



Effect of scale on trait predictors of species responses to agriculture

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Abstract: *Species persistence in human-altered landscapes can depend on factors operating at multiple spatial scales. To understand anthropogenic impacts on biodiversity, it is useful to examine relationships between species traits and their responses to land-use change. A key knowledge gap concerns whether these relationships vary depending on the scale of response under consideration. We examined how local- and large-scale habitat variables influence the occupancy dynamics of a bird community in cloud forest zones in the Colombian Chocó-Andes. Using data collected across a continuum of forest and agriculture, we examined which traits best predict species responses to local variation in farmland and which traits best predict species responses to isolation from contiguous forest. Global range size was a strong predictor of species responses to agriculture at both scales; widespread species were less likely to decline as local habitat cover decreased and as distance from forest increased. Habitat specialization was a strong predictor of species responses only at the local scale. Open-habitat species were particularly likely to increase as pasture increased, but they were relatively insensitive to variation in distance to forest. Foraging plasticity and flocking behavior were strong predictors of species responses to distance from forest, but not their responses to local habitat. Species with lower plasticity in foraging behaviors and obligate flock-following species were more likely to decline as distance from contiguous forest increased. For species exhibiting these latter traits, persistence in tropical landscapes may depend on the protection of larger contiguous blocks of forest, rather than the integration of smaller-scale woodland areas within farmland. Species listed as threatened or near threatened on the International Union for Conservation of Nature Red List were also more likely to decline in response to both local habitat quality and isolation from forest relative to least-concern species, underlining the importance of contiguous forests for threatened taxa.*

Keywords: avifauna, behavioral plasticity, cattle pasture, IUCN Red List, montane, rainforest, threatened species

El Efecto de la Escala sobre los Pronosticadores de Características de las Respuestas de las Especies a la Agricultura

Resumen: *La persistencia de las especies en terrenos alterados por el humano puede depender de factores que operan en múltiples escalas espaciales. Para entender los impactos antropogénicos sobre la biodiversidad, es útil examinar las relaciones entre las características de las especies y sus respuestas al cambio en el uso de suelo. Un vacío clave de conocimiento afecta si estas relaciones varían dependiendo de la escala de respuesta que se está considerando. Examinamos cómo las variables de hábitat en escala local y a gran escala influyen en las dinámicas de ocupación de una comunidad de aves en las zonas de bosque de niebla en la región Chocó-Andes en Colombia. Al usar datos colectados a lo largo de un continuo de bosque y agricultura, examinamos cuáles características predicen mejor las respuestas de las especies a la variación local en granjas y cuáles*

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características predicen mejor las respuestas de las especies al aislamiento de bosques contiguos. El tamaño de extensión global fue un buen pronosticador de las respuestas de las especies a ambas escalas de agricultura; las especies con una amplia distribución tenían menos probabilidad de declinar si la cobertura de hábitat local disminuía y si la distancia al bosque aumentaba. La especialización de hábitat fue un buen pronosticador de las respuestas de las especies sólo en la escala local. Las especies de hábitat abierto tuvieron particularmente la probabilidad de incrementar si la pastura incrementaba, pero fueron relativamente inafectadas a la variación en la distancia al bosque. La plasticidad en la búsqueda de comida y el comportamiento de parvada fueron buenos pronosticadores de las respuestas de las especies a la distancia al bosque, pero no de las respuestas al hábitat local. Las especies con la menor plasticidad en el comportamiento de búsqueda de comida y las especies con seguimiento obligado de parvada tuvieron mayor probabilidad de declinar si la distancia al bosque contiguo incrementaba. Para las especies que exhibían estas últimas características, la persistencia en terrenos tropicales puede depender de la protección de bloques más grandes de bosque contiguo, en lugar de la integración de áreas en pequeña escala de bosque dentro de los terrenos agrícolas. Las especies enlistadas como amenazadas o casi amenazadas en la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza (UICN) también tuvieron una mayor probabilidad de declinar en respuesta a la calidad del hábitat local y al aislamiento del bosque en relación con especies de menor preocupación, lo que resalta la importancia del bosque contiguo para taxones amenazados.

Palabras Clave: avifauna, especies amenazadas, Lista Roja UICN, montano, pastura de ganado, plasticidad del comportamiento, selva

Introduction

Detailed knowledge of how species respond to anthropogenic stressors is fundamentally important for conservation (Phalan et al. 2011; de Lima et al. 2013). Identifying ecological and morphological predictors of species sensitivity to human-induced change particularly informs understanding of human impacts on biodiversity. By using species characteristics to predict cross-species variation in sensitivity to anthropogenic impacts, one can develop a clearer understanding of how community characteristics are altered by changes in land use. In turn, this understanding can provide important insights into ecosystem functioning and service provision (Elmqvist et al. 2003; Bregman et al. 2014).

Most studies use density- or abundance-based metrics to examine the relationships between species traits and their responses to anthropogenic stressors. For example, studies often relate species traits to measures of abundance or density variation across a gradient of human land-use intensity (Gray et al. 2007; Newbold et al. 2013). Typically, this approach views species responses as relatively fine-grain phenomena, where observed abundances are assumed to depend on local habitat characteristics. In reality, species abundances depend partially on local habitat features within a given location and partially on factors operating at larger scales. In farmland, for example, species abundances can also depend on the distribution of natural habitats in the surrounding landscape (Clough et al. 2009; Kennedy et al. 2010; de Lima et al. 2013). Surrounding natural areas can act as sources that buffer agricultural populations from extirpation via immigration (Pulliam 1988) or provide important resources to agricultural populations during some life stages (Evelyn & Styles 2003; Şekercioğlu et al. 2007).

For a more synthetic understanding of the links between species traits and their sensitivity to habitat change, it is necessary to tease apart such local- and landscape-scale influences on species occurrence. Until now, no one has examined whether the traits that predict species' responses vary depending on the scale of response being considered. Understanding how traits relate to local-scale responses (e.g., to within-farm habitat variation) can inform managers about the effectiveness of habitat-based conservation interventions. Similarly, understanding larger-scale responses can provide information on the likely impacts of landscape-scale habitat change. This can be particularly important for the design of protected area networks or prioritization of land-use policy (Harrison & Bruna 1999; Mattison & Norris 2005).

In the tropics, many studies have reported relationships between species' ecological and morphological characteristics and their tolerance of agricultural habitat. Among birds, for example, tolerance of agriculture correlates with many traits, including rarity, body mass, diet, reproductive strategy, range size, population size, and foraging guild (Cleary et al. 2007; Gray et al. 2007; Tscharrntke et al. 2008; Barbaro & Van Halder 2009; Şekercioğlu 2012; Newbold et al. 2013). Agreement across studies has been relatively weak (Ewers & Didham 2006), but general patterns include lower tolerance of agricultural expansion among larger-bodied and longer-lived species and species that feed largely on fruit or insects (Şekercioğlu et al. 2002; Gray et al. 2007; Newbold et al. 2013). It is unknown whether these relationships are mediated by species sensitivity to local habitats within farmland, sensitivity to large-scale patterns of habitat distribution, or both. This hampers informed conservation decision making about the scale at which efforts should be directed.

We analyzed avian community data from forests and cattle pasture habitats in the Chocó-Andes of Colombia, a zone straddling 2 global biodiversity hotspots (Myers et al. 2000). We examined species responses to agricultural development with hierarchical community models, which allowed us to evaluate the influence of agricultural habitat change at 2 scales: the relative cover of woodland at the local scale immediately around our sample points and the degree of isolation of a sample point from contiguous forests at the landscape scale. We compared species responses at both scales to a set of ecological and morphological traits, including foraging microhabitat preference, diet, foraging plasticity, migratory habits, global range size, and body mass. We considered the implications of our findings for agricultural development policies in tropical forest landscapes.

Methods

We collected field data from 3 areas in the Western Andes of Colombia within the departments of Antioquia, Risaralda, and Chocó (Supporting Information). Each area spans an altitudinal zone dominated by subtropical and submontane cloud forest (1290–2680 m above sea level), a range occupied by a high diversity of endemic and threatened taxa (Armenteras et al. 2003). Within each area, we sampled farmland and forest, including intact primary forests along with some secondary forest cover (age range 6–30 years). All study areas were alongside extensive contiguous forest tracts (>1,000,000 ha) stretching well beyond study area boundaries, which we confirmed using the ALOS/PALSAR pantropical cloud-free forest cover data set (Supporting Information) (Shimada et al. 2010). Our forest sampling locations therefore represented controls with which to compare the effects of agriculture. Cattle grazing is the principal agricultural land use in the region, accounting for more than 95% of farmed land use in each study area. It is also the primary agricultural activity throughout the Colombian Andes (Etter et al. 2006; Gilroy et al. 2014a). Farmland across all 3 study areas was typical of the region and contained a range of small-scale woodland features such as forest fragments, riparian strips, hedgerows, and gardens. We henceforth refer to these within-farm areas as *woodlands* and to contiguous forest habitats as *forest*.

Point Count Sampling

We sampled bird communities with 100 m radius point counts of 10-minute duration following Gilroy et al. (2014a, 2014b). We visited each point on 4 separate mornings from 06:00 to 12:00. We avoided conditions of rain or high winds. We varied the routes taken by observers each day to ensure that each point was visited both early and late in the sampling window. Points were arrayed within 400 × 400 m squares placed randomly

across all major habitat types. In each square, we located 3 points 200 m apart along a triangular transect. There was at least 300 m between squares in different habitats and 400 m between squares in the same habitat. In total, we sampled 20 squares in farmland, 23 squares in primary forest, 6 squares in mature secondary forest (15–30 years old), and 9 squares in younger secondary forest (<15 years old) for a total of 174 sampling points (Supporting Information). All point counts were conducted by experienced observers (J.J.G. and D.P.E.). We recorded all unknown vocalizations with Sennheiser ME66 microphones and Olympus LS11 recorders and identified them later through the use of extensive reference material (e.g., www.xeno-canto.org). To ensure that species occurrence could be meaningfully related to habitat characteristics within the study areas, we excluded records of highly mobile or transient species from the data set (e.g., large raptors and swifts and nonbreeding, trans-continental migrants). All sampling was carried out from January to March and June to July 2012, corresponding with the relatively dry period in the region.

Species Trait Data

We compiled data on body mass, range size, altitudinal range breadth, foraging, diet, flocking behavior, and seasonal movements for each species we encountered. Data on range size and generation length were taken from BirdLife International's World Bird Database (<http://www.birdlife.org/datazone>). We used extent of occurrence as an index of range size, which is the smallest continuous area encompassing all known, inferred, or projected sites of present occurrence of a species, excluding cases of vagrancy. Data on altitudinal ranges, body mass, foraging, diet, flocking, and migratory behavior were taken from species accounts in the Handbook to the Birds of the World Alive online repository (<http://www.hbw.com>). For each species, we calculated a score for foraging plasticity based on the range of foraging microhabitat preferences, foraging modes, and diet groups mentioned in each individual species account. For each of the habitat, mode, and diet categories in Table 1, we scored each species 1 or 0 depending on the nature of wording in the account. We then summed these values to given an overall plasticity score for each species.

Additionally, we identified the principal microhabitat specialization and diet group of each species (Table 1), again based on the wording of each species account, and recorded these as categorical variables. In cases where no clear principal microhabitat or diet could be identified, we classified species as generalists. We also determined whether species were obligate followers of mixed-species foraging flocks based on use of the words *usually*, *mostly*, or *invariably* in flocking descriptions (this excluded species moving in single-species flocks). We recorded this as a binary variable. We also classified

Table 1. Foraging traits used to evaluate plasticity in foraging behavior across species.*

<i>Trait</i>	<i>Description</i>
Microhabitat specialization	
Open areas	use of grassland, clearings, or other non-forested areas
Forest terrestrial	use of forest floor
Forest understory	use of vegetation close to the ground, shrubs
Forest midstrata	use of forest between understory and canopy
Forest canopy	use of all parts of forest canopy, including lower canopy
Foraging modes	
Soil or leaf litter gleaner	food taken from within soil or litter layer
Trunk or branch gleaner	food taken by gleaning from bark or epiphytic plants
Foliage gleaner	food taken by gleaning from foliage or from plant material itself
Aerial	food taken in mid-air
Diets	
Nectar	nectar resources, species described as nectarivorous
Seeds	seed resources, species described as granivorous
Fruit	fruiting bodies, excluding seeds, species described as frugivorous
Insects	any invertebrate prey
Vertebrates	any vertebrate prey

*Each species was assigned a binary indicator for each trait, which were then summed to generate an index of foraging plasticity across species.

species as seasonal movers if their accounts described regular seasonal or altitudinal movements.

Habitat Variables

We visited all areas within a 100 m radius surrounding each sampling point to visually map the distribution of habitats (following Gilroy et al. 2014a, 2014b). We estimated the ages of secondary forest stands through informal interviews with reserve managers and locals. When reported ages differed, we used the mean (Gilroy et al. 2014a). For points in farmland, we mapped all areas of woodland habitat, including fragments (size range 0.1–27 ha), riparian corridors, hedgerows, isolated trees, and other wooded features (e.g., gardens), and grazed pasture and other habitats. Using digitized copies of each map, we calculated the proportionate cover of pasture surrounding each point relative to the cover of woodland habitats. We used this value as an index of within-farm habitat quality surrounding each point (henceforth local habitat index). The index ranged from 0, representing a landscape completely covered by woodland habitats, to 1, representing a landscape completely covered by grazed pasture. Other habitat types (e.g., roads, rivers) were excluded from consideration in the index.

To measure the large-scale effect of isolation from natural habitat tracts, we estimated the linear distance from each sampling point to the nearest contiguous forest edge based on data from the ALOS/PALSAR pantropical cloud-free forest cover data set (Shimada et al. 2010). As ground truthing revealed some inaccuracies in the remotely sensed data, we also directly mapped the limits of contiguous forest on the ground with handheld GPS units or by visually mapping forest edges for parts of study areas that were inaccessible. We combined these

observations with the ALOS/PALSAR map to create a best-estimate layer delimiting the current extent of contiguous forest (i.e. all primary and secondary forests with direct connectivity to large forest tracts, excluding isolated fragments) across each site in ArcMap version 10 (Gilroy et al. 2014c). We used this layer to calculate distances from the forest edge for each sampling point.

Statistical Analyses

We modeled species occurrence probabilities across our sample sites as a function of habitat variables with a community-level hierarchical framework in which we controlled for cross-species variation in detection probability (Dorazio et al. 2006; Zipkin et al. 2009). In this model we applied a state-space formulation in which true species occurrence probabilities were modeled alongside an observation model that was fitted to observed data. This allowed species-specific detection probabilities to be estimated as a function of the number of times each species was detected over repeat visits to each individual sampling point (Dorazio et al. 2006). We assumed that detection probabilities varied in relation to the timing of visits, because most species are easier to detect at times closer to dawn, and included a random intercept indexed by species and study area to control for region-level autocorrelation.

For each species, we modeled true occurrences across all point count locations as a binomial response to 2 predictor variables: the local habitat index and the linear distance to contiguous forest. We centered and standardized both these predictor variables prior to analysis, ensuring direct comparability of model parameter estimates (Schielzeth 2010), and incorporated linear and quadratic terms for each predictor to account for

potential nonlinearity in species responses. The model for each species also included a categorical term indicating whether sampling points were located in primary forest, secondary forest, or farmland; a parameter accounting for altitudinal variation in species occurrence; and a random intercept indexed by species and study area to account for region-level variation in species occurrence probabilities.

The model was hierarchical at the community level, such that all species-level parameters (occurrence and detection) were treated as random effects with values drawn from hyper-parameter distributions representing the full spectrum of variation across the community (Kéry & Royle 2008). We assigned diffuse uniform (0,1) priors for hyper-parameter means and inverse-gamma (0.1, 10) priors for hyper-parameter variances (Dorazio et al. 2006). We fitted the model with WinBUGS version 1.4 (Spiegelhalter et al. 2003) and sampled the posterior distribution of each parameter for 50,000 iterations following a burn-in of 30,000 iterations.

To facilitate direct comparison of species responses across the 2 scales of interest, we generated standardized response indices for each species at each scale. We used the fitted hierarchical model to predict species occurrence probabilities for sets of simulated sites where the habitat predictor in question (either local habitat index or distance from forest) was allowed to vary across a uniform distribution representing the extent of variation we sampled in the field and other variables were held constant (1000 replicates for each species at each scale). We then compared these predictions to equivalent values for sets of simulated sites in contiguous forest. We took the mean proportionate difference between these occurrence probabilities as a standardized index of response for each species at each scale. We refer to these indices as the local habitat response and forest distance response hereafter.

We assessed relationships between species response indices and species traits using generalized linear mixed models (GLMMs) with family included as a random effect to control for potential phylogenetic non-independence. GLMMs were used at this stage because, unlike the Bayesian framework used in the first stage of modeling, there are established methods for model selection and multimodel inference associated with GLMMs (Burnham & Anderson 2002). We treated body mass, global range size, and foraging plasticity score as continuous predictor variables (Table 1), which were centered and standardized prior to analyses. We treated foraging microhabitat, diet, flock following, and migratory status as categorical variables (Table 1). For both of the response indices (response to local habitat index and response to forest distance), we conducted a full exploration of parameter space by fitting every possible combination of these variables. We derived model-averaged parameter effect sizes and unconditional standard errors by ranking model coefficients according to their AIC weight

Table 2. The relative importance of species traits explaining observed species responses to agriculture based on a local habitat index (proportion of pasture cover relative to woodland area) and the linear distance from the edge of contiguous forest.*

Trait	Local habitat response ΣAIC_w	Forest distance response ΣAIC_w
Global range size	0.999	0.999
Altitudinal range	0.451	0.597
Body mass	0.341	0.312
Plasticity index	0.382	0.952
Seasonal movements	0.459	0.567
Flocking	0.551	0.988
Foraging microhabitat	0.999	0.574
Diet	0.642	0.981

*Importance is estimated as the sum of Akaike's information criterion (AIC) weights of all models including a given trait from a full set of possible model combinations. Species responses are modeled from observation data, controlling for variation in detection probability.

(Burnham & Anderson 2002). We also summed AIC weights for models containing each predictor (ΣAIC_w) as an index of likelihood that each variable should be included in the best model. Finally, we assessed whether the responses of species listed as threatened or near threatened on the International Union for Conservation of Nature (IUCN) Red List (IUCN 2008) differed on average from those of species classified as least concern via *t* tests. A schematic diagram detailing the analysis rationale is in Supporting Information.

Results

We modeled the responses of 319 bird species from 38 families across our 3 study areas. Most species declined in agriculture relative to forest (78% of species). On average, species occurrence probabilities were 59% lower at sampling locations within farmed areas (mean across all species) than in contiguous forest. Species responses to local habitat and distance from forest varied widely across the community (Figs. 1a & 1b) and were only weakly correlated (Fig. 1c), indicating considerable variation in the relative sensitivity of species to local- and large-scale habitat change. Across the whole community, species occurrence probabilities were predicted to decline on average by 26.8% as distance from forest increased from 500 to 1000 m. Similarly, predicted occurrence probabilities declined by 27.1% as the proportion of local pasture cover increased from 40% to 60%.

Relationships between species traits and their responses to agriculture were highly sensitive to the response scale considered (Fig. 2). Habitat specialization, for example, was strongly linked to local habitat responses but showed limited predictive power for forest distance responses (Table 2). The relationship between

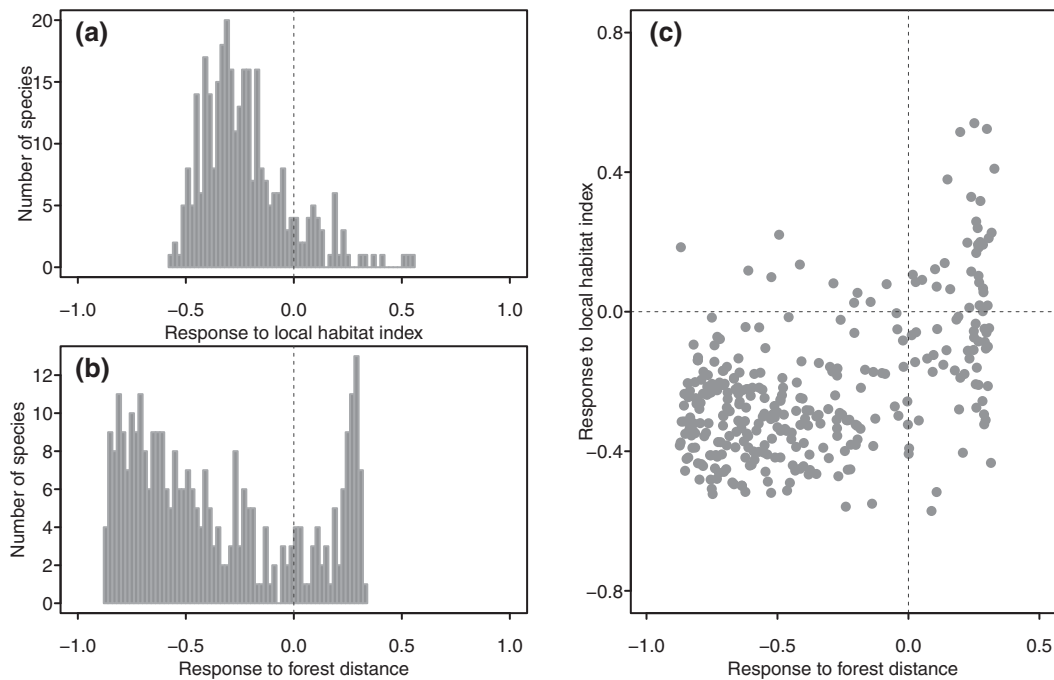


Figure 1. Species responses to (a) the local habitat index and to (b) large-scale isolation from contiguous forests. Responses to the local habitat index reflect the mean proportional change in species occurrence as cover of pasture increases, relative to woodland. Responses to forest distance reflect the mean proportional change in occurrence as linear distance from the edge of contiguous forest increases. Both responses are standardized to allow direct comparability; effects of other variables are controlled. (c) Correlation between the 2 responses across all 319 species considered.

habitat specialization and the local habitat response was largely driven by a strong effect of species that use open habitats; these species were more likely to respond positively to decreasing woodland cover at the local scale (Fig. 2c). Conversely, terrestrial and undergrowth specialists were more likely to decline as local woodland cover decreased (Fig. 2c). Although a similar link was evident between habitat specialization and species responses to distance from forest (Fig. 2b), the effects were of a smaller magnitude and had a much lower level of support in model selection (Table 2).

Foraging plasticity and flocking behavior, by contrast, were stronger predictors of responses to distance from forest than responses to local habitat (Table 2). Species with low scores for foraging plasticity were more likely to decrease in farmland as distance from contiguous forest increased (Table 2 & Fig. 2b). Similarly, obligate flock-following species showed a higher tendency to decline as isolation from forest increased, relative to nonflocking species (Fig. 2a). Foraging plasticity and flocking were unrelated to local habitat responses (Table 2 & Fig. 2).

Responses at both scales were strongly related to global range size. Species with large global ranges were more likely to show positive responses to increasing pasture cover at the local scale and to increasing distance from contiguous forest than species with small ranges (Table 2 & Fig. 2). We found weaker support for effects of body

mass, altitudinal range breadth, and seasonal movements on the response scales considered; model-averaged parameter standard errors always spanned zero (Table 2 & Fig. 2). Similarly, species dietary specializations were weakly related to responses at either scale (Table 2 & Fig. 2). We found some evidence for a phylogenetic signal in the random effects from both model sets, suggesting considerable cross-family variation in the strength of responses to local habitat and isolation from contiguous forest (Supporting Information).

We detected 20 near-threatened or threatened species across our study areas. On average, these species had significantly stronger negative responses to the local habitat index and forest distance than species listed as least concern (local habitat: $t = 2.37$, $df = 29.97$, $P = 0.025$; forest distance: $t = 4.61$, $df = 25.15$, $P < 0.001$; Fig. 3). Compared with least-concern species, threatened and near-threatened species tended to have significantly smaller global ranges ($t = 4.07$, $df = 38.04$, $P < 0.001$), narrower altitudinal ranges ($t = 4.12$, $df = 21.91$, $P < 0.001$), and lower plasticity scores ($t = 2.14$, $df = 23.75$, $P = 0.043$), although they did not differ significantly in body mass ($t = -1.24$, $df = 22.39$, $P = 0.226$). Proportionately fewer threatened and near-threatened species were classed as obligate flock followers (4.7%) or seasonal movers (19.1%) than least-concern species (12.4% and 29.8%, respectively).

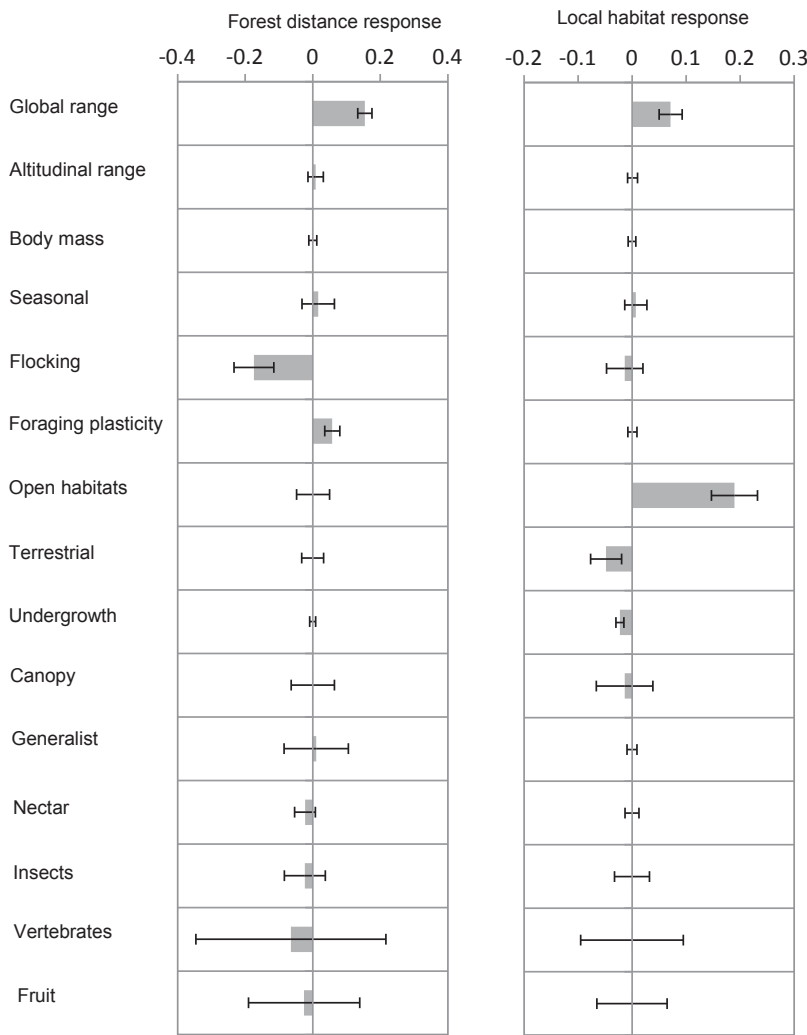


Figure 2. Model-averaged effect sizes (SE) indicating the relationship between species' traits and their responses to local habitat within farmland and the linear distance from each sampling point to contiguous forest.

Discussion

Some studies show that tropical agricultural landscapes retain relatively high biodiversity value when farmland is interspersed with wildlife-friendly areas (Daily et al. 2001, 2003; Ranganathan et al. 2008). However, it is often unclear whether these communities are sustained in part by immigration from surrounding natural habitats. In our study area, many bird species showed high sensitivity to distance from forest, suggesting that immigration could play an important role in structuring the avifauna of farmland. We are the first to find that the species traits associated with these large-scale habitat responses differ from those associated with local habitat sensitivity. Species responses to forest distance were strongly associated with 3 traits in particular: global range size, foraging plasticity scores, and flocking behavior. In contrast, responses to the local habitat index were strongly related to the primary habitat associations of species, alongside global range size.

These differences in trait-response relationships across scales have important implications for understand-

ing human impacts on agricultural communities. In particular, by teasing apart local- and large-scale responses, our methods allowed us to predict how communities may change as large natural areas become increasingly denuded in tropical landscapes. Our results highlight the potential for many species to decline or disappear from agricultural communities as they become isolated from large contiguous forests. The species most vulnerable to this isolation effect are those with small global ranges and lower foraging plasticity scores, in particular flock-following specialists. Our results suggest that species with these characteristics may be relatively less likely to benefit from increases in woodland habitat features within farmland unless larger forest blocks are nearby.

Although behavioral plasticity is an important predictor of species sensitivity to anthropogenic change (Miller & Cale 2000; Swihart et al. 2003; Tuomainen & Candolin 2011), the specific link between behavioral plasticity and isolation from natural areas has not been shown previously. Plasticity in foraging behavior is likely to be an important trait facilitating adaptation to novel agricultural habitats, increasing the likelihood of highly plastic

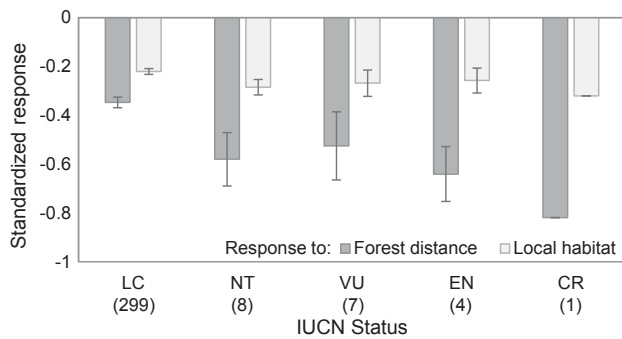


Figure 3. Comparison of species' mean responses to agriculture and distance from contiguous forest across International Union for Conservation of Nature (IUCN) Red List categories (LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered). Numbers of species in each category are in parentheses. Local responses to pasture cover reflect the mean proportional change in occurrence as local cover of pasture increases relative to woodland habitats, whereas forest distance responses reflect the mean proportional change in occurrence as linear distance from the edge of contiguous forest increases. Both responses are standardized to allow direct comparability; effects of other variables are controlled.

species establishing populations within farmland. Specialist foragers, in contrast, appear to be less likely to occupy farmland unless contiguous forests are nearby. Dietary specializations—particularly insectivory and frugivory (Cleary et al. 2007; Vetter et al. 2011; Newbold et al. 2013)—can be important predictors of species persistence in tropical agriculture and of overall extinction likelihood (Şekercioğlu 2011). However, we found little evidence of a link between specific diets and species responses at either scale. Our results suggest that narrowness of diet composition and foraging tactics, rather than diet specialization itself, is an important predictor of species responses to agriculture.

Flocking behavior was also a strong predictor of species responses to distance from forest. It suggests that flock-obligate species are more likely to decline in farmland isolated from contiguous forest. The lack of a corresponding link between flocking and responses to local habitat suggests that flock followers may benefit relatively little from increased within-farm habitat quality, unless farmland is close to forest. High sensitivity of flocking specialists to habitat degradation has been demonstrated previously in tropical avifaunas (Stouffer & Bierregaard 1995; Laurance 2004; Peters et al. 2008), further underlining the vulnerability of flock species to anthropogenic change. Understory flock specialists show heightened reluctance to cross open areas (e.g., logging roads, Laurance et al. 2004; Lees & Peres 2009), hinting that agriculture could

also represent a barrier to dispersal, which would limit the colonization of within-farm woodlands. The loss of obligate flocking species from agricultural communities isolated from forest could have substantial consequences for community assembly—an issue deserving of further study (Daily et al. 2001).

A strong link between species habitat associations and their responses to local habitat variation is perhaps to be expected (Newbold et al. 2013). In our study, this link was largely driven by open habitat specialists, which showed strong positive responses to increasing pasture cover (and hence decreasing woodland) in the local area surrounding sampling locations. However, understory and, in particular, terrestrial species also responded negatively to increasing local pasture cover, underlining the sensitivity of these groups to forest loss (Stratford & Stouffer 1999; Laurance et al. 2004; Lees & Peres 2009). Other studies suggest canopy specialists have limited tolerance of agriculture in the tropics (Sodhi et al. 2004; Gray et al. 2007), but we found no relationship between canopy specialization and species responses at either spatial scale.

Although previous studies have shown larger-bodied species to be more sensitive to habitat loss (Owens & Bennet 2000; Cleary et al. 2007; Tscharnatke et al. 2008), we found little evidence for a link between body mass and species responses at either spatial scale. This could be because our models accounted for a broader range of traits than most previous studies. A recent global analysis of species responses to agriculture also found little effect of body mass after accounting for the effects of other variables (Newbold et al. 2013). We found no effects of altitudinal range breadth or migratory behavior, but global range size was a strong predictor of species responses at both scales. Species with smaller ranges were more likely to decline with increasing pasture cover and distance from forest, indicating strong sensitivity of range-restricted species to agricultural habitat change. This echoes the findings of previous studies linking range size to species sensitivity to agriculture (Renjifo 1999).

Threatened and near-threatened species tended to be more sensitive to agriculture at both local and large scales than species classified as least concern. The IUCN's classification criteria require information on the magnitude of declines in range and population size in response to environmental change (Rodrigues et al. 2006; IUCN 2008), which are typically inferred from rates of habitat loss. In the absence of detailed data on species responses, these inferences are often based on best-guess estimates of the sensitivity of each taxon to agricultural conversion. Our study provides rigorous quantification of these sensitivities for a highly threatened avian community in the tropical Andes (Supporting Information) and should therefore be of substantial value for conservation prioritization. Our observation that threatened and near-threatened species tended to have lower plasticity scores than least-concern

species further highlights the importance of behavioral plasticity as a predictor of vulnerability to agriculture.

Management Implications

Understanding how species traits correlate with their responses to agriculture will facilitate better predictions of the functional effects of different land-use scenarios (Newbold et al. 2013). Diversity itself is an important component of ecosystem resilience because diverse communities are more likely to hold multiple species capable of contributing to a single given function (Nystrom et al. 2000; Elmqvist et al. 2003; Hooper et al. 2005). Our work highlights the need for studies of functional diversity to account for both local- and large-scale factors that influence community structuring. Farmed landscapes in close proximity to contiguous forests are more likely to support diverse communities, including specialized and range-restricted species, than farmlands isolated from forest. Inferences about functional diversity and ecosystem resilience derived from studies in farmed landscapes may be misleading if the effects of forest proximity on species occurrence are not taken into account. In particular, community functional diversity within small-scale woodland habitats in farmland could be overestimated if the buffering role of surrounding natural areas is overlooked.

Our results suggest that actions promoting the wider adoption of wildlife-friendly farm management, for example by leaving a greater proportion of land as woodland fragments or shade trees (Manning et al. 2006), are likely to be of most benefit to a subset of species that show a strong response to local habitat quality (Perfecto & Vandermeer 2010). However, these measures may be insufficient to sustain a further array of species that are sensitive to isolation from contiguous forest. The future of these species may be strongly dependent on the protection of large contiguous forest reserves within tropical landscapes (Gibson et al. 2011). Our results suggest that these reserves could play extremely important roles in sustaining community diversity within surrounding agricultural lands, with potentially important knock-on effects for agricultural ecosystem service provision (Hooper et al. 2005). Our results strongly underline the need for measures to protect remaining contiguous forests within the Chocó-Andes region, given the clear importance of these areas for a large number of highly threatened taxa.

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Supporting Information

A study area map, an analytical workflow diagram, a summary of family-level random effects (Appendix S1) and a table of species-specific response values (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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