

Resilience and stability in bird guilds across tropical countryside

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The consequences of biodiversity decline in intensified agricultural landscapes hinge on surviving biotic assemblages. Maintaining crucial ecosystem processes and services requires resilience to natural and anthropogenic disturbances. However, the resilience and stability of surviving biological communities remain poorly quantified. From a 10-y dataset comprising 2,880 bird censuses across a land-use gradient, we present three key findings concerning the resilience and stability of Costa Rican bird communities. First, seed dispersing, insect eating, and pollinating guilds were more resilient to low-intensity land use than high-intensity land use. Compared with forest assemblages, bird abundance, species richness, and diversity were all ~15% lower in low-intensity land use and ~50% lower in high-intensity land use. Second, patterns in species richness generally correlated with patterns in stability: guilds exhibited less variation in abundance in low-intensity land use than in high-intensity land use. Finally, interspecific differences in reaction to environmental change (response diversity) and possibly the portfolio effect, but not negative covariance of species abundances, conferred resilience and stability. These findings point to the changes needed in agricultural production practices in the tropics to better sustain bird communities and, possibly, the functional and service roles that they play.

agriculture | avian | compensation | countryside biogeography | intensification

Diversity in biological communities is linked to ecosystem function in complex ways, making it difficult to project the consequences of biodiversity loss to humanity (1–7). Still, ecological theory and empirical findings have shown that high levels of biodiversity provide more pollination (8), seed dispersal (9), primary production (10), erosion control (6), decomposition (6), insect abundance regulation (11), and fish biomass production (12). Understanding how biodiversity will respond to expected future land-use intensification (13) will be crucial to predicting the future of Earth's life support systems (14). Although interest in the resilience of ecosystem processes to anthropogenic disturbance is burgeoning (2, 7), few studies have explicitly considered the resilience and stability of the communities of organisms involved in these ecosystem processes (15).

Resilience has traditionally been defined as the ability of an ecosystem process to recover from temporary disturbances or more recently, withstand more permanent disturbances (1, 2). Stability has been defined as constancy in ecosystem processes over time (3, 16). Rather than ecosystem processes, here, we assess the resilience of communities to land-use intensification. Specifically, we group Costa Rican birds into guilds involved in four key ecosystem processes—seed dispersal (frugivores), seed predation (granivores), insect abundance regulation (insectivores), and pollination (nectarivores)—and assess the resilience of guild structure to land-use intensification. Guild structure is determined by the total number of constituent individuals (abundance) and species (species richness) as well as the distribution of abundances across constituent species (diversity). We define resilience as the degree to which guild structure is

maintained across a land-use intensification gradient, and we define stability as constancy in guild structure over time.

What determines the resilience of biological communities remains largely unanswered. Multiple mechanisms have been put forth (2, 7), including the degree to which communities exhibit response diversity and/or the preponderance of negative correlations in abundance between species pairs over space or time. First, response diversity is defined as the variability in responses among organisms to an environmental disturbance (7). It may confer resilience, because if species react differently to disturbances, then there is a higher likelihood that guild abundance will remain constant after ecosystems change (7, 17). Second, negative covariation in abundance between species in the same guild can confer resilience by causing the total abundance of a guild to remain constant through disturbances (17–19). For example, the decline of one insect-eating bird after a disturbance could be offset by an increase in abundance of another species within the same guild. Such negative correlations may arise either through competition (referred to as density compensation) (17–19) or differing responses to abiotic conditions.

Determinants of community stability are better understood. In addition to serving as an indicator of guild resilience, species richness has been theoretically and empirically linked to community stability (3, 4, 12, 16, 20, 21). Two proposed drivers of the richness–stability relationship are the portfolio effect and negative covariance. The portfolio effect shows that a statistical consequence of many species fluctuating in abundance can be that total abundance remains constant (3). Additionally, diverse communities may also remain stable in total abundance if they may contain more competitors than species-poor communities and thus, exhibit more negative covariance (16, 20).

We use a 10-y dataset (1999–2008) of bird transect censuses in Costa Rica to examine whether bird communities are resilient and stable across a gradient of land-use intensity. The gradient extends over four 30-km-diameter regions, within which are replicated sites of forest ($n = 10$), low-intensity land use ($n = 16$), and high-intensity land use ($n = 15$). The four regions span Costa Rica's diverse life zones and agricultural systems: Guanacaste (lowland dry forest; melon, rice, and cattle), Puerto Viejo (lowland wet forest; heart of palm, banana, and cattle), San Isidro (midelevation wet forest; coffee, pineapple, and sugar cane), and Las Cruces (premontane wet forest; coffee, cattle, and mixed gardens). Compared with low-intensity sites, high-intensity sites had lower forest cover at 100- and 200-m radii, fewer crop species, fewer and lower quality hedgerows, larger and fewer agricultural plots, and fewer vegetation strata.

We assess avian resilience to intensification by examining trends in abundance, richness, and diversity for large (>100 g)

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seed-dispersing, seed-predating, insect-eating, and pollinating guilds. We analyze patterns in guild structure stability along the land-use intensity gradient by calculating (i) yearly variation in total bird detections within each guild and (ii) yearly variation in the number of constituent species within each guild. We then explain trends in bird community resilience by quantifying how birds react to land-use intensification (response diversity) and the frequency with which birds exhibit negative correlations with each other. Finally, we investigate whether species richness causes abundance to remain stable through the portfolio effect and/or negative covariance.

Results

We found more resilience to low- than high-intensity land use for three of four avian guilds (Fig. 1 *A–C* and Table S1). Consistent with prior research (22, 23), frugivores and nectarivores were slightly affected by low-intensity land use (compared with forest),

whereas insectivores declined significantly (Fig. 1 *A–C*). All three guilds, however, were significantly less abundant, species-rich, and diverse (exhibiting a less even distribution) in high-intensity land use than in forest. Unlike the other guilds, granivores proliferated outside of forest, peaking in abundance, species richness, and diversity in low-intensity land use (Fig. 1 *A–C*).

Effects of land-use intensity on stability varied by guild (Fig. 1 *D* and *E*). Frugivores and insectivores had the highest stability in

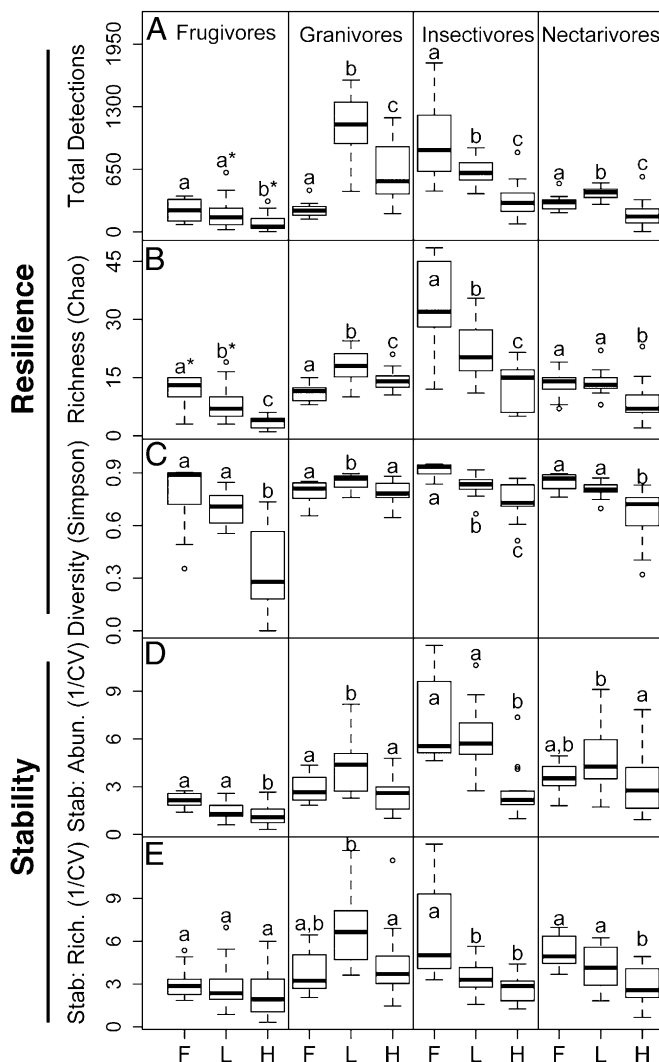


Fig. 1. Resilience of guild structure [(A) total detections, (B) species richness, and (C) diversity] and stability [the inverse of 10-y variation in (D) total detections and (E) species richness] along a land-use gradient (F, forest; L, low intensity; H, high intensity). Letters denote significance under Tukey posthoc or Wilcoxon signed rank tests ($P < 0.05$). Asterisks denote significance of $0.05 < P < 0.1$. Whiskers represent minimum and maximum values without outliers (circles) defined as two times the interquartile range subtracted and added from the first and third quartile (the bounds of boxes). Box and whisker plots show that birds were more resilient and stable in low- than high-intensity land use (Table S1).

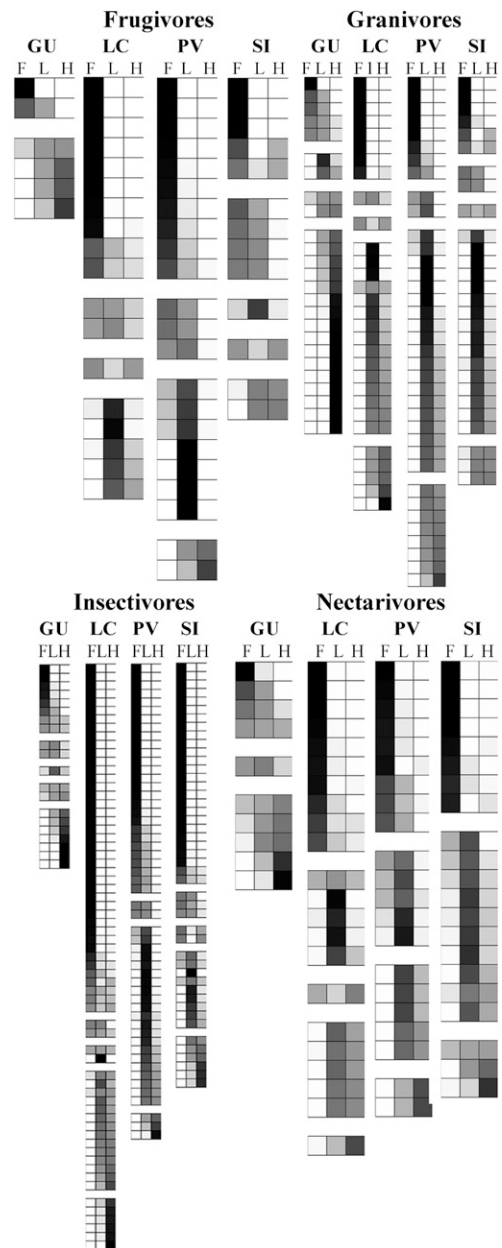


Fig. 2. Cluster analyses based on relative abundances of species in forest (F), low-intensity land use (L), and high-intensity land use (H). Rows are individual species, and columns are regions: Guanacaste (GU), Las Cruces (LC), Puerto Viejo (PV), and San Isidro (SI). Dark filled boxes indicate higher relative abundance. Species are grouped together by similar responses to land-use intensification (all species within the same group have >0.25 correlation coefficients). Groups of species are separated from each other with empty rows. Because multiple groups are present for each guild and region, it is clear that species within each guild respond differently to land-use intensification and thus, exhibit response diversity.

total yearly detections in forest and low-intensity land use, whereas nectarivores and granivores were most stable in low-intensity land use. For stability in species richness, frugivores exhibited no trends, insectivores were most stable in forest, granivores were most stable in low-intensity land use, and nectarivores were most stable in both forest and low-intensity land use.

We assessed determinants of guild resilience by searching for signs of response diversity and through analyses of negative covariance. To test for response diversity, we asked whether or not species identity determines relative abundance in each land-use intensity treatment. Separate analyses were conducted for each region because of differences in their species pools. In all cases, responses to land-use intensity treatments varied significantly by species identity ($P < 0.0001$), indicating that species within guilds exhibit response diversity in each region. To visualize response diversity, we separated guilds into clusters of species based on their relative abundance in each land-use treatment (Fig. 2). The fact that species exhibited significant response diversity is not surprising (17); although previously unexpected, high avian abundance and diversity in countryside is now well-established at our study sites (24, 25) and elsewhere (26).

Although response diversity was present, we found little evidence that negative covariance contributes to guild resilience. Variance-ratio tests showed that species pairs tended to co-occur and not negatively correlate over space (Fig. 3). Further, negative correlations possibly driven by diffuse competition were also absent: no more than 5% of populations correlated negatively with the rest of their guild (Fig. 3). Because defining guilds is subjective (27), we also asked whether species pairs more similar in traits were more likely to correlate negatively over space. Few significant trends were observed; however, for several years in several regions, frugivores more similar in traits were more likely to correlate negatively (Fig. 4). Negative correlations could also be evident in energy use and biomass rather than abundance (28). We reanalyzed our data, multiplying species' abundances by mass, but did not observe noticeable changes (Fig. S1).

To determine drivers of guild structure stability, we regressed stability in total yearly detections [1/coefficient of variation (CV)] against Chao species richness. Except for nectarivores, regressions were significant, indicating that a richness–stability

effect may be operating (3–5, 20, 21) (frugivores: $R^2 = 0.49$, $\beta = 0.09$, $P < 0.01$; granivores: $R^2 = 0.13$, $\beta = 0.13$, $P = 0.02$; insectivores: $R^2 = 0.45$, $\beta = 0.16$, $P < 0.01$; nectarivores: $R^2 = 0.03$, $\beta = 0.08$, $P = 0.29$) (Fig. S2). We explored whether this relationship may have resulted from the portfolio effect and/or increased negative covariance in species-rich communities. The portfolio effect has been shown to operate when variation in population abundance among years scales with mean population size among years with an exponent (z) greater than one (12, 20). Using yearly variation in total detections and mean detections as proxies for abundance, we found scaling parameters above one (frugivores: $z = 1.59$, $R^2 = 0.83$; granivores: $z = 1.36$, $R^2 = 0.80$; insectivores: $z = 1.02$, $R^2 = 0.71$; nectarivores: $z = 1.03$, $R^2 = 0.72$).

In contrast, we found that assemblages with higher species richness did not exhibit more negative covariance (frugivores: $\beta < 0.01$, $R^2 < 0.01$, $P = 0.90$; granivores: $\beta < 0.01$, $R^2 < 0.01$, $P = 0.78$; insectivores: $\beta < 0.01$, $R^2 < 0.01$, $P = 0.63$; nectarivores: $\beta = 0.06$, $R^2 = 0.07$, $P = 0.10$). In fact, we found no evidence that populations exhibit negative covariance in population size over time (17–19, 29), although positive correlations were sometimes present (Fig. 3). Repeating temporal analyses using the summed abundance of guilds rather than species pairs yielded the same result (Fig. 3). Moreover, the lack of negative correlations over time was not an artifact of how we defined our guilds: species more similar in traits did not exhibit more negative covariance over time (Fig. 4).

Discussion

We found that guilds were more resilient to low- than high-intensity land use, but negative covariance in abundance was not responsible for these patterns. Rather, we more often observed positive correlations between species pairs over space and time. Species within the same guild may have co-occurred spatially for several reasons. First, guilds may be comprised of closely related species with similar habitat requirements. Second, species may jointly peak in abundance where shared resources are abundant (30, 31). Third, many species, especially insectivores, form mutualistic mixed species flocks, traveling in concert in search of food (32). Over time, positive correlations in abundance may also arise because of common responses to abiotic factors (33–35). For example, because climate influences insect populations

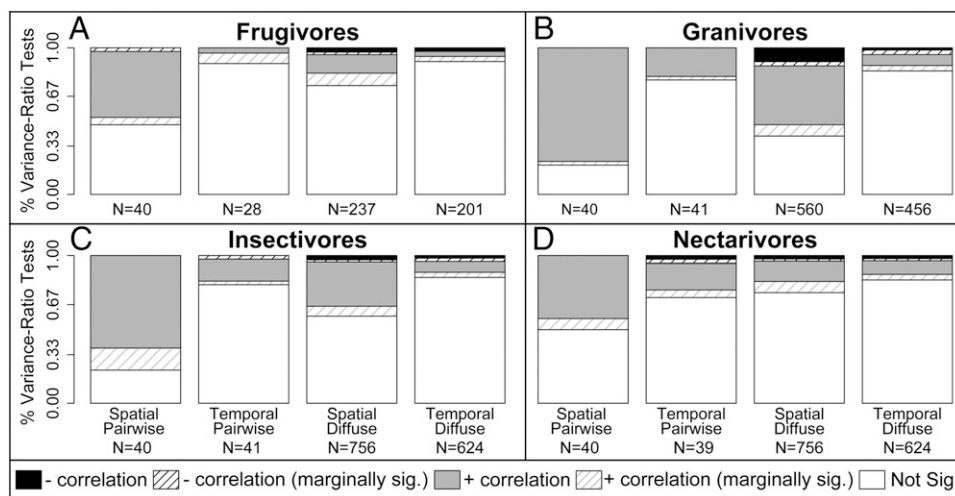


Fig. 3. Proportions of significant ($P < 0.05$) variance ratio tests for species pairs (pairwise) and between individual species and the rest of their guild (diffuse) over space (spatial) and time (temporal). (A) Frugivores, (B) granivores, (C) insectivores, and (D) nectarivores. For pairwise spatial analyses, one variance ratio test is used for each region ($n = 4$) and year ($n = 10$). For pairwise temporal analyses, one variance ratio is used for each transect ($n = 41$); however, transects without at least three constituent species are excluded. For diffuse spatial analyses, one test is used for each region ($n = 4$), each year ($n = 10$), and each species that meets a detection threshold (Methods). Similarly, diffuse temporal analyses are characterized by one test for each transect ($n = 41$) and species that meet the detection threshold. Marginal correlations are when $0.05 < P < 0.1$. The few negative correlations indicate an absence of negative covariance structure.

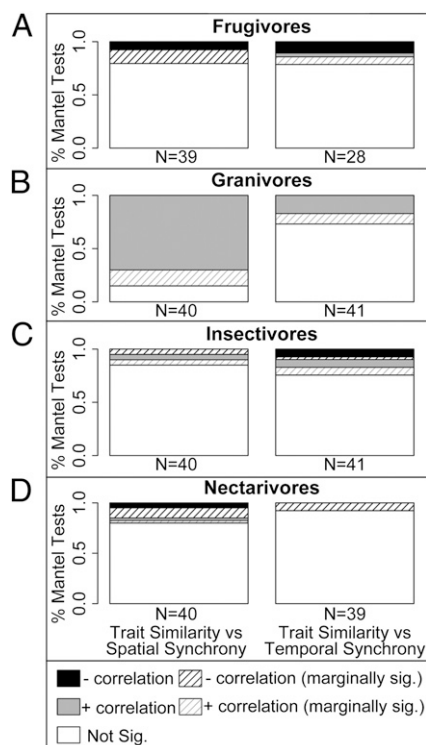


Fig. 4. Summary of correlations between (i) functional trait similarity of species pairs and (ii) the spatial/temporal co-occurrence of species [(A) frugivores, (B) granivores, (C) insectivores, and (D) nectarivores]. Species pairs were restricted to those pairs within the same guild to examine the influence of guild construction on finding signatures of negative covariance. Spatial mantel tests are used for each region ($n = 4$) and year ($n = 10$); temporal mantel tests are used for each transect ($n = 41$). Trait similarity and spatial/temporal co-occurrence were not consistently correlated; therefore, negative covariance structure was not more common between species that were more functionally similar.

and fruit availability (30, 32, 36), many species may increase in abundance when conditions are favorable.

Regardless, response diversity and possibly the portfolio effect seem to have played a larger role in conferring resilience and stability than negative covariance, and they may be responsible for contrasting patterns in guild resilience and stability among land-use intensity treatments. Although subsets of each guild were detected in all treatments, the number of species able to persist in high-intensity agriculture was limited. Correlations exist between bird diversity and insect abundance regulation (11), seed dispersal (9), and pollination (8), meaning that high-intensity land use may threaten these processes. Furthermore, because we found that species richness was related to guild stability, decreased species richness could potentially result in less stable provision of ecosystem processes over time (14).

Declines in guild abundance and richness, however, do not necessitate declines in ecosystem processes. The absence of negative correlations in abundance does not preclude compensation through changes in behavior (37, 38). For example, Spotted Antbirds (*Hylophylax naevioides*) assumed the behavior role of Ocellated Antbirds (*Phaenostictus mcleannani*) after their extirpation from Barro Colorado Island, Panama (38). Additionally, although negative correlations may not be evident over the time span of our study, negative correlations could still occur over longer timescales (38). Finally, within each functional group, some species may play larger roles than others (39). Certain ecosystem processes could persist if particularly important species are resilient to intensification, or alternatively, they

could exhibit rapid declines if important species are lost first (15, 39). Therefore, future studies aimed at predicting ecosystem function should assess species' roles in ecosystems on a per species basis.

Land-use intensification threatens birds, and compensatory changes in abundance do not seem to operate across the diversity of biomes and agricultural production systems investigated here. However, changes in guild structure and stability were generally significant only in high-intensity land use. Low-intensity land use systems, with small-scale polycultures that maintain tree cover and structurally diverse hedgerows (24), have the potential to retain diversity and stability in avian guilds. Future investigations would profitably focus on specific landscape-level attributes (e.g., extent, configuration, identity, and proximity of native vegetation) that may affect resilience and stability of bird communities (40). Because avian pollination, pest control, and seed dispersal are ecologically and economically valued (41), rationale exists for adjustments in land-use practices that decrease intensification to promote avian diversity and potentially augment and stabilize ecosystem service provision.

Methods

Study Sites. We characterized resilience and stability with avian censuses across Costa Rica. In 1999, we arrayed transects in four regions of Costa Rica with diverse climates and land-use histories: Puerto Viejo (PV), San Isidro (SI), Las Cruces (LC), and Guanacaste (GU). In each region, the predominant land use was originally subsistence farming (PV: 1700–1800s; SI: late 1800s; LC: 1950s; GU: 1700–1800s), with cattle farming increasing in the 1950s. In the 1970s, cash crops became popular (banana in PV, coffee in SI and LC, and rice in GU), and over the past decade, pineapple cultivation in PV and SI and sugar cane cultivation in GU have increased substantially. Deforestation has been largely halted since the 1980s in PV, the 1970s in LC, and earlier in SI and GU.

Within each region, we haphazardly stationed 12 200-m transects. Transects were placed along small roads and trails that are very numerous (making them representative of countryside) for ease of access. Forest transects were placed within tracts of continuous forest or large forest fragments. Non-forest transects were placed in agricultural plots and pastures and near small farmhouses, although agriculture predominated. We used cluster analysis (unweighted average pair group mean on Gower dissimilarity) to define land-use treatments using vegetation surveys from 1999 and a land-use map provided by Fondo Nacional de Financiamiento Forestal. Variables used to define Gower dissimilarities included number of planted crop species, number vegetation strata, quality and extent of hedgerows, size of agricultural plots, number of agricultural plots, and forest cover at 100- and 200-m radii. Nonforest transects formed two clusters (Analysis of Similarity: $R = 0.58$, $P < 0.01$): low-intensity ($n = 17$) and high-intensity ($n = 19$) sites. We excluded from analyses transects that were unstable (changing in classification) or spatially autocorrelated (Mantel tests: $P < 0.05$), although results were robust to their inclusion. We therefore report analyses from 41 transects: 10 forest and 16 low- and 15 high-intensity sites.

Avian Censuses. Starting in 1999 and continuing until 2008, sites were visited biannually, one time in the wet and one time in the dry season. Each transect was surveyed three times per season, with three transects surveyed each day. The order of surveying replicates was alternated each day to distribute the highly productive dawn hours across replicates and treatments. Later, total detections over the 3 d at each replicate were summed into a master species detections list to avoid pseudoreplication.

All birds seen and heard within 50 m of either edge of the path or road were recorded. Birds identified outside 50 m, flythrough birds (except for hummingbirds), and flyovers were noted but not included in the censuses. The first census began approximately at sunrise and lasted 30 min. Transects were walked continuously until the 30-min time period was reached. If time remained, the survey was continued, walking in the reverse direction. New individuals were counted if they could be distinguished from ones already counted (e.g., by sex, age, or simultaneous detection).

Using information from the work by Stiles and Skutch (42) and expert opinion (J.Z.), we classified birds into four feeding guilds, each important for a particular ecosystem service or process: large (>100 g) frugivores ($n = 34$, seed dispersal), granivores ($n = 61$, seed predation), insectivores ($n = 107$, insect abundance regulation), and nectarivores ($n = 43$, pollination). We restricted guild lists to species that are not nomadic and not in migratory

flux during our censuses periods. Published radio telemetry programs with three species at our study sites showed that species do not regularly commute from agricultural plots to large forest patches (43).

Resilience and Stability. We analyzed resilience by calculating total detections, Chao species richness, and Simpson diversity for each guild at each transect, summing over all years of data. For analyses of stability, we calculated two metrics for each guild and transect: the inverse of yearly variation in total detections and the inverse of yearly variation in species richness (CV). We used raw detections instead of modeling abundance to account for variability in detection probability for several reasons. First, transects were along roads and trails, making distance sampling unreliable (44). Second, data were not compatible with multiple observer (45) and time of detection methods (46). Finally, repeated survey methods do not accommodate small sample sizes (47), and abundance estimation with N mixture models resulted in high error rates. Instead, we minimized bias through surveying constancy: J.Z., an expert in Costa Rican avifauna, conducted all censuses.

In addition, we found all analyses robust to the exclusion of birds detected greater than 25 m from transects, where detection probability decreases rapidly. Furthermore, results were robust to excluding flock-forming birds, for which temporal changes in sociality could influence measured stability. Finally, we adjusted relative abundances according to estimates of detection probability for a subset of species ($n = 7$ frugivores, $n = 7$ granivores, $n = 25$ insectivores, and $n = 9$ nectarivores) from surveys conducted by the same observer (J.Z.) in the Las Cruces study circle (48). After excluding transects without at least two species, we found that several trends in abundance and diversity became not significant because of low sample size, but none changed in direction (except that granivores were detected slightly more in forest than high-intensity agriculture).

We used ANOVA with Tukey posthoc tests to examine how land-use intensity affects total detections, species richness, diversity, and $1/CV$ for total detections and species richness. For several analyses, residuals were not normally distributed; therefore, we fourth root-transformed the data to meet ANOVA requirements. When data could not be transformed, we used Kruskal–Wallis nonparametric tests with planned Wilcoxon signed rank contrasts. All statistical analyses were done in R (49).

Drivers of Resilience. Because our land-use intensity treatments are categorical and we include analyses of many species, we assess response diversity using contingency tables rather than the generalized linear models used by Winfree and Kremen (17). We pooled all observations of each species over 10 y of surveys by land-use type, forming contingency tables for each guild and region. We used Fisher exact tests and Monte Carlo randomization procedures to test whether land-use intensity and species identity were independent. The Monte Carlo procedure is conditional on row and column totals, and P values result from the proportion of simulated tables more extreme than observed data. To visualize response diversity, we then calculated pairwise correlation coefficients among all species in each guild based on their relative abundances in each land-use intensity treatment. We used these correlation coefficients in cluster analyses (unweighted average pair group mean), arbitrarily separating clusters based on a fixed threshold (<0.25 correlation coefficient between clusters) for clarity in visualization. If response diversity is absent, we expect that all species would similarly react to land-use intensification, and no separation of clusters would be possible; alternatively, the presence of multiple clusters indicates response diversity to land-use intensification.

We assessed whether communities exhibited negative covariance with a variance-ratio test and a Monte Carlo simulation that calculates a null variance ratio after randomization (17). We report these analyses in terms of total detections; however, replacing detections with biomass (total detections \times body mass) did not change our results. To test whether species pairs exhibited spatial asynchrony (tended to be located in different places), we pooled observations of each species on each transect within 1-y periods and fourth root-transformed abundances. Species were excluded from analyses if fewer than 10 individuals were observed per region or fewer than three transects were occupied per region. We then used 40 variance ratio tests, one for each region ($n = 4$) and year ($n = 10$), to test whether or not all the species pairs in each guild exhibited overall significant negative covariance over space.

For analyses of negative co-variance over time, we again pooled observations of species on each transect over 1-y periods, excluding species that were not detected at least three times per transect. We then used one

variance-ratio test per transect to assess the frequency of negative correlations in abundance between species pairs over time ($n = 41$). We excluded transects that did not host at least three species.

Diffuse competition could drive negative correlations between individual species and the summed abundance of their functional guild, rather than between species pairs. We therefore also examined whether spatial and temporal asynchrony was evident between individual species and the summed abundance of their functional guild. For spatial analyses, species were excluded from analysis if fewer than 10 individuals were observed per region or fewer than three transects were occupied per region. For temporal analyses, species were excluded from analysis if detected fewer than three times at a given transect. One variance-ratio test was conducted for each remaining species and transect.

Classifying species into feeding guilds is in part arbitrary, and it is possible that negative covariation could be evident only among species that are functionally similar and thus, compete more often. To address this concern, we compiled information on traits thought to influence resource use and acquisition for each species (42): size (mass and length), sociality (solitary, pairs, monospecific groups, and heterospecific groups), foraging strata (water, ground, lower, middle, and upper canopy, and above canopy), and foraging behavior (aerial, sallying, foliage gleaning, bark gleaning, ground rummaging, berry plucking, and stalking) (50, 51). Based on these traits, we calculated trait dissimilarity between every combination of species pair within each guild, thereby creating a matrix of dissimilarity in species traits. We used a Gower Dissimilarity Index, because it easily incorporates continuous, categorical, and binary data.

For each region ($n = 4$) and each year ($n = 10$), we calculated spatial co-occurrence (Pearson correlation coefficient) between all combinations of species pairs in each guild using the same criteria for exclusion as for spatial variance-ratio tests. For each transect ($n = 41$), we also calculated temporal co-occurrence (Pearson correlation coefficient), using the same criteria for exclusion as for temporal variance-ratio tests. Using the matrices of similarity in spatial/temporal co-occurrence and matrices of similarity in functional traits, we then related pairwise trait similarity to pairwise spatial/temporal co-occurrence with Mantel tests. We repeated all analyses, sequentially excluding functional traits to test whether our conclusions were robust. All significant relationships were robust to the traits considered: several relationships became nonsignificant, but none changed in direction.

Drivers of Stability. To assess the influence of species richness on stability, we regressed stability against species richness. Finding a significant relationship, we then attempted to identify underlying mechanisms by testing for the presence of the portfolio effect and/or increased negative covariance. The work by Tilman et al. (20) showed that the portfolio effect operates when variance in total yearly abundance scales with mean abundance among years with an exponent greater than one. For each guild, we summed species detections by year and transect, excluding species that were not found at least 3 of 10 y at any given transect. We then calculated mean total detections and variance in total detections among years for each species. Using these values, we parameterized the model by Tilman et al. (20) to discern whether mean detections scale with variance in detections with an exponent greater than one.

Additionally, negative covariance could drive species richness–stability relationships if species-rich transects boast more competitors than species-poor transects. We used the variance-ratio from temporal variance-ratio tests as an indicator for the strength of negative correlation between all of the species pairs in the community. Using transects as replicates, we regressed the variance ratio against estimated species richness to test whether species-rich transects boasted higher negative covariance than species-poor transects.

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