RESEARCH ARTICLE

Foraging ecology and flocking behavior of insectivorous forest birds inform management of Andean silvopastures for conservation

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ABSTRACT
Wildlife-friendly agricultural practices, such as agroforestry, can play an important role in conserving biodiversity by providing and connecting habitat across working landscapes. Silvopastures (i.e. pastures with substantial tree cover), in particular, possess considerable potential for conserving biodiversity due to the dominance of pastoral landscapes in many regions. However, to balance tradeoffs between the conservation and agricultural values of these anthropogenic systems, better information on wildlife use and how it relates to habitat quality is needed. To improve our mechanistic understanding of silvopastoral habitat quality, and to develop management recommendations, we evaluated the foraging behavior of insectivorous forest birds in Andean silvopastures compared with forest fragments. Focal species' prey attack rates were >25% lower in silvopastures than in forest fragments, suggesting that arthropod prey were less abundant or accessible in silvopastures than in forest fragments. In forest fragments, birds in mixed-species foraging flocks attacked prey more frequently than solitary birds. In silvopastures, flocking and solitary birds attacked prey at similar rates, and birds foraged in flocks half as frequently as in forest fragments. Insectivorous birds preferentially foraged in a small subset of tree genera in forest fragments, but did not exhibit selective foraging in less botanically diverse silvopastures. Insectivorous species that used silvopastures foraged in microhabitats such as vine tangles and hanging dead leaves less frequently than species that did not use silvopastures. Forest species that used silvopastures may have been negatively affected by a breakdown of beneficial interspecific interactions in silvopastures, highlighting the potential for cascading effects of species loss in anthropogenic habitats. Managing silvopastures to include preferred tree species and microhabitats could improve their habitat quality for forest species, but strategies to enhance the conservation value of managed landscapes with silvopastures must also include preservation of forest fragments.

Keywords: avian community ecology, anthropogenic habitat, interspecific interactions, land-sharing, mixed-species flocks, mutualism, wildlife-friendly agriculture

La ecología de forrajeo y el comportamiento de bandada de aves insectívoras de bosque aporta al manejo y la conservación de los sistemas silvopastoriles andinos

RESUMEN
Las prácticas agrícolas amigables con la vida silvestre, como la agro-forestería, pueden jugar un rol importante en la conservación de la biodiversidad al ofrecer y conectar el hábitat a través de paisajes antrópicos. En particular, los sistemas silvopastoriles (i.e., pasturas con una cobertura sustancial de árboles) poseen un potencial considerable para conservar la biodiversidad debido a la dominancia de paisajes pastoriles en muchas regiones. Sin embargo, para balancear los costos y beneficios entre la conservación y el valor agrícola de estos sistemas antropogénicos, se necesita mejor información sobre el uso de la fauna silvestre y cómo esto se relaciona con la calidad del hábitat. Para mejorar nuestra comprensión mecanicista de la calidad de hábitat de los sistemas silvopastoriles, y para desarrollar recomendaciones de manejo, evaluamos el comportamiento de forrajeo de aves insectívoras de bosque en sistemas silvopastoriles en comparación con fragmentos de bosque en los Andes. Las tasas de ataque de especies focales fueron >25% más bajas en los sistemas silvopastoriles que en los fragmentos de bosque, sugiriendo que las presas de artrópodos fueron menos abundantes o accesibles en los sistemas silvopastoriles que en los fragmentos de bosque. En los fragmentos de bosque, las aves que participaron en bandadas de especies mixtas de forrajeo atacaron presas más frecuentemente que las aves solitarias. En los sistemas silvopastoriles, las aves en bandada y solitarias atacaron presas a tasas similares, y las aves participaron de las bandadas de forrajeo la mitad de las veces que en los fragmentos de bosque. Las aves insectívoras forrajearon preferentemente en un pequeño subgrupo de géneros de árboles en los fragmentos de bosque, pero no exhibieron forrajeo selectivo en los sistemas silvopastoriles botánicamente menos

diversos. Las especies insectívoras que usaron los sistemas silvopastoriles forrajearon en micro-hábitats como cúmulos de enredaderas y hojas muertas colgantes menos frecuentemente que las especies que no usaron los sistemas silvopastoriles. Las especies de bosque que usaron los sistemas silvopastoriles pueden haber estado impactadas negativamente por una ruptura de las interacciones inter-específicas benéficas en los sistemas silvopastoriles, resaltando el potencial de los efectos de cascada en la pérdida de especies en los hábitats antropogénicos. El manejo de los sistemas silvopastoriles que apunte a incluir las especies de árboles y los micro-hábitats preferidos podría mejorar su calidad de hábitat para las especies de bosque, pero las estrategias para realzar el valor de conservación de los paisajes manejados con presencia de sistemas silvopastoriles también debe incluir la preservación de los fragmentos de bosque.

Palabras clave: agricultura amigable con la fauna silvestre, bandadas de especies mixtas, ecología de comunidades de aves, hábitat antropogénico, interacciones inter-específicas, mutualismo, usos múltiples del suelo

INTRODUCTION

Habitat conversion is the primary threat to biodiversity across the tropics (Bradshaw et al. 2009). In the Neotropics, the majority of deforested land is converted to cattle pasture (Lambin et al. 2003, Wassenaar et al. 2007), which threatens biodiversity by destroying, fragmenting, and degrading habitat (Steinfeld et al. 2006). The adoption of silvopastoral practices (i.e. the incorporation of trees into pastures) can alleviate some of the negative impacts of agricultural production by reducing extractive pressure on forests, increasing connectivity among forest fragments, and providing habitat for forest species (Perfecto and Vandermeer 2008, Murgueitio et al. 2011).

Silvopastures provide habitat for more species of birds (Sáenz et al. 2006, Mastrangelo and Gavin 2012), insects (Giraldo et al. 2011, Rivera et al. 2013), and plants (MacLaren et al. 2014) than conventional pastures. For example, live fences—a key silvopastoral feature wherein living trees are used as fence posts—have repeatedly been identified as important repositories of biodiversity (Harvey et al. 2006, Pulido-Santacruz and Renjifo 2011). Silvopastures also provide habitat for more avian forest species than conventional pastures (Mendoza et al. 2014). However, compared with forests and other agroforestry systems, silvopastoral avian communities consist of more generalists and include fewer species of conservation concern (Mendoza et al. 2014, Colorado Zuluaga and Rodewald 2015, Greenler and Ebersole 2015). Silvopastures have also been shown to be of lower habitat quality than forests and other agroforestry systems, as indicated by lower male to female ratios of some avian forest species, an often reported indicator of habitat quality (Latta and Faaborg 2002, Catry et al. 2004, McDermott and Rodewald 2014). Furthermore, mixed-species foraging flocks (hereafter, 'mixed flocks') are less common in silvopastures than in forests (Colorado Zuluaga and Rodewald 2015), and consist of fewer individuals and species than in shade coffee, cardamom, or secondary forests (McDermott and Rodewald 2014). A breakdown of mixed flocks in silvopastures could affect flocking species that use

silvopastures because flocks benefit members by reducing mortality and improving foraging success through prey flushing, sharing of information about food resources, and reducing time lost to vigilance behavior (Morse 1977, Sridhar et al. 2009, Colorado Zuluaga 2013). Silvopastures may provide lower-quality habitat than other agroforestry systems due to their need for greater light availability and more open understory to accommodate livestock production (Andrade et al. 2004, Mastrangelo and Gavin 2012). However, cattle production in the Neotropics occupies 85 times the land area of coffee and cacao production combined (FAO 2013), suggesting that silvopastures could play a larger role in conservation than other agroforestry systems at landscape and regional scales (Rice and Greenberg 2004). Understanding how forest species use silvopastures (e.g., foraging behaviors) could facilitate efforts to balance tradeoffs between production and conservation goals, and may ultimately determine the extent to which silvopastoral systems can contribute to conserving biodiversity.

Foraging studies provide an integrated and mechanistic way to measure silvopastoral habitat quality because they directly quantify prey acquisition, an essential element of fitness (Lindell 2008, Marshall et al. 2013). Moreover, metrics of foraging behavior, such as attack and movement rates, more accurately assess habitat quality than measures of prey abundance because they reflect actual prey encounter rates, thereby synthesizing prey abundance and accessibility (Hutto 1990). Studies of foraging behavior can also identify key resources, such as plant species (Holmes and Robinson 1981, Pejchar et al. 2005) or microhabitats (Cruz 1988, Strong 2000), and have shown that species interactions, including flocking behavior, can be influenced by habitat quality (Knowlton and Graham 2011). In sum, foraging behavior studies can elucidate mechanistic drivers of habitat quality, advance our understanding of flocking behavior–habitat quality relationships, and identify critical habitat elements for biodiversity conservation.

We evaluated the foraging behavior of insectivorous forest birds in silvopastures and forest fragments of the

Colombian Andes to quantify prey availability, investigate how interspecific interactions influenced foraging success, and identify critical habitat elements. We used forest fragments because conversion to agriculture in the region has resulted in a landscape with many small forest fragments, but no large tracts of contiguous forest (Pagiola et al. 2004). The coincidence of extensive human development and high biodiversity and endemism in the region suggests that many species could be at risk of extinction or extirpation (Brooks et al. 2002), prompting the need to understand how working landscapes that consist of degraded forest remnants and presumably wildlife-friendly agricultural practices such as silvopastoralism can better conserve biodiversity (Chazdon et al. 2009). Many cattle producers in the La Vieja River watershed in the Colombian Andes adopted silvopastoral practices between 2002 and 2007 as part of an international pilot project (hereafter, 'the Silvopastoral Project'; World Bank 2008) to determine whether silvopastoral practices could promote sustainable cattle ranching and benefit biodiversity. We tested the predictions that: (1) insectivorous forest birds would forage less successfully in silvopastures than in forest fragments; (2) the rarity or species-poor nature of mixed flocks in silvopastures would contribute to lower foraging success; and (3) tree species preferences of insectivorous forest birds would vary between silvopastures and forest fragments. We also documented the behavior of forest-restricted insectivores to identify tree species that could be incorporated into silvopastures to improve habitat quality.

METHODS

Study Sites

We studied the foraging behavior of avian insectivores on farms in the La Vieja River watershed on the western slope of the central range of the Colombian Andes (Valle del Cauca Department). Mean annual precipitation for the region is 2,300 mm, with peak rainfall in April–May and October–November, and dry seasons during July–August and January–February (https://www.cenicafe.org/). The region is largely deforested, with forest remaining in only 21% of the watershed (Pagiola et al. 2004). Historically, coffee was produced under shade trees throughout the region, but coffee production shifted to full sun methods, and then to cattle ranching (Calle and Piedrahita 2007).

The Silvopastoral Project resulted in the establishment of >800 ha of silvopasture and 350 km of live fence across the region (Pagiola and Rios 2013). Most silvopastures were planted with tree species such as *Gliricidia sepium*, *Psidium guajava*, *Inga edulis*, and *Samanea saman*, although planted species varied among farms, and some silvopastures included remnant forest trees. The most common naturally recruiting tree species in silvopastures

were *Zanthoxylum* spp. and *Cupania americana*. Forest remnants were uncommon, small (mostly <10 ha), and restricted to riparian zones and steep slopes (Calle and Méndez 2009, Calle et al. 2009). Most forest fragments were dominated by *Cupania americana* and *Anacardium excelsum*, while common understory species included *Oreopanax cecropifolius*, *Aiphanes* spp., and *Trophis caucana*.

In 2013, we identified study sites on farms that had participated in the Silvopastoral Project. We established 6 sites in silvopastures and 6 sites in forest fragments (0.8–9.7 ha, and 950–1,250 m above sea level) on 8 farms. Sites of the same habitat type were separated by at least 300 m (mean = 2.9 km). During site selection we attempted to control for slope and aspect as much as possible. Slopes were generally greater in forest fragments (mean = 16%) than in silvopastures (mean = 9%), but the difference was statistically insignificant ($P = 0.06$). There was no consistent difference in aspect between treatments. Both forests and silvopastures were evenly split between west- and east-facing slopes, with few facing north or south. The matrix surrounding our sites was a mosaic of conventional pastures, other agricultural crops (e.g., banana, coffee, pineapple, citrus), home gardens, rural communities, and bamboo forests, with conventional pastures being most prevalent.

Vegetation Sampling

To determine the availability of tree species for foraging, vegetation was sampled in 4 random 8-m radius (0.02 ha) plots per site. In each plot, we measured the diameter at breast height (DBH), and density, frequency, and identity of all trees >5 cm DBH. We used these data to calculate importance values for each tree species by summing the relative density, frequency, and cover. Cover was calculated by converting DBH to basal area and multiplying basal area by tree density divided by the total number of trees sampled (Gabbe et al. 2002). Importance values provide an estimate of the proportion of total foraging surface provided by each tree taxon, which can then be used to determine whether birds are foraging selectively, and to identify tree taxa that are preferred or avoided (Holmes and Robinson 1981, Gabbe et al. 2002). To quantify the general vegetation structure of silvopastures and forest fragments, we measured tree stand basal area, canopy cover, and understory stem density (DBH <5 cm) at 1.6-m intervals along 16-m perpendicular transects within each plot (Morrison and Lindell 2011).

Foraging Observations

To determine whether foraging success (movement rates, prey attack rates, and prey size) was lower in silvopastures than in forest fragments, we selected 5 insectivorous species (hereafter, 'focal species') for study: *Todirostrum*

cinereum (Common Tody-Flycatcher), *Pachysylvia semibrunnea* (Rufous-naped Greenlet), *Vireo olivaceus* (Red-eyed Vireo), *Polioptila plumbea* (Tropical Gnatcatcher), and *Hemithraupis guira* (Guira Tanager). Most observations of *V. olivaceus* were of the resident, endemic subspecies *V. o. caucae*, although a few observations in December were likely of the boreal migrant *V. o. olivaceus* (Hilty and Brown 1986). We chose to study insectivorous passerines because they dominate mixed flocks and are highly sensitive to habitat degradation (Powell 1985, Gray et al. 2007). In addition, we selected these 5 focal species because they were the only insectivorous forest species regularly encountered in our silvopastoral sites. They are predominately canopy foragers; however, across our study sites, there was not a clear demarcation between canopy and understory foraging flocks, as has been reported elsewhere in the northern Andes (Colorado Zuluaga and Rodewald 2015).

To analyze tree species preferences, we observed an additional 15 insectivorous avian species and split all 20 species into 2 groups: sensitive or adaptable (Appendix Table 1). Our rationale for making this distinction was to examine potential differences in foraging preferences between insectivorous forest species that used silvopastures and those that that did not. As such, sensitive species were defined by their absence from silvopastures (observed <5 times in silvopastures over the course of the entire study), and their presence in forested habitats. Most of our sensitive species were also considered of medium sensitivity to deforestation (Stotz et al. 1996; Appendix Table 1). For further description of the avian communities in our study region, see Fajardo et al. (2009).

All foraging surveys were conducted by B. Tarbox, thereby ensuring consistent identification and behavioral assessments. Observations were made from June, 2013, to October, 2015, predominantly during the dry season (70% and 72% of search effort in silvopastures and forest fragments, respectively). Sites were visited once or twice per week, and systematically searched between 06:00 and 18:00 hours, with most visits occurring between 07:00 and 11:00 hours (71% in silvopastures, and 78% in forest fragments). Observations of the same species at the same site on the same day were only included when individuals could be differentiated by sex, age, or distance (>100 m; Gabbe et al. 2002). Observations lasted as long as the observer could be certain that they were observing the same individual (range = 20–193 s, mean = 44 s). Observations <20 s in duration were removed from analyses (Robinson and Holmes 1982). For each observation, we recorded avian species, mixed flock membership, number and type of movement, number and type of prey attack, prey size and order (when visible), tree species, and microhabitat. Birds were considered to be mixed flock members if they moved within 10 m of and in the same

direction as at least 2 other individuals of at least 1 other species; as such, monospecific family groups were not considered mixed flocks unless joined by other species (Moynihan 1962). Movements were categorized as hops, short flights (<1 m), and long flights (>1 m). Attack maneuvers were categorized as gleaning, reaching, lunging, leaping, hanging, flutter-chasing, flush-pursuing, or sallying (Remsen and Robinson 1990). Prey size was estimated in relation to bill size. Attack and movement rates were calculated by dividing the numbers of attacks and movements by observation time. Only the first tree species in which an attack occurred was included in analyses of tree species preferences (Bell et al. 1990). Similarly, only the first movement or attack in an observation period was used for analyses of differences in movement types and attack maneuvers between habitats. Our data refer only to birds that were actively foraging and were not singing, preening, or engaged in any other activity that might have affected foraging behavior. Thus, we cannot address additional variables that may have changed between forests and silvopastures, such as time spent singing or preening.

Statistical Analysis

We used generalized linear mixed models (GLMMs) to analyze the fixed effects of habitat type, mixed flock membership, and their interaction on 3 different aspects of foraging success (movement rates, prey attack rates, and prey size). We also included the random effects of site and bird species to account for differences between sites in prey availability and accessibility and differences between species in foraging behavior (Gelman and Hill 2007). We report on bird species differences when they differ from the overall pattern. Additionally, some sites produced few foraging observations, so combining data from all species allowed us to better account for site as a random effect. We used separate models for each response variable (movement rates, prey attack rates, and prey size), and, because our response variables were continuous and nonnegative, we used a gamma distribution with a log link function. To fit our models, we used Hamiltonian Monte Carlo methods via the rstanarm package in R (Stan Development Team 2016, R Core Team 2017). We assigned weakly informative priors (Normal [0, 1]; Gelman et al. 2008, 2017b) and sampled 4 chains for 5,000 iterations each, with target average acceptance probability set to 0.95. To assess convergence, we visually inspected chain mixing and checked for $\hat{R}$ values >1.01 (Appendix Figure 5; Gelman et al. 2013). To assess model fit, we compared the distributions of simulated data under the fitted model to the distribution of observed data (Appendix Figure 6; Gelman and Hill 2007, Stan Development Team 2016), and calculated conditional and marginal R^2 values (Gelman et al. 2017a). Sex and age were not included in our models due to the difficulty of distinguishing between the sexes

and ages of some of our focal species (e.g., *Vireo olivaceus*, *Todirostrum cinereum*).

To assess tree species and microhabitat preferences, we combined into one group all avian species that used both habitat types (adaptable species; 11 species), and into a second group all species that were observed only in forest fragments (sensitive species; 9 species). The additional species were included only in analyses related to tree species and microhabitat preferences. We used chi-square goodness-of-fit tests based on log-likelihood statistics to determine if each group foraged selectively or foraged in tree species as available (Manly et al. 2002). Expected frequencies were calculated by multiplying the relative importance value of each tree species by the total number of foraging observations for each group (Gabbe et al. 2002). To meet minimum expected frequency standards for chi-square tests, tree species with relative importance values lower than 4% were analyzed at the genus or family level (e.g., *Croton*, Lauraceae), or in an 'other' category (Koehler and Larntz 1980, Jelinski 1991). Trees in the genera *Inga* and *Machaerium* were not lumped into the 'other' category because observed frequencies were much higher than expected frequencies; thus, we included them separately in our analyses. Because chi-square tests were significant for both foraging groups in forest fragments, we calculated Bonferroni confidence intervals for each tree species category to determine whether there were preferences or aversions to particular tree taxa (Byers et al. 1984, Manly et al. 2002). To analyze differences between avian species groups in microhabitat use, we used Pearson's chi-square tests (with Yates' continuity correction for small expected frequencies) on the proportions of observations that occurred in vine tangles or hanging dead leaves.

To analyze differences in vegetation between habitats, we used Welch's *t*-tests to account for unequal variances. To analyze differences between habitats in movement types and attack maneuvers, we used chi-square tests. To meet minimum expected frequency standards for chi-square tests, long and short flights were combined for analyses of movement types. For the same reason, sally attacks were lumped into the 'other' category when analyzing differences in attack maneuvers of *Todirostrum cinereum* and *Hemithraupis guira* (Koehler and Larntz 1980, Jelinski 1991). All data and analysis code are available online (see Data deposits in Acknowledgments).

RESULTS

Vegetation Structure and Composition
Silvopastures were far less structurally complex than forest fragments. Tree density was greater in forest fragments (815 trees ha^{-1}) than in silvopastures (199 trees ha^{-1}; $P <$ 0.001). Similarly, basal area was greater in forest fragments (21.4 m^2 ha^{-1}) than in silvopastures (7.6 m^2 ha^{-1}, $P <$ 0.001). Canopy cover in forest fragments (85%) was almost double that in silvopastures (48%, $P <$ 0.001), and understory stem density was more than an order of magnitude greater in forest fragments (4,923 stems ha^{-1}) than in silvopastures (186 stems ha^{-1}; $P =$ 0.001). Forest fragments also contained ~3 times as many tree species (17.5 species per site) as silvopastures (5.5 species per site; $P <$ 0.001; Appendix Table 2).

Foraging Success
In total, 275 foraging observations of the 5 focal species were recorded (Appendix Table 1). Overall, movement rates were not different across habitat types (Figure 1A; mean difference = 0.14, 95% Bayesian uncertainty interval: −0.08 to 0.37). However, movement rates of *Polioptila plumbea* (mean difference = 0.22, 90% Bayesian uncertainty interval: 0.04 to 0.41) and *Todirostrum cinereum* (mean difference = 0.20, 90% Bayesian uncertainty interval: 0.02 to 0.43) were higher in silvopastures than in forest fragments (Figure 2A). Overall, attack rates were 26% lower in silvopastures than in forest fragments (Figure 1B; mean difference = −0.26, 95% Bayesian uncertainty interval: −0.48 to −0.02), and there was little variation in response to this variable among species (Figure 2B). Prey size was recorded for 48 observations, limiting the ability to detect overall differences between habitat types (Figure 1C; mean difference = 0.12, 95% Bayesian uncertainty interval: −0.97 to 1.17). However, *Vireo olivaceus* captured larger prey in silvopastures than in forest fragments (mean difference = 1.12, 90% Bayesian uncertainty interval: 0.13 to 2.28; Figure 2C), whereas *Pachysylvia semibrunnea* may have caught smaller prey in silvopastures (Figure 2C), although model results were ambiguous (mean difference = −2.36, 90% Bayesian uncertainty interval: −2.09 to 0.18). A high degree of model variance was explained by random effects (Figure 1), particularly by bird species. This is not surprising, given that our focal species included members of 4 different families (Tyrannidae, Vireonidae, Polioptilidae, and Thraupidae), resulting in considerable variation in foraging behavior and prey preferences. For attack and movement rates, differences between bird species accounted for the majority of variation explained by random effects, whereas for prey size, a greater proportion of variation was explained by site.

Focal species were less likely to join mixed-species foraging flocks in silvopastures (20% of observations) than in forest fragments (46%; $P <$ 0.001). Across habitat types, mixed flock membership had no effect on movement rates, attack rates, or prey size (Figure 1). However, there was a significant interactive effect between habitat type and mixed flock membership on attack rates (Figure 1B; mean difference = −0.3, 95% Bayesian uncertainty interval: −0.55 to −0.02), such that mixed flock membership had a positive
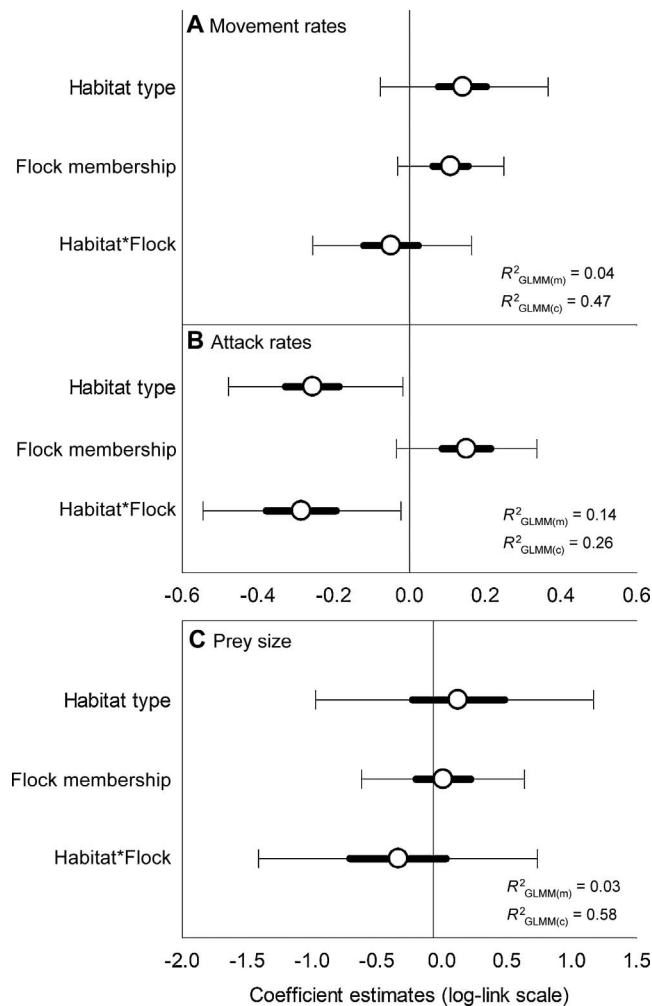
FIGURE 1. Mean coefficient estimates, with 50% and 95% Bayesian uncertainty intervals, for the influence of habitat type (silvopasture), mixed-species foraging flock membership, and their interaction on (**A**) movement rates, (**B**) attack rates, and (**C**) prey size of 5 focal avian species in the Colombian Andes. Values indicate the relative magnitude (on the log-link scale) and direction (positive or negative) of the influence exerted by the predictor variable on each response variable. Values are the results from generalized linear mixed models (GLMMs) using 5,000 Markov chain Monte Carlo (MCMC) iterations to generate posterior sample sizes of 10,000 for each model run (i.e. each response variable). Marginal (m) and conditional (c) R^2 values are shown for each model. Further details on MCMC convergence and model fit can be found in Appendix Figures 5 and 6.

FIGURE 2. Mean $\pm$ SE and raw data values of (**A**) movement rates, (**B**) prey attack rates, and (**C**) prey size of 5 focal avian species in forest fragments and silvopastures in the Colombian Andes.

first movement in an observation was too infrequently a long or short flight to meet minimum expected frequency standards of chi-square tests (Koehler and Larntz 1980). However, inspection of means and standard errors suggested that there was no difference in movement types between habitats for *H. guira* (Appendix Figure 7).

Foraging Preferences

Adaptable and sensitive species both selectively used tree species in forest fragments ($\chi^2 \geq 33.4$, $P < 0.001$). Adaptable species preferentially foraged in *Anacardium excelsum*, *Croton* spp., *Inga* spp., and *Machaerium* spp., while sensitive species preferentially foraged in *Inga* spp. and *Machaerium* spp. (Figure 4). In addition, adaptable

influence on attack rates in forest fragments, but had no effect in silvopastures (Figure 3).

Proportions of movement types and attack maneuvers did not differ between habitat types for our focal species (Appendix Figures 7 and 8), although *Polioptila plumbea* used a marginally greater proportion of gleaning and reaching attacks in silvopastures than in forest fragments ($P = 0.05$; Appendix Figure 8). For *Hemithraupis guira*, the
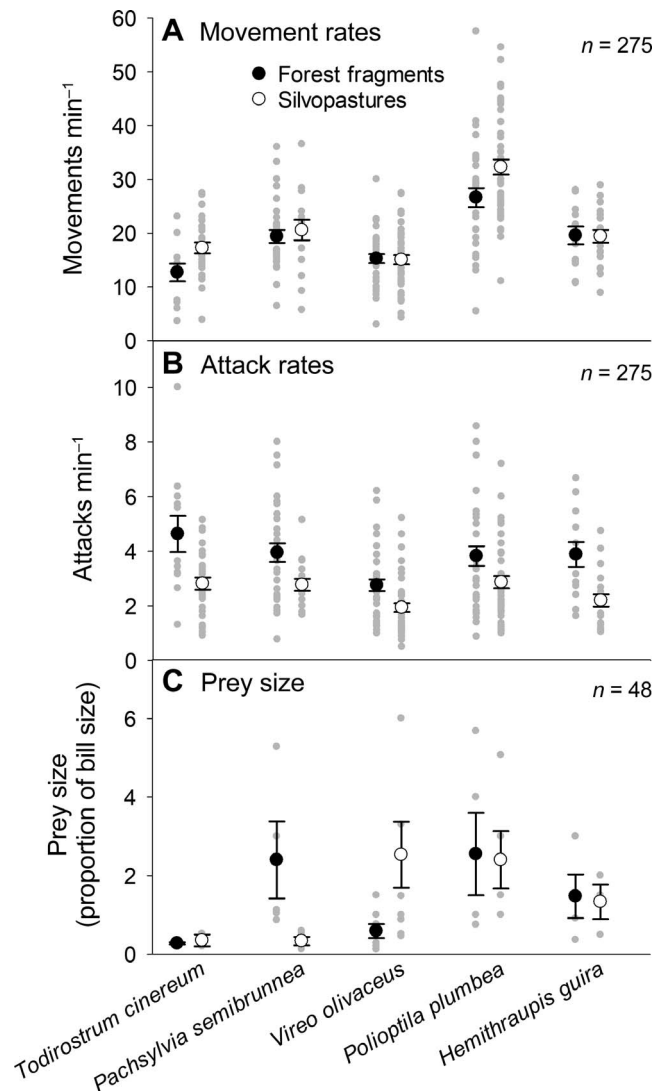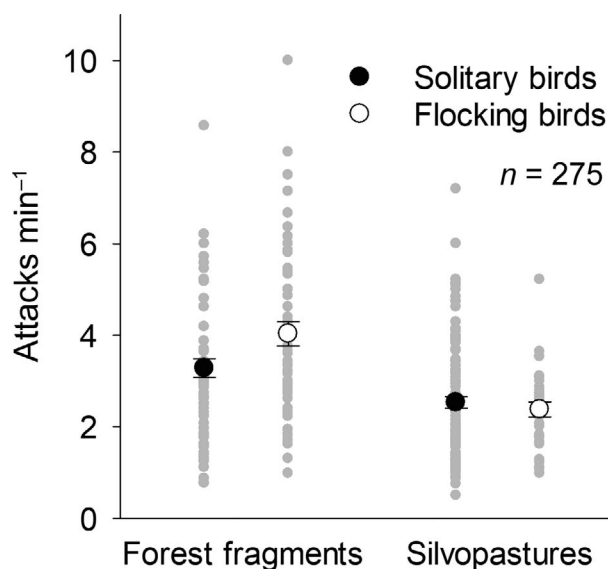
FIGURE 3. Mean ± SE and raw data values of prey attack rates of 5 focal avian species when foraging alone or in flocks in forest fragments and silvopastures in the Colombian Andes.

FIGURE 4. Tree species preferences of insectivorous forest birds in forest fragments and silvopastures in the Colombian Andes. Values for adaptable and sensitive avian species represent the percentage of foraging observations that occurred in each tree taxon, and percentage importance values indicate the availability of tree taxa. Sensitive species foraged selectively in forest fragments ($P < 0.001$) and were not observed in silvopastures, whereas adaptable species were observed in both habitats, but foraged selectively only in forest fragments ($P < 0.001$). Calculation of Bonferroni confidence intervals resulted in different values for each avian species group, so are not shown here. Instead, significance at $\alpha = 0.05$ is depicted by asterisks.

species avoided uncommon tree species as a group ('other' spp.; Figure 4). In silvopastures, adaptable species did not selectively use tree species ($\chi^2 = 9.7$, $P = 0.28$; Figure 4). In forest fragments, sensitive species used vine tangles more frequently than adaptable species (17% and 6% of observations, respectively; $\chi^2 = 6.8$, $P = 0.009$). Sensitive species did not use hanging dead leaves more frequently than adaptable species (5% and 4% of observations, respectively; $\chi^2 = 0.005$, $P = 0.95$). However, *Pachysylvia semibrunnea* was the only adaptable species to use hanging dead leaves (20% of observations in forest fragments); when *P. semibrunnea* was removed from analyses, sensitive species used hanging dead leaves more often than adaptable species ($\chi^2 = 4.1$, $P = 0.04$).

DISCUSSION

Our results show that silvopastures offer low-quality foraging habitat for many of the forest species that use them (Hutto 1990), and that degradation of beneficial interspecific interactions in silvopastures may exacerbate the effects of lower prey availability (Sridhar and Sankar 2008, Goodale et al. 2015). In support of our first prediction, that insectivorous forest birds would forage less successfully in silvopastures than in forest fragments, we found that prey attack rates were lower in silvopastures than in the small (<10 ha) forest fragments that were available in the region. We also found supporting, though not entirely conclusive, evidence for our prediction that the rarity or species-poor nature of mixed-species flocks in silvopastures would contribute to lower foraging success.
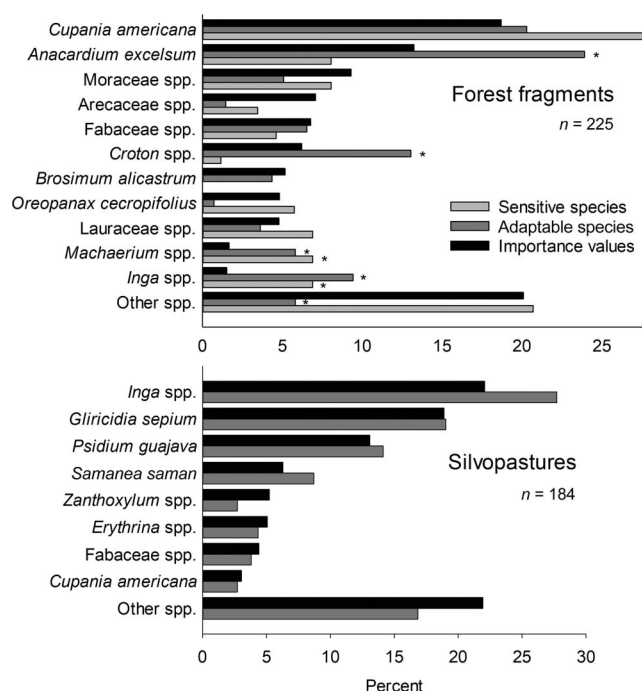
Focal species were less likely to join mixed-species foraging flocks in silvopastures. Moreover, we found that while mixed flock members attacked prey more frequently than solitary birds in forest fragments, there was no difference in attack rates between flocking and solitary birds in silvopastures, suggesting that flock function was impaired in silvopastures. We also found support for our last prediction that tree species preferences of insectivorous forest birds would vary between habitat types. While birds foraged selectively in forest fragments, they did not do so in silvopastures, and instead used trees as they were available. We also identified tree species and microhabitats that could improve silvopastoral habitat quality. Our findings illustrate (1) the potential to enhance silvopastoral habitat quality; (2) that breakdowns in interspecific interactions are likely occurring in anthropogenic habitat; and (3) the vital importance of protecting forest fragments in agricultural landscapes.

In the absence of an increase in prey size, lower prey attack rates of focal species in silvopastures suggest poor

habitat quality compared with small, degraded forest fragments. All focal species attacked prey less frequently in silvopastures than in forest fragments, and some species moved more frequently or captured smaller prey in silvopastures, suggesting that they acquired less food in silvopastures per unit effort (Davies and Houston 1981, Robinson and Holmes 1984, Hutto 1990). However, lower attack rates may not indicate lower habitat quality if they are offset or driven by the capture of higher-quality (i.e. larger) prey (Powell et al. 2015). In our study, this appeared to be the case for one species, *Vireo olivaceus*, which exhibited lower attack rates in silvopastures but caught substantially larger prey (predominantly larvae of Lepidoptera). The apparent success of *V. olivaceus* in silvopastures is not surprising given the broad geographic extent of this species' range and the wide variety of habitats in which it occurs (BirdLife International 2016a). However, the rest of our focal species did not appear to follow this pattern. For 3 of the 5 focal species, there was no difference in prey size between habitats. While small samples may have impeded our ability to detect a statistically meaningful difference in prey size for these species, mean values of prey size in each habitat type were similar for these 3 species. Changes in attack maneuvers employed between habitat types also could indicate changes in prey quality, yet we detected no significant differences in attack maneuvers. *Pachysylvia semibrunnea* actually appeared to catch smaller prey in silvopastures than in forest fragments, potentially compounding the negative effect of lower attack rates. As a near-endemic species, the poor performance of *P. semibrunnea* in silvopastures is consistent with assertions that silvopastures provide low-quality habitat for species of potential conservation concern (Colorado Zuluaga and Rodewald 2015, Greenler and Ebersole 2015, BirdLife International 2016b).

The differences between habitats in the prevalence and function of mixed flocks demonstrate the importance of considering interspecific interactions when assessing habitat quality (Tuomainen and Candolin 2011). As we predicted, birds in forest fragments joined mixed flocks more frequently than those in silvopastures, and benefited from flock membership through higher prey attack rates (Herrera 1979, Goodale et al. 2015), which could have been due to shared information about prey (Morse 1977, Munn 1984) or reduced vigilance effort (Pomara et al. 2003, Bell et al. 2009). In contrast, birds in silvopastures did not attack prey more frequently when in flocks, possibly due to the species-poor nature of mixed flocks in silvopastures. Absence of species that share information about prey and predators (i.e. nuclear and sentinel species) may impede flock formation (Zhang et al. 2013, Cordeiro et al. 2015) and impair flock function (Dolby and Grubb 1998, Goodale et al. 2015). Across our study sites, family groups of *Tachyphonus luctuosus* (White-shouldered Tanager)

appeared to be critical components of mixed flocks in forest fragments, but were absent from silvopastures. Indeed, conspecific flocking species frequently serve as nuclear species for mixed flocks because other species eavesdrop on the information that they share with each other (Magrath et al. 2007, Goodale and Beauchamp 2010). Numerous other flocking species (e.g., *Pachysylvia semibrunnea*, *Hemithraupis guira*, *Tolmomyias sulphurescens* [Yellow-olive Flycatcher], *Tangara* spp.) were also absent or uncommon in silvopastures in our study. By reducing the presence and function of mixed-species foraging flocks, the limited diversity and abundance of avian forest species in silvopastures (Colorado Zuluaga and Rodewald 2015; McDermott and Rodewald 2014) may have a cascading effect on insectivorous forest birds that use silvopastures (Goodale et al. 2015). An alternative hypothesis is that our focal species experience less predation risk in silvopastures than in forest fragments, obviating the primary need for joining mixed flocks (Goodale et al. 2015). Habitat structure in silvopastures is more open than in forest fragments, which may make it easier for birds to see predators before they get close enough to be a danger. Alternatively, the lack of dense cover for shelter in silvopastures might make birds even more dependent upon flocks to detect and escape predators. We cannot evaluate these hypotheses because we did not gather data on time spent watching for potential predators. Surprisingly, we never observed any of the avian predators most likely to be a threat to foraging insectivorous birds in either habitat type (e.g., *Accipiter* spp. [hawks], *Glaucidium* spp. [pygmy owls], or *Micrastur* spp. [forest falcons]), although one species, *Accipiter striatus* (Sharp-shinned Hawk), has been observed in our area (eBird 2018).

While general vegetation structure (e.g., canopy cover, basal area) may largely determine silvopastoral habitat quality for forest birds (Sáenz et al. 2006, McDermott et al. 2015), our study highlights the conservation value of specific tree species and microhabitats. On shade coffee farms, *Inga* spp. are an important resource for Neotropical migrants (Bakermans et al. 2012, Newell et al. 2014), and our results suggest that *Inga* spp. are also important for resident species within structurally complex and diverse forest fragments. We expected *Inga* spp. to be preferentially used in silvopastures as well. However, while the proportion of attacks that occurred in *Inga* spp. was greater than the percentage importance value of the species, adaptable species generally did not forage selectively in silvopastures. Lower density and species diversity of trees in silvopastures may force birds to forage in whatever trees are available, rather than selecting preferred taxa. Hartung and Brawn (2005) found similar differences in foraging selectivity between more open savanna habitats and closed-canopy forests. Other pre-

ferred tree species that could be incorporated into silvopastures include *Anacardium excelsum*, *Croton magdalenensis*, and *Machaerium* spp. Some of these tree species could provide benefits to landholders and wildlife. For example, *A. excelsum* is a valuable native timber species (Fournier 2003), and *C. magdalenensis* provides abundant fruit for avian and other frugivores (Z. Calle personal communication). While sensitive species as a group did not show a statistically significant preference for *Cupania americana*, it may also be an important tree species contributing to the wildlife value of silvopastoral systems because >30% of all *Pachysylvia semibrunnea* observations occurred in *C. americana*, far outweighing its relative importance value of 19%. *P. semibrunnea* also frequently foraged in clusters of hanging dead leaves in forest fragments, but this microhabitat was rare in silvopastures, suggesting that the impaired foraging of *P. semibrunnea* in silvopastures could have been related to the absence of hanging dead leaves. Sensitive species (i.e. species that did not use silvopastures) also frequently foraged in clusters of hanging dead leaves, as well as in vine tangles (another missing microhabitat in silvopastures). Thus, managing for the regeneration of preferred trees and formation of particular microhabitats, such as vine tangles and hanging dead leaves, could improve silvopastoral habitat quality for forest insectivores (Enríquez-Lenis et al. 2007, Sáenz et al. 2006).

Our study shows that silvopastoral systems provide low-quality habitat for some forest species, and suggests that a breakdown of interspecific interactions could amplify the impacts of species loss within agricultural landscapes. Furthermore, because our findings are in reference to degraded forest fragments rather than blocks of contiguous forest, we may have underestimated the deficiencies of silvopastures compared with intact ecosystems. Forest preservation, even of small fragments, thus remains the most critical element for conserving biodiversity in our study region. However, small forest fragments alone may not be sufficient to conserve biodiversity (Mendenhall et al. 2014). Despite their poor habitat quality, silvopastures may still enhance the ability of forest remnants to conserve biodiversity at regional scales by augmenting the abundance and diversity of species that forest fragments host and by reducing local extirpations (Şekercioğlu et al. 2002, Stouffer et al. 2011, Visco et al. 2015). Furthermore, silvopastures offer an economically and culturally viable means for improving the conservation value of vast expanses of otherwise ecologically inhospitable land (Rice and Greenberg 2004, Murgueitio et al. 2011), meaning that their widespread establishment may be more feasible than large-scale reforestation in some cases. Of course, our results indicate that silvopastures would be more likely to achieve conservation goals if managed for higher tree species diversity and greater structural complexity, partic-

ularly of specific microhabitats (e.g., vine tangles). Additionally, demographic studies of mortality rates and nesting success in silvopastures and behavioral studies of sensitive species' dispersal through silvopastures are needed to further understand how silvopastoral systems can best support avian metacommunities (Hanski 1998, Johnson 2007).

Ultimately, forest preservation remains paramount to conserving Neotropical biodiversity, but silvopastures can be a valuable component of regional conservation efforts, especially if paired with forest protection and restoration. If silvopastures are managed to meet specific biodiversity conservation objectives, they could provide critical habitat for some forest species and improve the ecological function of agricultural landscapes.

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APPENDIX TABLE 1. List of avian species included in foraging preferences analysis of insectivorous forest birds in silvopastures and forest fragments of the Colombian Andes. Focal species are highlighted in bold font. Study group is based on presence (adaptable) or absence (sensitive) in silvopastures. Sensitivity refers to sensitivity to deforestation per Stotz et al. (1996). For status, M = boreal migrant, NE = near-endemic, and R = resident. Sample sizes (*n*) are broken down by habitat type (i.e. pastures (p) or forest fragments (f)).

Scientific name	Common name	Study group	Sensitivity	Status	*n* (p)	*n* (f)
Thamnophilus multistriatus	Bar-crested Antshrike	Adaptable	Low	NE	14	5
Thamnophilus atrinucha	Black-crowned Antshrike	Sensitive	Low	R	0	22
Cercomacra nigricans	Jet Antbird	Sensitive	Medium	R	0	2
Myiopagis viridicata	Greenish Elaenia	Adaptable	Medium	R	4	10
Mionectes oleagineus	Ochre-bellied Flycatcher	Sensitive	Medium	R	0	5
Leptopogon superciliaris	Slaty-capped Flycatcher	Sensitive	Medium	R	0	4
Poecilotriccus sylvia	Slate-headed Tody-Flycatcher	Sensitive	Low	R	2	21
Todirostrum cinereum	**Common Tody-Flycatcher**	**Adaptable**	**Low**	**R**	**28**	**12**
Tolmomyias sulphurescens	Yellow-olive Flycatcher	Sensitive	Medium	R	0	8
Pachyramphus rufus	Cinereous Becard	Adaptable	Low	R	6	1
Pachysylvia semibrunnea	**Rufous-naped Greenlet**	**Adaptable**	**Medium**	**NE**	**16**	**30**
Vireo olivaceus	**Red-eyed Vireo**	**Adaptable**	**Low**	**R, M**	**43**	**36**
Polioptila plumbea	**Tropical Gnatcatcher**	**Adaptable**	**Low**	**R**	**45**	**32**
Hemithraupis guira	**Guira Tanager**	**Adaptable**	**Low**	**R**	**20**	**13**
Tachyphonus luctuosus	White-shouldered Tanager	Sensitive	Medium	R	1	21
Mniotilta varia	Black-and-white Warbler	Adaptable	Low	M	1	2
Oreothlypis peregrina	Tennessee Warbler	Adaptable	Low	M	1	0
Setophaga pitiayumi	Tropical Parula	Sensitive	Medium	R	0	2
Setophaga petechia	Yellow Warbler	Adaptable	Low	M	9	2
Basileuterus culicivorus	Golden-crowned Warbler	Sensitive	Medium	R	0	3

APPENDIX TABLE 2. Mean values (SE) of vegetation structural and compositional metrics in forest fragments and silvopastures in the Colombian Andes.

| Vegetation characteristic	Forest fragments	Silvopastures
Basal area (m^2 ha^{-1})	21.4 (2.0)	7.6 (0.7)
Tree density (number per ha)	815 (95)	199 (43)
Tree species richness (number per site)	17.5 (2.2)	5.5 (1.2)
Canopy cover (%)	85 (3)	48 (5)
Understory stem density (number per ha)	4,923 (758)	186 (100)
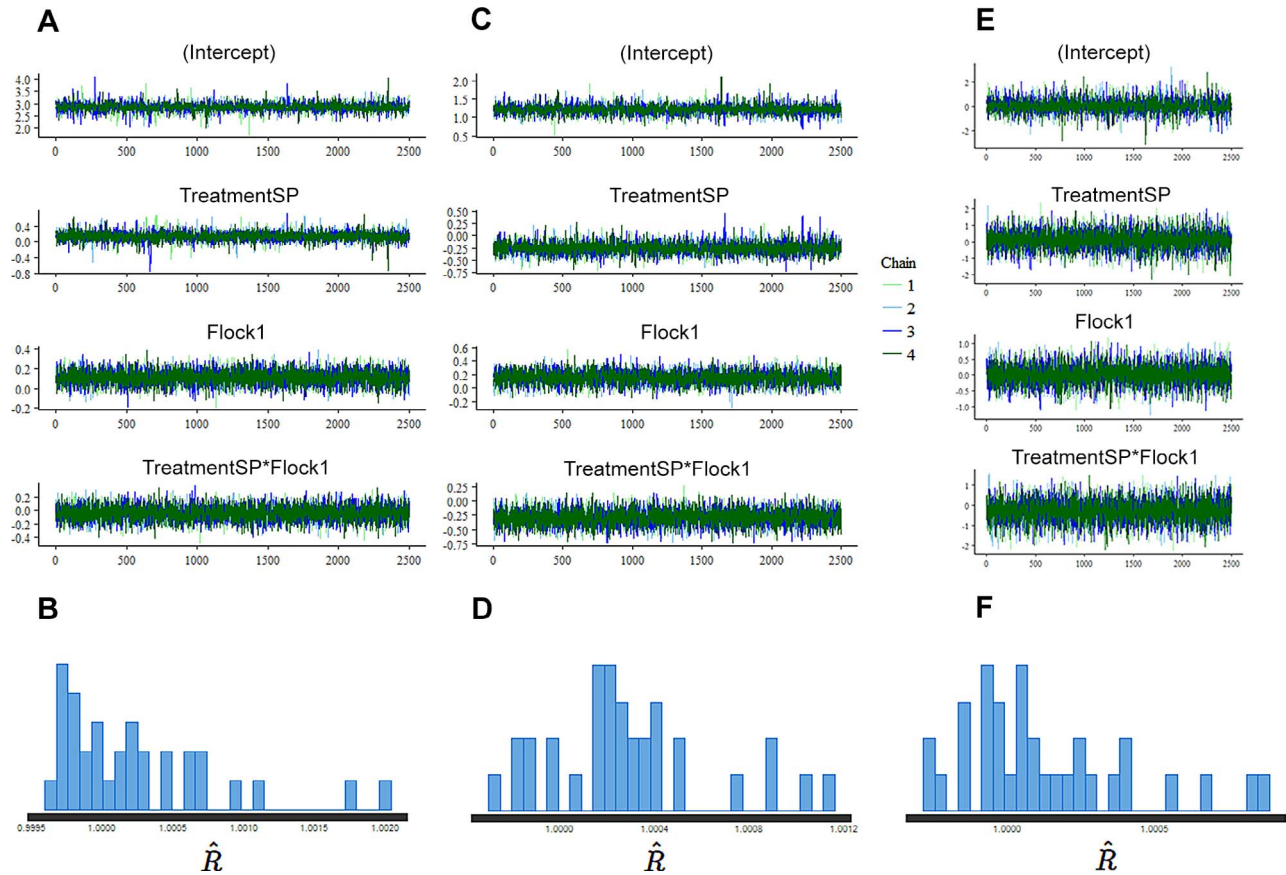
APPENDIX FIGURE 5. (**A**, **C**, **E**) Trace plots, and (**B**, **D**, **F**) $\hat{R}$ values for each generalized linear mixed model (GLMM) for the influence of habitat type (TreatmentSP), mixed-species foraging flock membership (Flock1), and their interaction (TreatmentSP*Flock1) on (**A**, **B**) movement rates, (**C**, **D**) prey attack rates, and (**E**, **F**) prey size of 5 focal avian species in the Colombian Andes indicated that Markov chain Monte Carlo (MCMC) iterations converged on their target distributions. The $\hat{R}$ statistic is the ratio of the average variance of draws within each Markov chain to the variance of pooled draws across all chains. Values >1 indicate that chains may not have converged on an equilibrium distribution and were minimal in our models (i.e. no $\hat{R}$ values exceeded, or even approached, the suggested threshold of 1.1; Gelman et al. 2013).
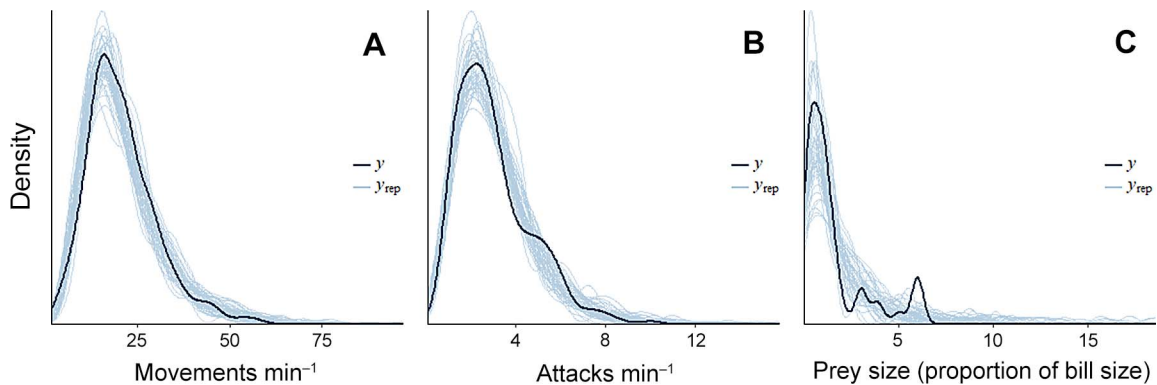
APPENDIX FIGURE 6. Kernel density plots generated to conduct posterior predictive checks for (**A**) movement rates, (**B**) prey attack rates, and (**C**) prey size of 5 focal avian species in the Colombian Andes. Results of simulated data generated under each generalized linear mixed model (y_{rep}) are plotted against the distributions of the observed data (y).
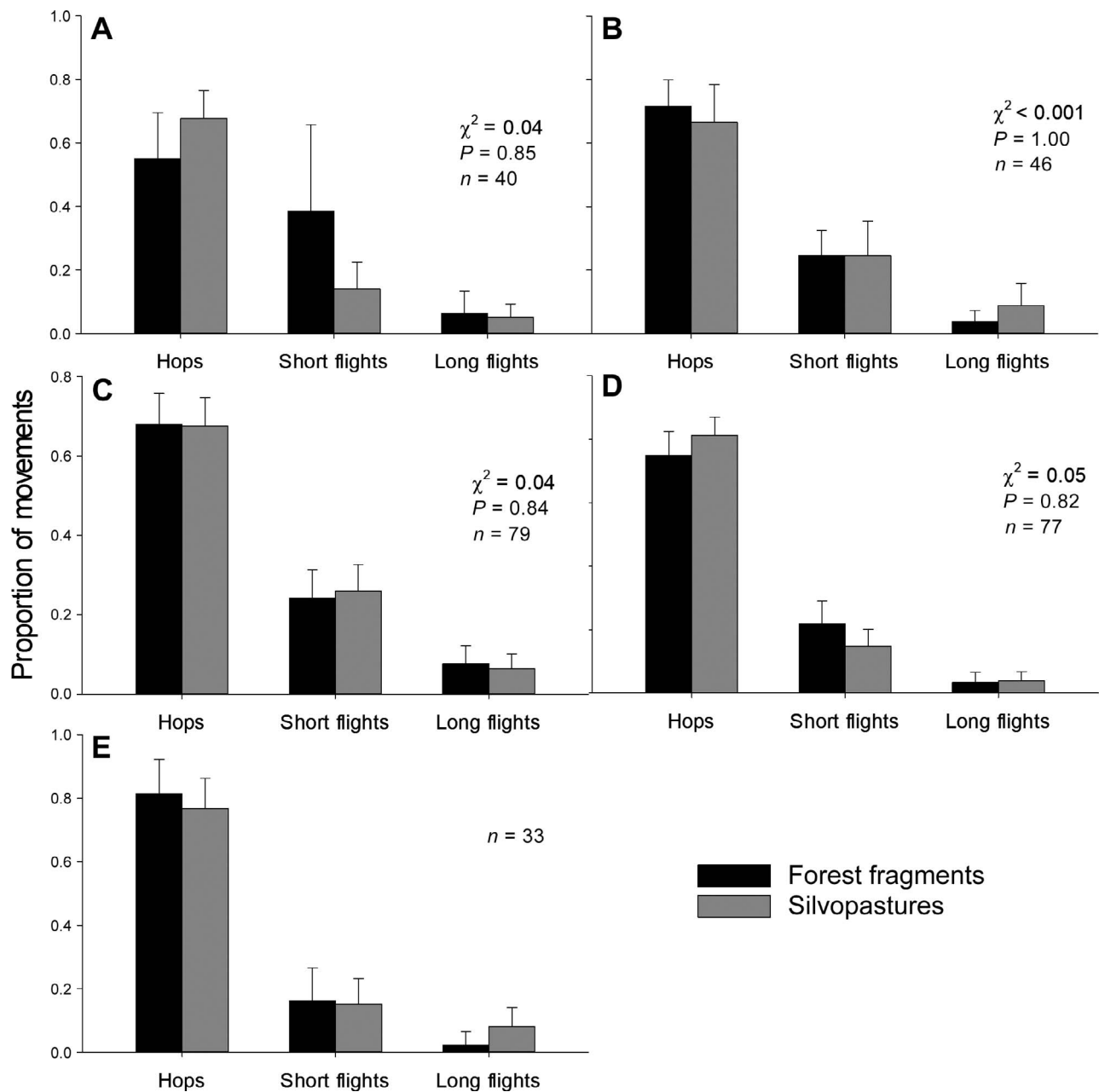
APPENDIX FIGURE 7. Differences in focal species' movement behavior between forest fragments and silvopastures: (**A**) *Todirostrum cinereum*, (**B**) *Pachysylvia semibrunnea*, (**C**) *Vireo olivaceus*, (**D**) *Polioptila plumbea*, and (**E**) *Hemithraupis guira*. Values depicted are mean proportions with standard error bars for hops, short flights (<1 m), and long flights (>1 m). Short and long flights were combined to meet minimum expected frequency standards for chi-square tests. *Hemithraupis guira* observations did not meet minimum expected frequency standards even after combining flights, so no test statistic (χ^2) is reported.
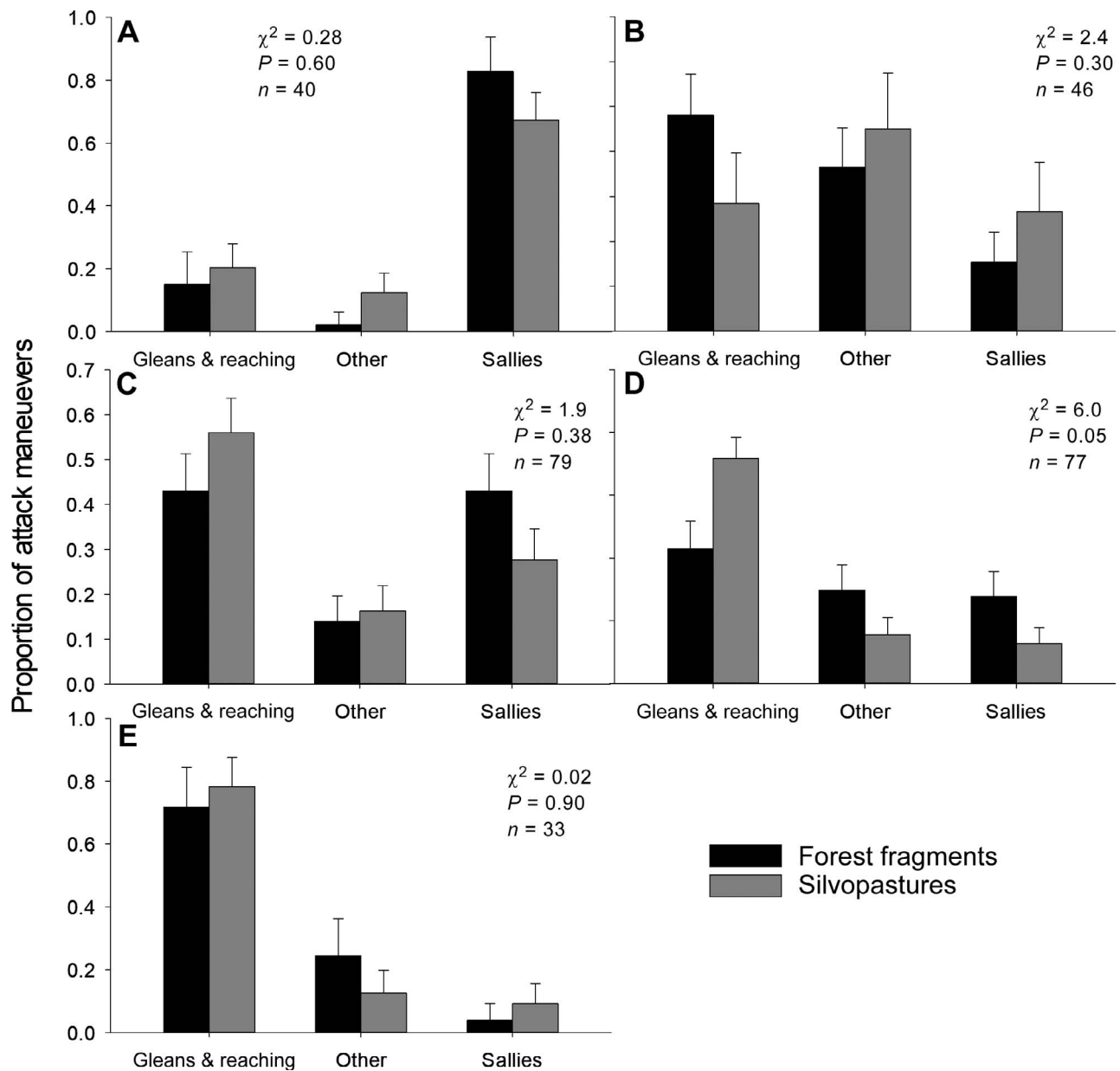
APPENDIX FIGURE 8. Differences in focal species' use of attack maneuvers between forest fragments and silvopastures: (**A**) *Todirostrum cinereum*, (**B**) *Pachysylvia semibrunnea*, (**C**) *Vireo olivaceus*, (**D**) *Polioptila plumbea*, and (**E**) *Hemithraupis guira*. Values depicted are mean proportions with standard error bars for gleaning and reaching (near-perch) attacks, sallies (flight-based attacks), and other (a variety of intermediate) attack maneuvers (e.g., hang, leap).