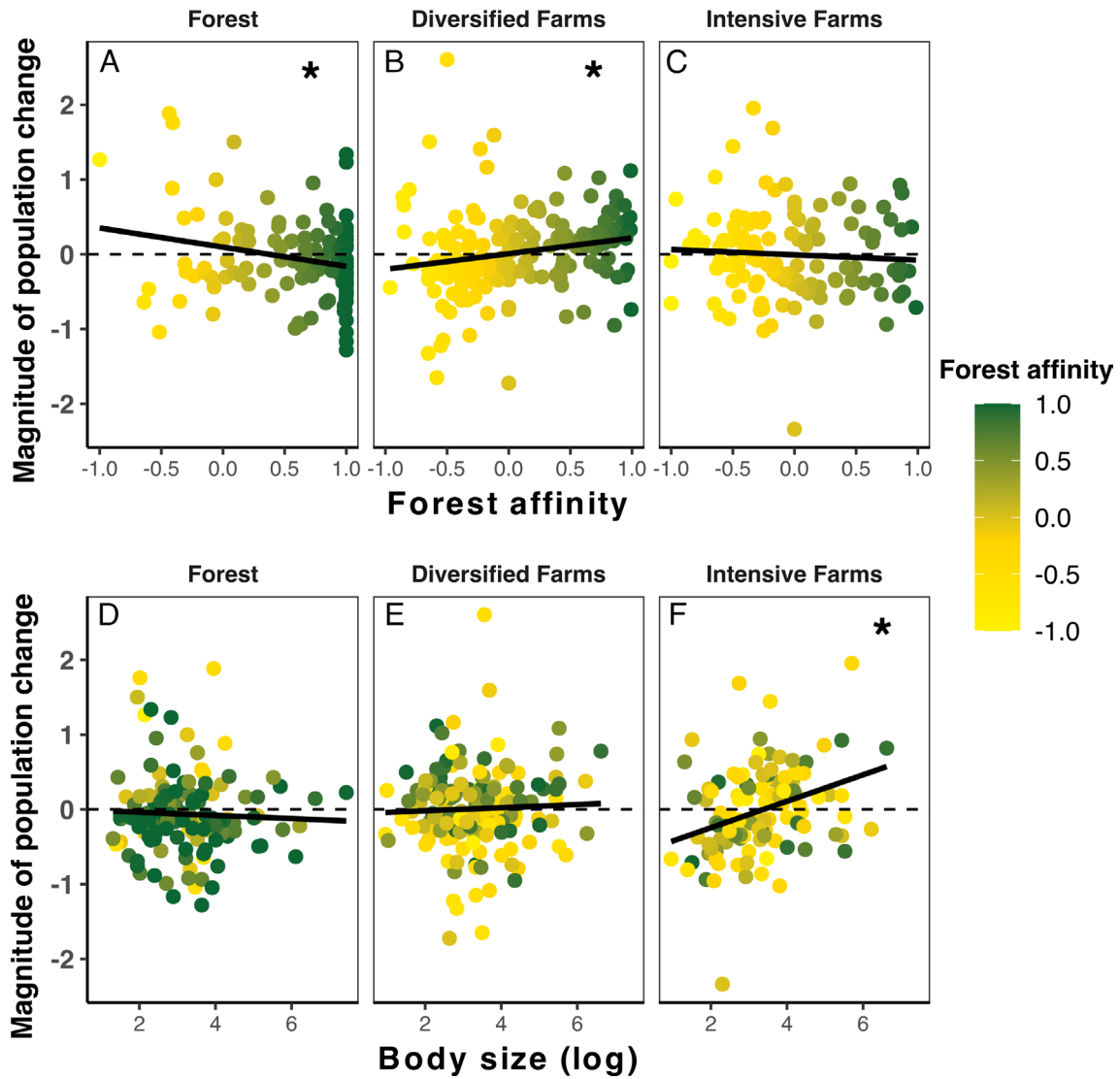
Forest Affinity and Body Size. Both forest affinity [LRT = 21.961, Pr(>Chi) = 1.703e-05] and log-transformed body size [LRT = 11.243, Pr(>Chi) = 0.004] explained important heterogeneity in long-term population trends. These effects differed by land use type. Forest association was an important predictor of long-term population trends in forest and diversified farms only (Fig. 3 *A* and *B*). In forests, population declines were negatively correlated with forest association (mean = –0.167, SE = 0.057, *P* = 0.004), such that population declines were on average greatest in the most forest-dependent species (Fig. 3*A*). In diversified farms, there was a strong positive association between forest affinity and population growth (mean = 0.358, SE = 0.077, *P* = 3.55e-06), with long-term growth greatest in forest-associated birds and lowest in agriculture-affiliated birds (Fig. 3*B*). In intensive farms, there was no strong association between forest affinity and long-term population trends (mean = 0.131, SE = 0.084, *P* = 0.117; Fig. 3*C*). Body size was important for explaining long-term population changes in intensive farms only (Fig. 3*F*), where large-bodied birds showed the greatest increases through time (mean = 0.107, SE = 0.035, *P* = 0.003).

Trophic Niche. Across the different trophic niches and land use types, the magnitude of population declines was most pronounced in forest-affiliated and agriculture-affiliated invertebrate-eating birds (Fig. 4 *A*, *B*, *D*, and *F*). Forest-affiliated invertivores within forest habitats showed the greatest declines within a single land use type (Fig. 4*A*), with 45 species showing significant long-term declines, and only 24 showing long-term growth. Even though agriculture-affiliated invertivores exhibited large declines in diversified farms (Fig. 4*D*), these were balanced by increases in forest-associated invertivores (Fig. 4*C*), with 32 species showing long-term population growth and nineteen exhibiting long-term declines. In intensive farms, declines were most pronounced in agriculture-affiliated invertivore species.

After invertivores, fruit-eating and omnivorous birds showed the most unbalanced variation in population changes across land use types (Fig. 4 *C*, *E*, and *F*). For frugivores, a disproportionate number of forest-associated species exhibited growth in diversified farms (Fig. 4*C*). In contrast, a disproportionate number showed declines in intensive farms (Fig. 4*E*), highlighting the contrasting effects that management practices have on long-term population trends in this group.

Omnivorous birds were the only group that had a statistically unequal number of species increasing relative to decreasing across multiple land use types (Fig. 4 *C* and *F*), and the only group to show disproportionate growth in intensively managed farms (Fig. 4*F*). In diversified farms, there was long-term growth in forest-associated, but not agriculture-affiliated, omnivores (Fig. 3*C*). In intensive farms, eleven agriculture-affiliated omnivorous species showed long-term population growth, whereas only four species showed long-term declines (Fig. 4*F*); four forest-associated omnivores increased in intensive farms and zero showed declines, though the limited sample size precluded formal statistical estimation of this effect (Fig. 4*E*).

Finally, nectar-feeding hummingbirds and the Bananaquit (*Coereba flaveola*), and granivorous birds, showed disproportionate population declines in a single land use type only (Fig. 4 *A* and *D*).

Fig. 3. Forest affinity and body size mediate population trends across land use types. Panels show the relationship between (*A–C*) forest affinity and (*D–F*) body size with population trends in (*A* and *D*) forests, (*B* and *E*) diversified agriculture, and (*C* and *F*) intensive agriculture. In (*A–F*), points depict species-specific population trends in each land cover type. (*A–C*) Forest affinity for each species was quantified using a multispecies occupancy model. (*D–F*) Body size was log-transformed before use as predictor in linear mixed-effects models. Black lines depict predicted relationship between forest affinity and population trends, with 95% Bayesian Credible intervals from a linear mixed-effects model. Color of points represents forest affinity, with green denoting high forest affinity, and yellow low forest affinity. (*A*, *B*, and *F*) Asterisks denote importance of linear relationship from linear mixed-effects model.

In forests, ten forest-associated nectarivores declined over the study, and only two showed long-term growth (Fig. 4*A*). Among agriculture-affiliated granivores in diversified farms, fourteen species showed long-term declines and only four increased (Fig. 4*D*).

Our analysis revealed differing population trends across habitats for forest-affiliated invertivores and frugivores. Among the 32 forest-affiliated invertivores increasing in diversified farms, seven species also showed population gains in forest habitats, while ten exhibited declines. Furthermore, only 10 of the 32 species exhibited population increases in intensive farms. Similarly, for the 18 forest-affiliated frugivores showing population growth in diversified farms, eight also exhibited population increases in forest habitats, while four showed declines

Discussion

Population data for 429 resident and migratory Neotropical bird species over 18 y reveal widespread population changes across forest and agricultural landscapes in Costa Rica. Contrary to our

expectations, community-wide population trends tended to be balanced in the number of species showing population growth and declines. However, moving beyond species identity to incorporate species traits revealed functional shifts in bird communities resulting from population changes.

The relative magnitude of declines by land use type was greatest in forest habitats, adding increasing evidence pointing toward the declining state of Neotropical forest biodiversity (9, 10, 14, 28), with the largest declines occurring in forest-affiliated invertivores. In agricultural landscapes, bird populations showed diverging trends by land management type. Specifically, in diversified farms, populations of some forest-affiliated species encompassing diverse ecological functions exhibited growth over nearly two decades.

However, population growth in diversified farms did not counterbalance declines in forest habitats, as many of the species showing growth in diversified farms were distinct from those declining in forest habitats. In intensive agriculture, population trends were characterized by declines in the population size of many forest-affiliated species and the selection for agricultural-affiliated
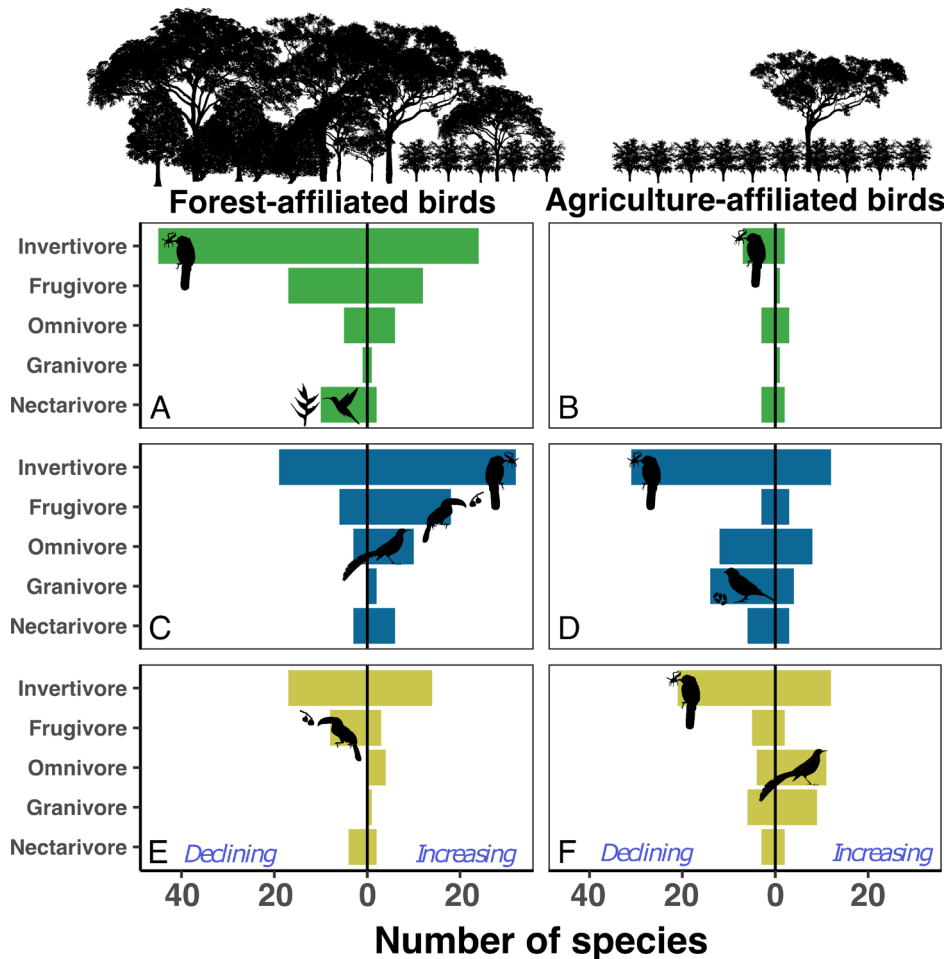
Fig. 4. Population trends by land use and trophic niche reveal general declines in primarily insect-eating (invertivore) birds across all land uses, with some growth in diversified farms. Guild-specific comparisons in the number of species showing population declines (negative x axis values) vs. population growth (positive x axis values) in (A and B) forests, (C and D) diversified farms, and (E and F) intensive agriculture. Panels in the left column (A, C, and E) represent guild-specific changes in forest-affiliated species, and panels in the right column (B, D, and F) represent agricultural-affiliated species in each land use type. Bird icons denote guilds with unbalanced (nonzero) variation in the number of species increasing vs. decreasing, as quantified using a Bayesian binomial proportion test. Bird icons within negative x axis values represent a greater number of species decreasing than increasing in a given guild, and icons within positive x axis values denote a greater number of species increasing than decreasing.

omnivores, such as the Tropical Mockingbird (*Mimus gilvus*) and the Red-winged Blackbird (*Agelaius phoeniceus*).

Forests. In forest habitats, we observed an alarming trend of biodiversity loss: Nearly 65% more species were decreasing than increasing over the 18 y across Costa Rica. The steepest declines were observed in forest-specialized invertivores, a group known to be particularly sensitive to the effects of deforestation and fragmentation (14, 29), and matching findings from other Neotropical forests (14, 28). A recent global analysis of avian population declines found that severe population fragmentation was the best predictor for declines in nonmigratory birds in South America (30). In this system, for example, the Rufous Mourner (*Rhytipterna holerythra*) and the Northern Nightingale-wren (*Microcerculus philomela*) are sensitive to habitat fragmentation, effects that have driven local extirpations throughout Costa Rica (15, 31); these same species were characterized by rapidly declining population sizes in this study. Even though the forest habitats sampled did not experience deforestation during this study, these declines support the hypothesis that this system is still paying off an extinction debt decades after the initial loss of surrounding forests.

Given the high diversity and magnitude of species declines in forest bird populations, it is likely that multiple factors beyond historical changes in forest cover explain these losses (32, 33). For example, despite the forest plots in our study representing the highest quality forest available in each region (at elevations commensurate with agricultural plots), the initial condition of these forests may contribute to the observed declines. Moreover, adjacent agricultural activities could impact not only the ecological integrity of the forests but also the bird populations they support. Climate change, whether directly through physiological responses or indirectly through effects on phenology and abundance of food resources, may in part also explain these declines. A recent long-term study in one of the study circles found declines in the richness and density of forest insects since the 1970s (34), an effect which can cascade up to drive bird declines. As such, the observed declines in forest bird populations may thus reflect not just changes in forest cover but also the combined effect of these multiple pressures on the ecosystem. While the mechanisms behind these declines are clearly an area that requires future research, the widespread losses in forest bird populations reveal the declining condition of tropical forest bird diversity.

Across families, population growth of bird species in forest habitats was primarily driven by expanding population sizes of species within families that showed growth across all habitats, including Accipitrid hawks and several oscine families (Tanagers, Cardinals,

and Grosbeaks and Wrens) that are known to survive in cities or agricultural areas. In addition, population increases were found in some agricultural-affiliated, disturbed forest, and edge-specialist species (*SI Appendix,* Table S1). These changes indicate that forest communities may be losing many South American endemic suboscine and nonpasserine forest species, in turn replacing them with more common species that are increasing in all land use types. Our findings suggest that this transition is being driven by slow changes in population sizes through time.

Diversified Farms. While the short-term benefits of diversified farming practices for forest biodiversity are well documented (35–37), our results demonstrate that this value to forest-associated species appreciates through time. Although the conversion from forest to farmland selects for open country species, we found that these landscapes gradually recover populations of some forest-affiliated species, with subsequent declines in early colonizers of newly deforested habitats. By managing smaller plots separated by fence rows and integrating forest patches of varying sizes, these farms maintain a complex, multilayered vegetation structure. This not only offers a variety of habitats for different bird species but also likely increases food availability and nesting options, providing vital resources for bird populations. For example, the increase in frugivorous bird populations on diversified farms may, at least in part, be attributed to the richness and abundance of fruit resources resulting from greater on-farm plant diversity, increased forest cover, and diverse shade plants (38). Additionally, diversified farms may serve as buffer zones or connective corridors between forest fragments, enhancing overall landscape connectivity and mitigating the effects of habitat fragmentation (36). The increased capacity to support forest-bird populations through time ultimately improves the value that these farming systems have for conserving biodiversity outside of protected areas.

Interestingly, diversified farms did not show widespread declines in forest-associated birds; rather, they showed population increases. For example, species that require complex vegetation to persist increased in diversified farming landscapes, including the Gray-headed Chachalaca (*Ortalis cinereiceps*), Grey-necked Wood-rail (*Aramides cajaneus*), Fiery-billed Aracari (*Pteroglossus frantzii*), as well as globally threatened species such as the Great-green Macaw (*Ara ambiguous*; IUCN Endangered) and Great Tinamou (*Tinamus major;* IUCN Near Threatened). Across guilds, increases in forest-associated birds were driven most strongly by insectivorous, frugivorous, and omnivorous birds.

The increase in forest-associated invertivores in diversified farms was particularly surprising, as population declines in forest-invertivores have been well documented elsewhere (9, 14), and invertivores showed relatively large declines in forest and intensive farming landscapes. While the increases in forest-associated invertivores in diversified farming landscapes are promising from a conservation perspective, they do not counterbalance the declines of invertivores in forest habitats, as many of the most forest-specialized species are not found in farming landscapes, including those showing declines in forests in this study.

Declines in diversified farming systems were greatest in Emberizidae seedeaters and swallows, families which associate most strongly with agricultural-affiliated and nonforested habitats. In addition, we found declines in agricultural-affiliated specialists such as the Yellow-faced Grassquit (*Tiaris olivaceus*), which has expanded its range and local abundance following widespread deforestation (39), as well as some other widespread species commonly found in agricultural landscapes (e.g., pale-breasted Spinetail, *Synallaxis albescens*).

Intensive Farms. Population changes in intensive agriculture revealed sustained degradation of bird diversity. Long-term winners were characterized by invasive species, agricultural-affiliated granivores, agricultural-affiliated invertivores, as well as deforestation-driven range-expanding species (*SI Appendix,* Table S3). The lagged but persistent declines in forest-affiliated frugivores (Fig. 4*E*) and replacement by open-country omnivores (Fig. 4*F*) suggest that long-term success in these landscapes depends partly on a species' ability to forage and obtain resources in a flexible manner. For example, the Great Kiskadee (*Pitangus sulphuratus*) showed some of the greatest levels of population growth in intensively managed farms (*SI Appendix,* Fig. S1) and also employs the greatest diversity of foraging techniques of the Costa Rican flycatchers (40).

Cross-Habitat Trends and Core Species Dynamics. Across the three land-use types, nearly 45% of the species were "core species," or species detected in each of the three land use types. These species often displayed trends of stability or even population growth across all habitats (*SI Appendix,* Fig. S4). Despite this, intensive farming practices often negatively affected a substantial subset of these forest-affiliated core species. Noticeably dominant in this group were species with stable or increasing populations in forests and diversified farms but marked declines in intensive farms. This divergence underscores the negative impact of intensive farming on forest-affiliated species able to persist in farming landscapes.

Our study also highlights a notable trend of migratory bird declines across all land use types, likely reflecting the complex interplay of local and broader-scale influences. While local land-use changes may significantly impact these trends, it is likely that other factors throughout the entire life cycle of migratory species play an important role. These birds face myriad challenges, and the nature of these treats can change across breeding and wintering grounds. Therefore, the declines we observed may be indicative not only of the conditions in Costa Rica but also of far-reaching issues in other parts of migratory ranges. Future research is needed to illuminate the complex interplay of factors that determine population trends of migratory species across their entire life cycles.

The declining trends observed among forest-affiliated and agricultural-affiliated invertebrate-eating birds have broad implications for ecosystem services, in particular pest control. Birds play a significant role in regulating insect populations, and a decrease in these bird populations could result in an increase in pest insects, affecting crop productivity (41, 42). This underlines the importance of maintaining bird diversity and abundance in these environments not only for biodiversity conservation but also for the sustainable maintenance of agricultural productivity.

Conclusion. As the magnitude of wildlife population declines accelerates globally, understanding how agricultural landscapes can help improve the long-term status of wildlife outside of protected areas has never been more important. Our findings on bird population trends suggest that diversified farming practices can reduce the magnitude of wildlife declines in agricultural landscapes by stabilizing and promoting growth in bird populations. Particularly, some forest-affiliated invertivores, frugivores, and omnivores greatly benefited. Nonetheless, these benefits through time do little to mitigate, much less negate, the precipitous declines found in tropical forest bird populations, and action is needed to help address declines in these increasingly threatened ecosystems. Conserving wildlife populations in the coming decades will require transformative changes not only in how we protect

Earth's remaining forests but also in how we manage agricultural landscapes for biodiversity and people.

Methods

Study System. Field data were collected in 48 transects that were distributed across a combination of countryside landscapes and protected forest areas in Costa Rica. The study transects can be split into four distinct regions: Guanacaste (GU), Las Cruces (LC), San Isidro (SI), and Puerto Viejo (PV). Within each of the four study regions, twelve transects were distributed across a land use gradient that included protected tropical forest habitats, diversified farming systems (small-scale traditional farming practices), and larger-scale mechanized intensively managed farms. Each of the 48 transects was 200 m in length and 50 m in width. On average, transects were separated by 10.5 km within each of the four study regions (*SI Appendix*, Table S1). Transects were originally chosen in 1999 based off GIS. The size distribution of the forest patches within which the forest transects were embedded ranged from small forest patches of 78 ha (Los Cusingos Bird Sanctuary) to as large as 47,500 ha (Braulio Carrillo National Park), with a median size of 22,928 ha (mean 23,358 ha). The designation of sites as "Forest" was straightforward, whereas factor analysis using farm-level and landscape-level characteristics was used to group transects into either "Diversified" or "Intensive" Farming systems in ref. 17.

Specifically, vegetation analyses at each agricultural transect were used to categorize nonforest transects into diversified farms or intensive farms based in (26). Transect-level vegetation was first characterized in each agricultural transect in 1999 and 2002. These transect-level measurements were then supplemented by a land-use classification map obtained from Fondo Nacional de Financiamiento Forestal (FONAFIFO). Local-level factors included the number of crop species, the quality and size of hedgerows, the size of the farm plot, and the number of vegetation strata. At the landscape-level, factors included the percentage of forest cover at 100- and 200-m radii. Using these local- and landscape-level factors, pairwise dissimilarity between all agricultural transects was calculated using the Gower Dissimilarity index. Gower Dissimilarity is a measure of the pairwise dissimilarity in vegetation structure, for all nonforest transects. Subsequently, these vegetation dissimilarity values were used for cluster analysis, employing an unweighted average pair-group mean method. This led to the division of nonforest transects into two categories of farming intensity: "low intensity" (n = 17) and "high intensity" (n = 19) (26).

Over the course of the study, all forest transects and a majority of agricultural transects remained relatively similar in land management and vegetation cover (19). However, four of the agricultural transects changed substantially in management type and were excluded from all downstream analyses to avoid bias in results driven by changes in land use during the study. Previous work has demonstrated that the long-term dynamics of the bird communities found within agricultural transects correspond most strongly to other transects within the same land use designation (19), reinforcing the usefulness of these classifications for categorizing farming practices and the bird communities found within.

Based on our field observations, we can infer that the overall chemical input in intensive farms is considerably higher on average than in diversified farms. This difference in pesticide usage may contribute to the differential impacts on bird populations that we observe between these two types of land use, although further study would be needed to conclusively establish this link.

Bird Community Sampling. From 2000 to 2017, bird community sampling took place in each of the 48 transects. In each of the 18 y, expert Neotropical ornithologist Jim Zook (J.Z.) visited the transects six times, three times in the dry season (Jan. to Apr.) and three times in the wet season (Oct. to Dec.). Transect counts took place for thirty minutes, during which J.Z. would observe all the birds seen or heard. The identity and number of birds detected within the 50-m transect buffer were recorded. Birds detected flying over the transect or outside of the transect were noted as "flyovers" and "out." In this study, we chose to only include birds found within transects (i.e., found using substrate within the transect counts, not flying through) to conform with assumptions of statistical independence among transect locations and to limit the scope to local-scale analyses of forest and farmland bird communities. Over the 18 y, we detected a total of 506 bird species within the 48 transects across the four study regions. For this study, we estimated species population trends for species in which there

were greater than 10 counts. As a result, 77 of the species detected within our study transects were excluded from population trend analyses. This resulted in a total of 429 species that were included in downstream population-level analyses.

Population-Level Analyses. We developed a multispecies hierarchical model to estimate latent community- and species-specific population trends in each land use type (19, 43). In the model, transect-level counts $X_{i,j,t,k}$ represented the number of individual detections of each species i at site j during each replicate visit k in year t, such that $X_{i,j,t,k} \geq 0$. We assumed that the abundance of species i at site j in year t was a Poisson random variable, such that $X_{i,j,t,k} \sim \text{Poisson}(\lambda_{i,j,t})$, providing a latent population size estimate for each species in each site in each year. This latent site-level population size for each species in each year (hereafter "population size") was then modeled as a linear function of spatial and temporal coefficients (44). Specifically, the population size of species i at site j in year t was given by:

$$\log\left(\lambda_{i,j,t}\right) = \beta0_{i,\text{landuse}[j]} + \beta1_{i,\text{landuse}[j]} \times \text{year}[t] + \beta2_{i,\text{region}[j]} + \beta3_{\text{site}[j]}.$$

$\beta0_{i,\text{landuse}[j]}$ describes species-specific intercept in each land use type, or the relative effect of each land use type on population size, allowing each species to vary in their response to land management. For the parameters $\beta0_{i,\text{landuse}[j]}$, species-specific intercepts were assumed to be drawn from a normal distribution with a mean and SD that were independent and centered around zero. $\beta1_{i,\text{landuse}[j]}$ denotes the log-linear trend in population size across the 18-y study for each species i in each of the three land use types j. Species-specific population trends in each land cover type were not modeled independently, but instead followed a normal distribution with a mean and SD that were estimated for each of the three land uses j.

$$\beta1_{i,\text{landuse}[j]} \sim \text{Norm}\left(\mu. \beta1_{\text{landuse}[j]}, \sigma^2. \beta1_{\text{landuse}[j]}\right).$$

Model Implementation. The community trend model was developed and written in the probabilistic programming language Stan, and full Bayesian inference was carried out with MCMC sampling in the Stan language (SI stanModel). Weakly informative "vague-ish" normal priors were used for community hyper-parameters to ensure model convergence (44). Models were run using the RStan package (45). Three chains were run for 1,500 iterations after an initial burn-in of 750 iterations at a thinning rate of one. In total, 2,250 posterior draws [(1,500–750) × 3] were used to summarize the 344,106 estimated model parameters, including 1,287 land-use specific population trends. Model convergence was assessed based off visual inspection of parameter trace plots and based off the Gelman–Rubin statistic (R-hat values) less than 1.1. Run time for this model was over 108 h.

Trends by Forest Affinity and Body Size. We next addressed how population trends within forest and agricultural habitats relate to a species' affinity with forest habitats. Forest affinity scores for each species were derived using multispecies-occupancy models (18). Briefly, a species affinity for forest was estimated as the log odds of a given species occupying a forest habitat after controlling for detection probability and regional differences. For subsequent analyses in this study, these coefficients were centered around zero and scaled between negative one and one (−1,1). Values closer to −1 indicate low affinity (low probability) of being found in forest habitats, whereas values closer to 1 indicate species that are strongly affiliated with forest habitats.

We used a second-step modeling approach of the estimated population trends to test for the effect of forest affinity and body size on population trends. To ensure that latent (i.e., random slope) population trend estimates for species that did not occur in a given land use type did not affect trait analyses, land-use specific trend estimates were excluded if that species had fewer than five individuals in that land use type over the study. Additionally, we only included species in the model whose trend 95% credible intervals did not overlap with zero in a particular land use type. This approach enabled us to focus specifically on species with significant long-term population changes.

We used linear mixed-effects models (46) to model population-trend estimates as the response to the interactive effects of land use intensity, forest affinity (continuous values derived from multispecies occupancy models and described above), and the log-transformed average male body size from ref. 39. We initially chose to include all two- and three-way interactions to test for complex life-history responses. In the model, species responses were originally treated as normal random intercepts

(random effects). However, the inclusion of these species-specific random effects produced unusually small and identical SE across multiple parameters, and we chose to exclude this model component (46). The exclusion of species-specific random effects did not change the posterior point estimate or significance of any terms for the model coefficients; however, it did produce more variable and realistic SE. Models were estimated using the glmmTMB function in the package glmmTMB (47). Model performance was assessed using the "simulateResiduals" function in the DHARMa package (48), and a chi-square discrepancy test was used to test for the significance of the interaction terms using the drop1 function. All analyses were conducted with the statistical software R (v4.0.5) and RStudio (v1.4.1717)

Trends by Trophic Niche. We chose to use the foraging niche, as it captures variation in both resource availability and finer-scale habitat requirements, both of which have been shown to modulate species' responses to land use change. In addition, global analyses have indicated that these categories, which take into account multiple trait dimensions, are highly representative of similar ecological functions that have converged throughout the tree of life (49).

We assigned each of the 429 species included in this study trophic foraging niche assignments from ref. 49 based on binomial nomenclature. To understand how long-term niche dynamics differ between forest-affiliated and agricultural-affiliated species, species were further split by forest affiliation. Species with values greater than zero were designated as "forest-affiliated," whereas species with forest-affiliation scores less than zero were designated as "agricultural-affiliated species." These groupings correspond to species that are more commonly occupying forest habitats (forest-affiliated species) and species that more commonly occupy agricultural habitats (agricultural-affiliated species) in this system. A Bayesian binomial proportion test of the relative frequencies was used to test

for unbalanced variation in the number species increasing vs. decreasing in each guild by land cover type. Binomial tests were run using the *bayes.prop.test* in the BayesianFirstAid package (50).

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