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Research article

Managing the *farmscape* for connectivity increases conservation value for tropical bird species with different forest-dependencies

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ABSTRACT

Land clearing for agricultural use is a primary driver of biodiversity loss and fragmentation of natural ecosystems. Restoring natural habitat connectivity by retaining quality habitats and increasing on-farm tree cover contributes to species' mobility and persistence in agricultural landscapes. Nonetheless, remarkably few studies have quantified the impacts of on-farm practices for species' mobility measured as functional connectivity within the context of farm and broader spatial levels of landscape organization. We tested how adding and removing trees in different configurations on a farm comprised of coffee plantations and cattle pastures can help evaluate species' mobility at the *farmscape* level (an area comprising the farm plus a 1.5 km buffer area). We coupled bird capture data and scenario modeling to assess species mobility of five neotropical bird species with distinct life history characteristics representing a gradient of forest dependency. We used seven years of mist-netting data to estimate species habitat affinity and to predict species mobility using the Circuitscape model across a 4371 ha *farmscape* in Costa Rica. Circuitscape allowed us to estimate changes in movement probability and relative changes in resistance to movement that species experience during dispersal (measured as resistance distance and passage area through which species can move) under four *farmscape* management scenarios. The four land-use scenarios included: (a) the 2011 *farmscape* land-use composition and configuration, b) converting all existing live fences to post-and-wire fence lines in the farm c) converting simplified coffee agroforests to multistrata coffee agroforests in the farm, and d) placing multistrata live fences around the perimeter of every parcel and roads on the farm. Model results suggest that existing multistrata live fences maintain the sporadic movement of all five species irrespective of forest dependence. Likewise, adding multistrata live fences around individual fields presents a more efficient strategy for increasing species mobility than multistrata coffee agroforestry systems in the assessed *farmscape*, by doubling the passage areas available to all species, although it created labyrinths with "dead-ends" for two species. While retaining large habitat patches remains important for conservation, managing on-farm connectivity complements these efforts by increasing movement probability and reducing dispersal resistance for forest-dependent bird species.

1. Introduction

The expansion of agricultural land in more than one-third of Earth's ice-free terrestrial surface (Ramankutty et al., 2008) has resulted in habitat fragmentation and isolation, which consequently drive biodiversity loss (Haddad et al., 2015). Connectivity is essential for preventing local extinctions (Simberloff, 1976), thus incorporating conservation efforts in agricultural lands is vital given the role these landscapes play in maintaining between habitat patch connectivity (Mitchell et al., 2013; Tscharntke et al., 2005). The movement of species and genes between isolated patches of habitat and across agricultural landscapes can be promoted or enhanced by planning for connectivity through on-farm conservation practices. Supporting species dispersal and movement is also essential for sustaining the delivery of important ecosystem services that directly benefit agriculture-dominated landscapes, such as pest control and pollination services

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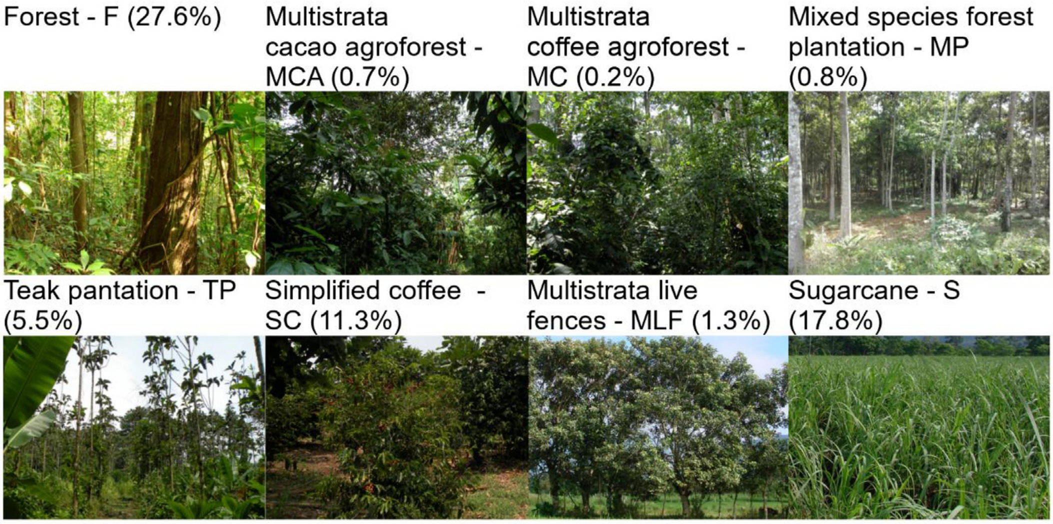

Fig. 1. Management intensification gradient of land uses monitored by CATIE's Bird Monitoring Program from high to lower complexity. Suggarcane is the only land use without tree cover. Percentage of the corresponding area occupied by each land used in relationship to the *farmscape* is shown in parentheses.

which are provided by mobile organisms (Whelan et al., 2008, 2015; Martínez-Salinas et al., 2016).

Increasing and managing on-farm natural vegetation, particularly tree density and diversity, can provide multiple benefits to farmers and wildlife. Managing on-farm natural vegetation is a common agroforestry practice, particularly in coffee, cacao, and livestock production systems across Mesoamerica (Chacón and Harvey, 2006; Harvey et al., 2006; Motzke et al., 2016). The use of agroforests is a proven means for increasing both high-quality habitat areas and dispersal corridors (MacDonald, 2003), however these are often abandoned in favor of simplified and often more intensified cropping systems (Perfecto et al., 1996; Philpott et al., 2008; Karp et al., 2012; De Beenhouwer et al., 2013).

Efforts to counterbalance the loss of forest habitat and tree diversity exist throughout Central America, engaging both public and private stakeholders. Costa Rica, for instance, supports nationalized conservation and financing programs that support farm-level conservation practices. These programs include certification schemes which recognize farmers' investing in biodiversity conservation efforts (DeClerck and Martínez-Salinas, 2011) and Costa Rica's well-known Payment for Ecosystem Services – PES (Garbach et al., 2012; Pagiola et al., 2007; Sánchez-Azofeifa et al., 2007). Areas eligible and prioritized for PES includes those within biological corridors, which are also Costa Rican mixed land use national conservation areas with a mandate to restore biological connectivity among national and regional protected areas (Canet Desanti et al., 2009). In most of these programs, the landscape context is overlooked even though connectivity (a spatially explicit process driven by the landscape composition and configuration) is best achieved through strategic placement of conservation elements to ensure unbroken routes between habitat patches in fragmented landscapes (Tscharntke et al., 2015). For instance, a critical knowledge gap that hinders more effective management of on-farm habitat elements to support species mobility is quantifying the contributions of on-farm conservation interventions to species mobility beyond the farm, while assessing the impact on species with different habitat preferences.

This study bridges this gap by estimating the contributions of both the type and placement of agroforestry plantings to the mobility of selected bird species. Species mobility, measured as functional connectivity is defined as the capacity of a species to move between habitat patches based on its life-history characteristics, landscape composition (patches of different land uses) and landscape configuration (spatial arrangement of land uses) (Tischendorf and Fahrig, 2000; Uezu et al., 2005).

This study focuses on evaluating the biodiversity conservation value of farmland management practices commonly used in Costa Rican cattle pastures and coffee fields: live fences (live trees lining the perimeter of fields and pastures), and coffee agroforests, where trees are embedded within the parcels (trees within parcels used to provide shade to crops). Based on the study site land-use composition and configuration, we hypothesized that live fences composed of trees with multiple strata (multistrata live fences) make limited contributions to birds' mobility due to the small area they cover ($< 1\%$ of the study area) and that increasing tree density and diversity within and around fields equally improve birds' mobility across this fragmented and agriculture dominated landscape. To test these hypotheses, we selected five neotropical bird species with distinct life history characteristics representing a gradient of forest dependency. We used seven years of bird mist-netting capture data from CATIE's Bird Monitoring Program (BMP) to estimate species' affinities and mobility across eight common land uses in the study site and the surrounding landscape.

2. Materials and methods

2.1. Study site

The study was conducted on the 1036 ha Tropical Agricultural Research and Higher Education Center (CATIE) farm located in Turrialba, Costa Rica (9° 53′ 56 N, 83° 39′ 03 W; 600 m.a.s.l.). We added a 1.5 km buffer to the farm perimeter thus extending the study area to 4371 ha, to consider connectivity beyond the direct boundaries of the farm, avoid biased calculations of net movement probabilities, and inflate movement cost. We designated this total area as the study *farmscape*. The delineation of the additional perimeter considers that habitat configuration within both the farm limits and adjacent habitat patches are interrelated and together influence species' ability to move through the landscape, i.e., a continuum. Studying connectivity on this farm is particularly relevant as it is situated at the core of the Volcanica Central Talamanca Biological Corridor (114,626 ha), with mixed land uses aiming to restore biological connectivity between Costa Rica's Central Volcanic and Talamanca mountain ranges (Canet Desanti et al., 2009).

More than 200 bird species (~8000 individuals) have been observed, captured and banded on the CATIE farm, as part of its long-term Bird Monitoring Program (BMP) which started operating in 2008 with the main goal of assessing the conservation contribution of eight distinct land uses following a management intensification gradient (Fig. 1). For this study, we have used seven years of capture data

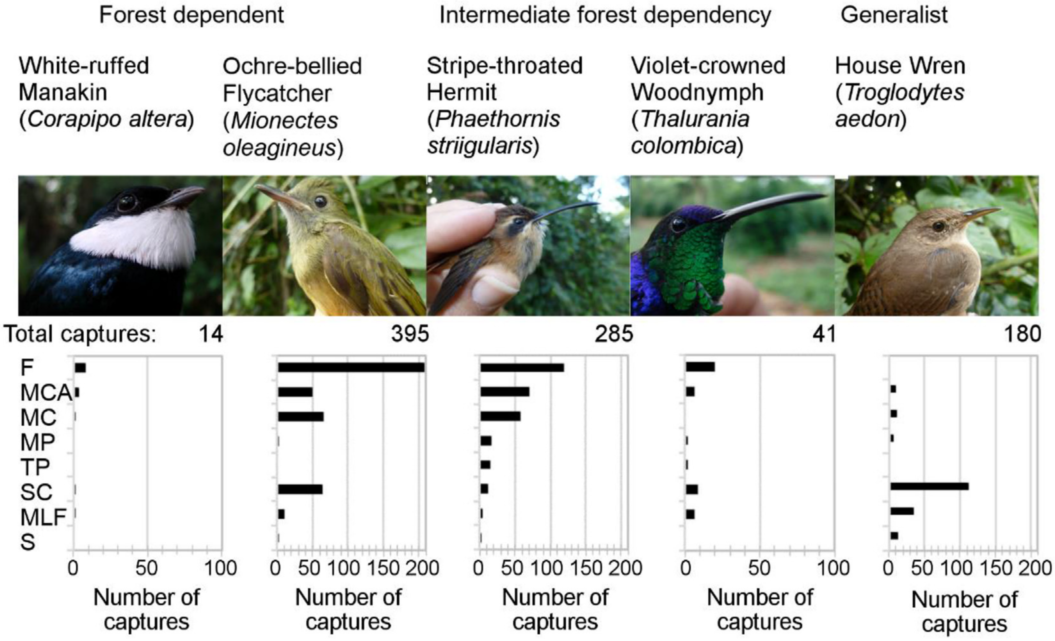

Fig. 2. CATIE's Bird Monitoring Program recorded captures for the selected bird species covering distinct life history characteristics. Total captures per species and land use including F: forest [4833 MH: mist-net hours, 21%], MCA: multistrata cacao agroforest [3025 MH, 13%], MC: multistrata coffee agroforest [2777 MH, 12%], MP: mixed species forest plantation [1290 MH, 6%], TP: teak plantation [217 MH, 1%], SC: simplified coffee agroforest [4712 MH, 21%], MLF: multistrata live fences [3554 MH, 15%], S: sugar cane [2487 MH, 11%].

(2008–2015) representing a sampling effort of 22,895 mist-net hours (1 mist-net hour = one net open for 1 h). The eight monitored land uses cover 65.2% of the total *farmscape* area (2851 ha), whereas the remaining unmonitored area (34.7%, 1519 ha) include other land uses such as open pasture (14.8% *farmscape* area), infrastructure (11.1%), water bodies (4.4%), cropland (11.6%), scrub (1.8%) and gardens (1.1%). The BMP activities follow standard mist-netting protocols (Ralph et al., 1993; monitoring methods described in detail in Martínez-Salinas et al., 2016).

2.2. Bird species selection

We selected five neotropical bird species which collectively represent a range of forest affinities and life history characteristics as described by Stiles and Skutch (1989), and observed in the capture data. These include two forest-dependent species: (1) White-ruffed Manakin (*Corapipo altera*) and (2) Ochre-bellied Flycatcher (*Mionectes oleagineus*); two intermediate forest-dependents: (3) Stripe-throated Hermit (*Phaethornis striigularis*), and (4) Violet-crowned Woodnymph (*Thalurania colombica*); and one generalist: (5) House Wren (*Troglodytes aedon*) (Fig. 2). The White-ruffed Manakin (Passeriformes, Pipridae) is mostly frugivorous but also takes insects (Stiles, 1985), inhabits subtropical evergreen forest interior and edges (Stiles, 1985) and it is considered as a least concern species (LC) with decreasing population trends (BirdLife International, 2017). The Ochre-bellied Flycatcher (Passeriformes, Tyrannidae) is predominantly frugivorous but also consumes insects and arillate seeds (Stiles, 1985), inhabits tropical evergreen forest interior, canopy and edges (Stiles, 1985) and is considered as an LC species with stable population trends (BirdLife International, 2017). The Stripe-throated Hermit (Caprimulgiformes, Trochilidae) is mostly nectarivorous but also consumes insects (Stiles, 1985), inhabits tropical deciduous and evergreen forests interior and edges (Stiles, 1985) and is considered as an LC species with unknown population trends (BirdLife International, 2017). The Violet-crowned-Woodnymph (Caprimulgiformes, Trochilidae) is mostly nectarivorous but also consumes insects (Stiles, 1985), inhabits tropical and subtropical evergreen forest interior, canopy and edges (Stiles, 1985) and is considered as an LC species with decreasing population trends (BirdLife International, 2017). Finally, the House Wren (Passeriformes, Troglodytidae) is a predominantly insectivorous (Stiles, 1985) non-forest species, and considered as an LC species that is increasing in population (BirdLife International, 2017).

2.3. Management scenarios

We digitized the *farmscape* land uses using a 2010 GeoEye image with a 0.46 m resolution at 1:1500 m scale. We visited every parcel and land use in the *farmscape* in August-September 2011 to validate the digitized land-use map and constructed four alternative management scenarios to estimate the impacts of on-farm practices on species mobility. These scenarios include: (1) the 2011 reference *farmscape* composition and configuration, referred to as *Business as usual* (BAU); (2) a *worst case* scenario converting all existing live fences to post-and-wire fence lines; (3) a *trees within* scenario converting simplified coffee agroforests to multistrata coffee agroforests equivalent to Smithsonian Bird-Friendly certification (DeClerck and Martínez-Salinas, 2011), and (4) a *trees around* scenario placing multistrata live fences around the perimeter of all coffee plots, pastures fields, and along all roads (Fig. 3).

All scenarios are realistic, representing a range of on-farm management practices commonly observed throughout Costa Rica and within the Volcanica Central Talamanca Biological Corridor. The *worst case* scenario represents an agricultural intensification scenario, where the CATIE's farm removes all existing live fences, reducing on-farm tree cover in about 58 ha (equivalent to ~ 116 linear km or ~23,200 trees assuming 5 m spacing between trees) (Fig. 3). The conservation scenarios, *trees within* and *trees around* only alter management practices by increasing tree density in, or around coffee fields or pastures while maintaining farm composition and configuration. Both conservation scenarios maintain the primary economic crops produced in CATIE's farm. The *trees within* implies the most significant change by converting 97 ha of simplified coffee agroforests and multistrata live fences to multistrata coffee agroforests. The *trees around* scenario, in contrast, implies the establishment of an additional 20 ha of multistrata live fences covering all possible areas within the farm for a total network of

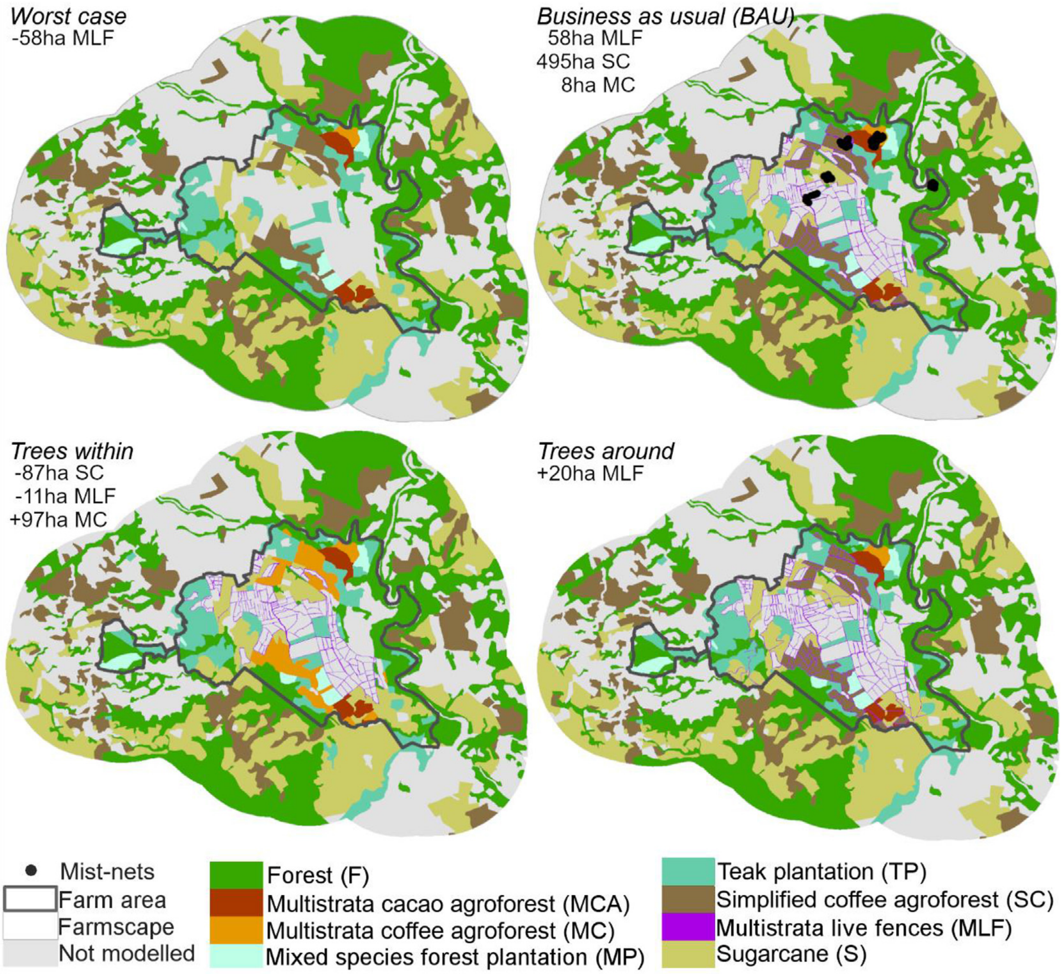

Fig. 3. Land use composition and configuration for the four management scenarios including farm and *farmscape* (1.5 km buffered farm) area. "Not modeled" refers to land uses not monitored by CATIE's Bird Monitoring Program such as cropland, gardens, infrastructure, open pastures, scrub and water bodies. Negative and positive values indicate area reductions or expansions in relationship to BAU respectively. Location of mist-nets where bird captures took place, shown as black dots in the BAU map.

78 ha (~156 linear km or ~31,200 trees) (Fig. 3).

2.4. Circuit theory and conductance values

We used Circuitscape *version 4.0* to model species mobility and *farmscape* permeability. Circuitscape links circuit and random walk theories (Shah and McRae, 2008). The model represents landscapes as electrical circuits and estimates expected net movement probabilities (measured as electrical current) between a species' preferred habitat while considering landscape composition and configuration (McRae et al., 2008; Shah and McRae, 2008). Circuitscape uses random movement under the assumption that species generally lack mental maps of landscape configuration (Koen et al., 2010) and accounts for multiple dispersal pathways (McRae et al., 2008). Circuitscape's capacity to consider multiple dispersal pathways is one of the main strengths of this model (Breckheimer et al., 2014; Pelletier et al., 2014; Shah and McRae, 2008).

By calculating species mobility with an additional 1.5 km buffer around the focal farm, we avoided inflating movement cost between habitat patches (Koen et al., 2010) and prevented biased calculations of net movement probabilities due to preferred habitat location within the *farmscape* (Koen et al., 2014). The added buffer comprises 26% of the total study area and is thus large enough to remove preferred habitat location bias (e.g., high current densities around the habitat) (Koen et al., 2014). In Circuitscape we used the pairwise habitat mode, with a 2-m resolution and averaged cost of movement through eight neighboring cells (4358 × 3389 pixels) (McRae et al., 2013). The pairwise mode calculates movement probability between all possible pairs of habitat patches.

Circuitscape uses each species' preferred habitat as focal nodes in the electrical circuit. Preferred habitat is defined for each study species by its natural history characteristics (Stiles and Skutch, 1989) confirmed by predominant BMP capture and recapture data. Movement probabilities are estimated between all pairs of preferred habitat patches (Koen et al., 2014) assuming a null cost of moving within preferred habitats. In this study, we consider forest to be the preferred habitat for forest-dependent species, the White-ruffed Manakin, and Ochre-bellied Flycatcher, and intermediate forest-dependent species, the Stripe-throated Hermit and Violet-crowned Woodnymph (Stiles and Skutch, 1989). Forest patches assigned as preferred habitat were > 100 ha (n = 2; mean = 340 ha; s.d. = 138 ha) separated by a maximum linear (Euclidean) distance of 5 km and a minimum distance of 1.3 km between patches (Fig. 3). We used forest patch area (ha) as a proxy for habitat quality (Stouffer and Borges, 2001). The House Wren, our fifth study species, is considered a generalist species well adapted to multiple habitat types. We designated the two largest agroforest patches, and scrubland uses (including multistrata cacao agroforests, gardens, scrubs, multistrata coffee agroforests, and simplified coffee agroforests)

Table 1

Mean land use conductance values and 95% confidence interval (CI) estimated from 915 bird captures (Fig. 2). CI values used to assess species mobility under conservative and optimistic conductance values. The R^2 adjust reflects the variability explained by the binomial model.

Land use	White-ruffed Manakin (*Corapipo altera*)	Ochre-bellied Flycatcher (*Mionectes oleagineus*)	Stripe-throated Hermit (*Phaethornis striigularis*)	Violet-crowned Woodnymph (*Thalurania colombica*)	House Wren (*Troglodytes aedon*)
Forest (F)	0.34 ± 0.28	0.72 ± 0.12	0.51 ± 0.14	0.11 ± 0.03	0.00 ± 0.00
Multistrata cacao agroforest (MCA)	0.14 ± 0.16	0.32 ± 0.12	0.37 ± 0.13	0.03 ± 0.01	0.06 ± 0.01
Multistrata coffee agroforest (MC)	0.05 ± 0.10	0.39 ± 0.13	0.34 ± 0.12	0.00 ± 0.00	0.07 ± 0.01
Mixed species forest plantation (MP)	0.00 ± 0.00	0.03 ± 0.05	0.19 ± 0.13	0.01 ± 0.01	0.08 ± 0.02
Teak plantation (TP)	0.01 ± 0.22	0.00 ± 0.00	0.66 ± 0.36	0.03 ± 0.02	0.00 ± 0.00
Simplified coffee agroforest (SC)	0.04 ± 0.07	0.30 ± 0.11	0.05 ± 0.04	0.03 ± 0.01	0.53 ± 0.04
Multistrata live fences (MLF)	0.05 ± 0.10	0.07 ± 0.06	0.01 ± 0.02	0.02 ± 0.01	0.22 ± 0.03
Sugarcane (S)	0.00 ± 0.00	0.02 ± 0.03	0.01 ± 0.02	0.00 ± 0.00	0.09 ± 0.02
R^2_{adjust}	**0.15**	**0.24**	**0.30**	**0.10**	**0.30**

as preferred habitat for the generalist House Wren ($n = 2$; mean = 83 ha; s.d. = 1 ha). We assumed habitat continuity when small roads i.e., ≤(≤5 m width) and canals (≤20 m width) separated preferred habitat patches (Moore et al., 2008).

Conductance values describe the ease or difficulty of movement through individual land uses (McRae et al., 2008). We derived the conductance values from the BMP capture data by calculating a species-specific conductance value for each land use. We estimated conductance values for each land use based on capture histories per land use for each species, rather than on capture-recapture histories per individual bird. The recapture rates of individual birds across land uses were very low, which made it impossible to model turnover and construct occupancy models. The selected approach, therefore, allowed us to use all presence-absence data available per species, which was critical in the case of forest-dependent species that are naturally infrequent in agricultural lands. For instance, the conductance values exclude turnover rate estimates across land uses and are based on occurrence probabilities for each species in each land use derived from binary presence/absence data.

We used a generalized additive mixed model (with Bernoulli distribution, a special case of the binomial) to estimate conductance values with 95% confidence intervals for each species by land use combination. The lowest and highest confidence intervals facilitate assessing species mobility while accounting for the most conservative and optimistic estimations. We used generalized additive mixed models due to their flexibility for modeling nonlinear temporal trends with smoothing functions while controlling for the lack of temporal and spatial independence of capture data (Zuur et al., 2010). Calculated species-specific land use conductance values included capture trends (sampling date) as a fixed effect, and the sample site land use as a random effect, while standardizing by sampling effort (mist-net hours). By using land use as a random effect, we assumed a correlation with compound symmetry in which all the variances and covariances are equal. We fitted three models for each species considering: (1) parallel effects of land uses over sampling time (random intercept); (2) different effects of land uses over sampling time and similar intercept (random slope), and (3) different intercept and effects for the land use on sampling time (both random intercepts and slopes). We selected the best-fitted model using the Akaike Information Criterion (AIC) and by evaluating diagnostic graphs (partial autocorrelation plots, residuals vs. predicted and QQ-plots; Figure S1). We used the gam function in the mgcv package in R (R Core Team, 2016) with Restricted Maximum Likelihood (REML) smoothing parameter, as recommended for modeling occurrence (Wood, 2008). Overall, conductance values and the land use maps for each scenario are the two primary input data in Circuitscape. For instance, we ran Circuitscape 60 times (five bird species, four scenarios, and three land use conductance values, i.e., lowest, mean, highest).

2.5. *Species mobility metrics*

We evaluated three metrics to assess bird mobility across the *farmscape*. First, we evaluated current densities, which indicate the expected probability (scaled between 0 and 100) that an individual will move through each *farmscape* cell as it moves between preferred habitat patches (McRae et al., 2008). This metric allows for visualizing areas used by the species as it moves across the *farmscape*. Second, we evaluated the relative change in resistance distance between scenarios. Resistance distance is a whole landscape metric that accounts for the distance between preferred habitat patches, the number of alternative paths available between all preferred habitat pairs, and the difficulty of movement along each path. Increasing the number of available paths lowers the resistance distance resulting in greater ease of movement through the *farmscape* (McRae et al., 2008). The relative change in resistance distance between scenarios (scenario-*Business as usual*/scenario + *Business as usual*) is bounded between −1 and +1 where negative values indicate resistance distances < BAU or a scenario that offers greater ease of movement than BAU. Positive values indicate resistance distances > BAU or reduced ease of movement than BAU. Third, we calculated the passage area (ha) in non-habitat areas with net movement probabilities greater than zero indicating areas where movement outside habitat is possible across the *farmscape* for each species.

3. Results

3.1. Conductance values models

As expected, the highest conductance values for the forest-dependent and intermediate forest-dependent birds were consistently found in the forest, except for the Stripe-throated Hermit with the highest conductance values in the teak plantation. The highest conductance value for the generalist House Wren was estimated in the simplified coffee agroforest. The White-ruffed Manakin and the Violet-crowned Woodnymph were rarely captured across land uses during the 22,895 mist-net hours which potentially explains the lowest R^2_{ajust} for the best-fitted model for both species (Fig. 1, Table 1). Two bird species, the Violet-crowned Woodnymph, and the House Wren were never captured in two of the land uses evaluated, yielding conductance values of zero for these land uses (Table 1). For example, the Violet-crowned Woodnymph was never captured in multistrata coffee agroforest (MC) whereas the House Wren was never captured in forest (F) or teak plantation (TP, Fig. 2). Forest, teak and the unmonitored land uses surround the preferred habitat of the House Wren, hence limiting the mobility of this species between preferred habitats (Fig. 3-BAU and Fig. 4e).

3.2. Farmscape land use composition and configuration in 2011: Business as usual scenario - BAU

The five-bird species, regardless of their forest dependency, were found to use different parts of the *farmscape* to move between preferred habitats (Fig. 4 - BAU). The modeled mobility across the *farmscape* for each species derived from the capture data indicate that the White-ruffed Manakin (forest dependent), the Violet-crowned Woodnymph (intermediate forest dependence) and the House Wren (generalist) move through the center of the farm (Fig. 4ade). In contrast, the Ochre-bellied Flycatcher and the Stripe-throated Hermit mainly use the south-east portion of the farm and *farmscape* area. Both species also moved along some areas in the north of the farm which may contain labyrinths with “dead-ends”. Areas with “dead-ends” contain redundant pathways and where preferred habitats remain disconnected (Fig. 4bc - BAU).

Business as usual – The BAU scenario supports the sporadic movement of all five species between preferred habitats according to the mean species-land use conductance values, leading to net movement probabilities values ≤ 1% (Table 1; Fig. 4). This represents a small but existing passage area (Fig. 4a-e; BAU). The only species with net movement probabilities > 1% was the Stripe-throated Hermit with a clear corridor located in the southern portion of the farm (Fig. 4c). This species and the House Wren had the smallest modeled passages areas which occupied 2.3% and 1.3% of the total *farmscape* area respectively, suggesting highly limited or constrained movement through non-habitat space across the *farmscape* (Fig. 4e; BAU and Fig. 5). Preferred habitats for two species, White-ruffed Manakin and Stripe-throated Hermit, were disconnected when using more conservative conductance values suggesting an existing but uncertain mobility (Fig. 5).

3.3. Removing all multistrata live fences – worst case scenario

The removal of 58 ha of multistrata live fences (6% farm area) in the *worst case* scenario interrupts the mobility of three of the five study species (Fig. 4 –*worst case*). For the two remaining species, the Ochre-bellied Flycatcher exhibited net movement probabilities < 1% but a reduced passage area compared to BAU (- 82 ha) with fewer alternative pathways and greater resistance values (increased relative resistance distance; Fig. 6). However, the Stripe-throated Hermit increased its passage area outside its habitat in 2 ha, with similar net movement probabilities to BAU (Figs. 4c and 5), but also with fewer and more resistant alternative pathways compared to BAU (Fig. 6). Nonetheless, the preferred habitats for both species also became disconnected when using more conservative conductance values (Fig. 5).

3.4. Converting simplified to multistrata coffee agroforest fields – “trees within” scenario

Converting 97 ha of existing simplified coffee agroforest to multistrata coffee agroforests in the farm limited the modeled mobility of the Violet-crowned Woodnymph. Despite this species’ forest dependence, it has never been recorded or captured in multistrata coffee agroforests (Table 1, Fig. 4 - *trees within*). The modeled passage area for the other four species increased slightly in this scenario, whereas net movement probabilities remained similar (Figs. 4 and 5). The passage areas expanded in non-habitat areas to 29, 16, 7 and 7 ha for White-ruffed Manakin, Ochre-bellied Flycatcher, Stripe-throated Hermit, and House Wren respectively, compared to BAU (Figs. 4 and 5). The *trees within* scenario offered a greater number of alternative pathways, lowering the resistance distance and increasing the ease of movement between preferred habitats than BAU for all species except Violet-crowned Woodnymph. This is reflected in the negative relative resistance distance values (Fig. 6). The mobility of the White-ruffed Manakin and Stripe-throated Hermit remained interrupted when using more conservative conductance values in the *trees within* scenario (Fig. 5).

3.5. Adding multistrata live fences around all coffee and pasture fields and along major roadways- “trees around” scenario

Adding an extra 20 ha of multistrata live fences on the farm increased by at least 1.9 times the passage area for all bird species (Fig. 5). Nonetheless, the net movement probability remained below 1% for all species (Fig. 4 - *trees around*), and the habitats for White-ruffed Manakin and Stripe-throated Hermit remained disconnected when using more conservative conductance values (Fig. 5). The clear corridor connecting both preferred habitats in the southeast part of the *farmscape* for the Stripe-throated Hermit was lost under this conservation scenario. Despite the larger passage areas (at least double that of BAU, Fig. 5), this scenario offers a smaller number of alternative pathways which increased relative resistance distance between preferred habitat for Ochre-bellied Flycatcher and Stripe-throated Hermit relative to BAU. This may suggest that rather than corridors connecting preferred habitats across different areas of the *farmscape,* the “trees around” scenario might create alternative and redundant pathways with “dead-ends” (Figs. 4b and 6).

4. Discussion

Assessing species movement across agricultural landscapes and quantifying the contribution of on-farm management practices to landscape connectivity is necessary to better inform conservation efforts (Tischendorf and Fahrig, 2000; Graham, 2001; Bélisle and Desrochers, 2002; Adriaensen et al., 2003). While randomly placed conservation elements can contribute to connectivity, planning these interventions at the *farmscape* level can increase movement probability with less effort and with a lower negative impact on farmers’ livelihoods and productivity objectives. This study demonstrates the value of planning the location of on-farm conservation elements and we discuss how the proposed approach can contribute to advancing on-farm conservation planning for species mobility beyond the farm as well as its limitations.

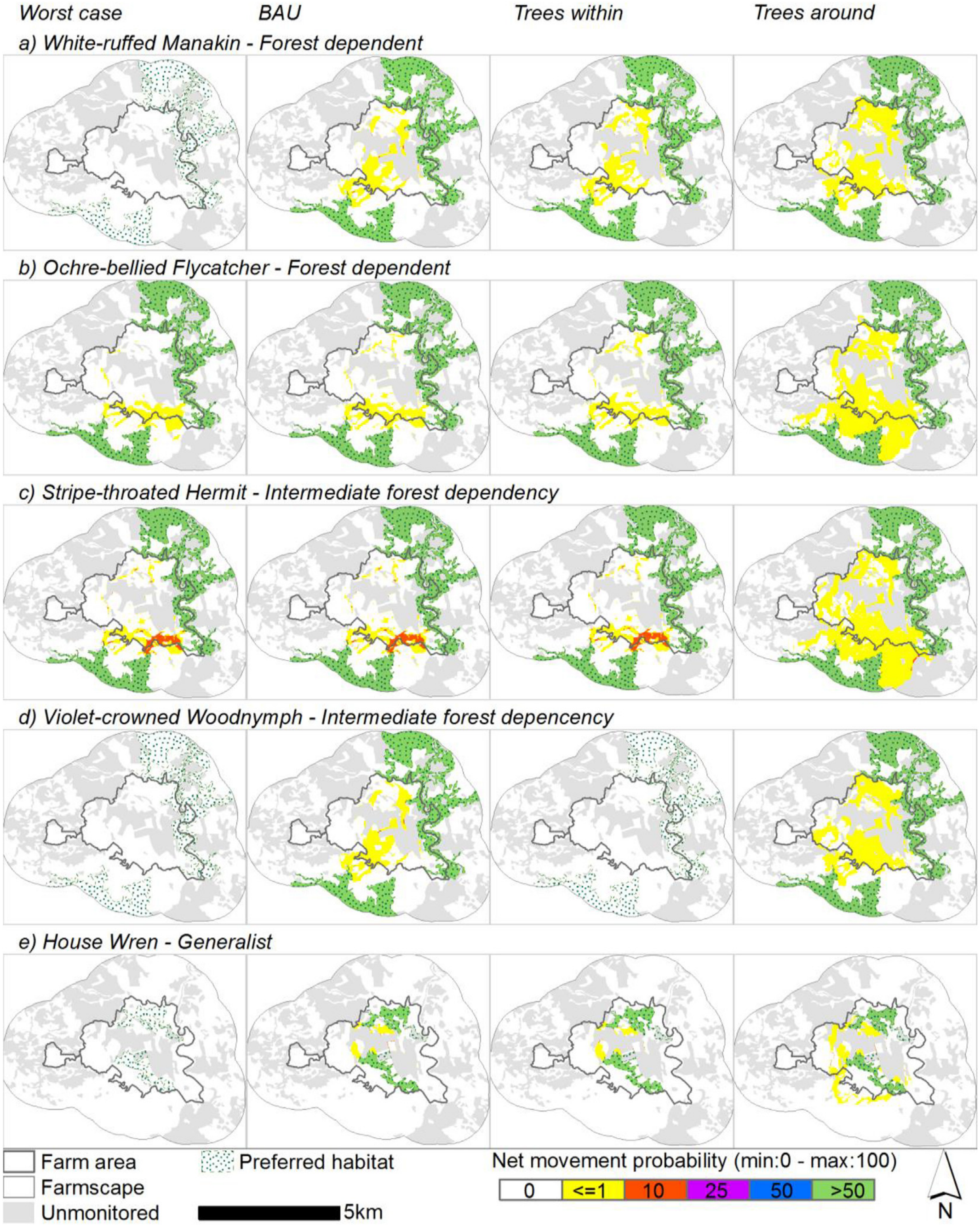

Fig. 4. Net movement probabilities for all five-study species according to the four modeled scenarios and the estimated mean species-land use conductance probabilities.

4.1. Retain and diversify existing live fences: a good starting point

Currently, the small portions of the farm and *farmscape* area (6% and 1% respectively) with live fences facilitate the movement for the five-bird species regardless of their forest dependency. Removing these linear elements through further conventional agricultural intensification would decrease on-farm contribution to bird species mobility, shifting from a previously connected to a disconnected *farmscape* with larger 'hostile' passage areas.

Live fences and tree cover embedded in agricultural landscapes provide several benefits to farmers (Morantes-Toloza and Renfijo, 2018). For example, live fences in silvopastoral systems provide naturally rot-resistant fence posts, shade, and fodder for livestock (Harvey et al., 2005) and have limited impact on pasture productivity due to the little land area they occupy (Garbach et al., 2012). Likewise, live fences in Central America are used to delineate pastures or crop parcels and are usually composed of a diversity of tree species offering multiple uses such as shade, fodder, carbon capture, and habitat (Harvey et al., 2005; Sánchez Merlos et al., 2005; Chacón and Harvey, 2006). The contribution to wildlife mobility from biodiversity-friendly on-farm conservation practices thus could complement rather than compete with farmer management priorities (e.g., Chacón and Harvey, 2006; Harvey et al., 2006; Motzke et al., 2016; Muñoz-Sáez et al., 2017).

Despite these benefits, deforestation, and removal of all types of tree cover is common in Central America due to the expansion of conventionally intensified production systems which disregard traditional, biodiversity-friendly practices (Hansen et al., 2013; FAO, 2015; Shaver et al., 2015; Kremen and Merenlender, 2018). Hansen et al., (2013)

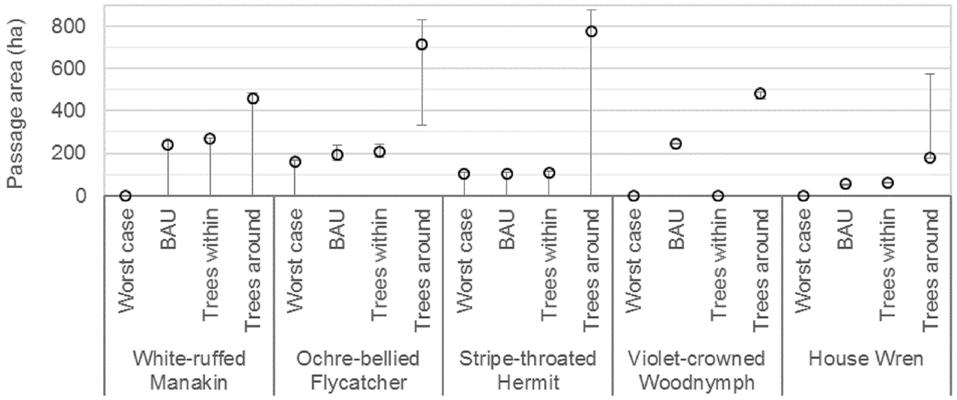

Fig. 5. Passage area (ha) for each bird species and management scenario estimated using the mean species-land use conductance values and the confidence interval (conservative and optimistic conductance values). Passage area indicates the area through which movement outside preferred habitat is possible for each species (See values in Table S1.).

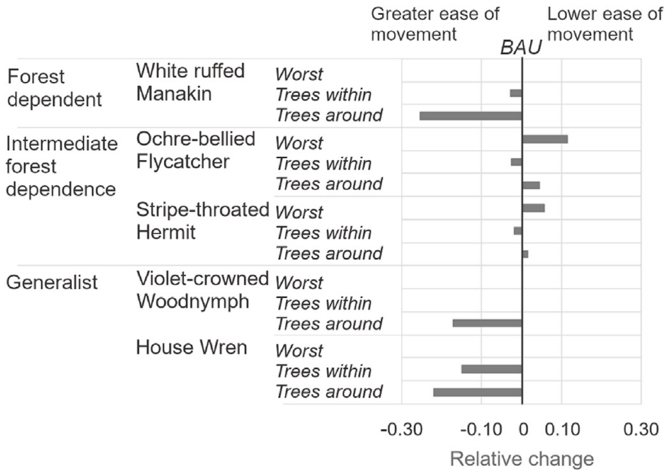

Fig. 6. Relative change in resistance distance between *Business as usual* - BAU and other scenarios (scenario-BAU/scenario + BAU). Negative values indicate scenarios that offer greater ease of movement (less resistance distance) than BAU. Positive values indicate that BAU offers greater ease of movement than alternate scenarios.

found high tree cover loss rates in the region since 2001 up to recently (see Global Forest Watch). Thus, the loss of tree cover, including live fences, is not only associated with the loss of conservation values but with the reduction or loss of ecosystem services benefitting farmers, affecting overall the ecological integrity of agricultural landscapes (DeClerck et al., 2010; Harvey et al., 2005).

Live-fence contributions are poorly recognized in conservation and agricultural development agendas. However, their biodiversity conservation value is considerable, particularly since conserving and diversifying existing live fences or other linear elements in agricultural landscapes are an effective conservation effort requiring a relatively small portions of the landscape (e.g., 6% in CATIE's *farmscape*) while producing significant conservation value in addition to multiple benefits to farmers (Morantes-Toloza and Renfijo, 2018). Restoring and enhancing live fences would improve the biodiversity conservation value of these agriculture dominated landscapes (Karp et al., 2019), as long as remaining natural habitat is protected and enhanced as well.

4.2. Increasing trees around or within fields for species' mobility at farmscape level: one, the other, or both

Increasing tree diversity and density as linear or embedded elements in agricultural lands contribute differently to species mobility. The two conservation scenarios tested here have distinct impacts on species mobility in CATIE's *farmscape*. Adding an extra 20 ha of multistrata live fences (*trees around* scenario) at least doubled the passage areas for all bird species across scenarios. Extending the multistrata live fences network increased pathway redundancy which is critical to functional connectivity (Fletcher et al., 2014). Nonetheless, we found that an increase in pathway redundancy and larger passage areas does not always lead to increasing connectivity (e.g., Ochre-bellied Flycatcher and the Stripe-throated Hermit). Our results support Fletcher et al., (2014) indicating that the configuration of pathway redundancy and the structure of the landscape matrix alters mobility. In contrast, converting 97 ha of simplified coffee agroforest to multistrata coffee agroforest (*trees within*) yielded much smaller increases in passage areas for four bird species and limited Violet-crowned Woodnymph mobility compared to *Business as usual*. Hence, *trees within* eased species movement between habitats for some birds in the same passage area whereas *trees around* is likely to be more effective for increasing the *farmscape* area used by birds with distinct life history characteristics, while simultaneously easing species movement among habitats for most but not all species.

On-farm conservation efforts targeted at increasing tree density and diversity through linear elements surrounding agricultural fields thus present an alternative conservation strategy, particularly where farmers are concerned with competition between tree shade and its impacts on reduced crop productivity (e.g., areas where topography, climate, and soils favor pests and diseases; Allinne et al., 2016). Coffee fields are often not bordered by trees, hence, implementing multistrata live fences around them presents an approach that both increases *farmscape* connectivity and limits coffee pest dispersal and movement (Avelino et al., 2012), at the same time increasing habitat for wildlife (Harvey et al., 2005, 2006).

However, maintaining and protecting multistrata shade coffee (*trees within*) should remain a priority due to their habitat value (Mas and Dietsch, 2004) and role as a refuge for diverse taxa (Perfecto et al., 1996; Philpott et al., 2008; Jha and Dick, 2010; Jha et al., 2014). Additionally, coffee fields with diversified shade canopies can ensure the provision of other ecosystem services beyond species mobility such as pests and diseases regulation, agroforestry products provisioning; soil fertility maintenance; and carbon sequestration (Cerda et al., 2017).

Overall, retaining and increasing habitat patches in agricultural landscapes is an essential strategy for conservation (Prevedello et al., 2017), since species mobility in the absence of preferred habitat is a moot point. Considering land use type, habitat connectivity, and landscape context in the management of *farmscapes* is imperative to support conservation efforts (Goldman et al., 2007; Dickson et al., 2013; Vaca et al., 2019). For instance, moving away from random tree location to targeted and strategic location of conservation elements within a *farmscape* can lead to significant improvement of conservation outcomes, while enhancing species mobility for several species with both high and intermediate forest dependencies.

Planning on-farm conservation efforts is particularly relevant to ecological certification. Certification schemes primarily promote increasing tree density and diversity within fields as a conservation strategy for improving habitat quality in agricultural landscapes (Quispe, 2007; DeClerck and Martínez-Salinas, 2011; Blackman and Naranjo, 2012). However, these strategies are often a compromise between an 'ecological gold standard,' and 'production-friendly' practices (Quispe, 2007). For instance, Smithsonian Bird Friendly emphasizes high levels of canopy cover and increased tree species diversity which has demonstrated habitat value (Mas and Dietsch, 2004) but whose impact on yields can be prohibitive for farmers (Philpott et al., 2007) thus affecting adoption and appropriation. On the other hand, the Rainforest Alliance's certification is more attainable for producers but has difficulties demonstrating positive impact for forest-dependent species (Mas and Dietsch, 2004; Quispe, 2007). Our modeling exercise demonstrates that *farmscape* spatial planning can have a positive effect on connectivity and complement habitat conservation strategies while complementing farmer's production objectives and goals.

4.3. Modeling species mobility in agricultural landscapes: novelty, limitations, and challenges

Seven years of capture data support our effort to model bird species' persistence and mobility. This modeling effort improves upon previous modeling approaches often based on more subjective methods (Spear et al., 2010; Zeller et al., 2012) and expert-based binary presence-absence values for evaluating critical connections and barriers in landscape planning (Dickson et al., 2013). Nonetheless, using capture data also includes some limitations including the lack of land use replicates and unbalanced sampling efforts. Both limitations were addressed by using novel methods such as subject-specific models (mixed models), and population averaged response patterns (Fieberg et al., 2009).

Our analysis is conservative and potentially underestimates the contribution of small forest patches, and unmonitored land uses in supporting species mobility across the *farmscape*. We purposely excluded 58 small forest patches (mean area = 15.3 ha; s.d. = 35 ha) and defined as preferred habitat only forest patches whose areas were greater than 100 ha following Stouffer and Borges (2001) findings which indicate understory birds require habitats greater than 100 ha despite that none of the selected birds are understory species (Stouffer et al., 2011). Likewise, the contribution from unmonitored uses (i.e., croplands, gardens, infrastructure, pastures, and scrub) to birds' species mobility was excluded due to capture data gaps, greatly reducing House Wren (generalist) mobility across the *farmscape* in particular.

Our proposed modeling approach provides a unique contribution despite the normal assumptions and limitations inherent in any modeling approach. First, it allows the estimation of land use mean conductance values and mobility uncertainty for each species evaluated based on seven years of capture data. Secondly, it allows the assessment of species' functional mobility based on individual species' live history characteristics, *farmscape* composition and, configuration. Thirdly, calculated metrics allow assessing different and complementary aspects of species mobility, which taken together, can enhance on-farm conservation planning interventions. For instance, the net movement probability facilitates identifying areas often used by species to move across the *farmscape*. Whereas the passage area and the relative change in resistance distance facilitate estimating the magnitude of the change in species' mobility due to on-farm conservation efforts, becoming a useful tool for impact assessment of conservation interventions in any given *farmscape*.

The proposed modeling approach accounts for the contribution of fine-scale elements and land use management to conservation beyond discrete and coarse land use categories (e.g., Lechner et al., 2015). Our approach (high spatial and thematic resolution) recognizes the contribution that one land use (e.g., coffee) could have to species mobility under different land management including for example mixing it with low versus high tree density and diversity. This approach is more in line with the realistic needs for managing agricultural land for conservation without limiting or affecting farmers' objectives and priorities. The selected scenarios represent alternative pathways for land use change in the region. The results from this modeling approach could facilitate engaging with multiple stakeholders to develop aligned conservation strategies including: 1) with farmers to identify other areas in the farm where multistrata live fences can be added to connect dispersal pathways, while considering the estimated cost of adopting each scenario; 2) with ecologists to identify monitoring strategies to test the efficacy of the proposed conservation scenarios with empirical data; and 3) with private sector actors and government agencies to guide incentive programs, with the goal of targeting conservation resources in landscape areas where we have the highest probability of a positive return on investment is more likely.

5. Conclusion

We coupled empirical evidence and a modeling approach to predict bird species mobility across an agricultural landscape under different on-farm conservation strategies (removing trees, adding trees in and around agricultural fields). Overall, our findings demonstrate that a very small area in CATIE's farm and *farmscape* with multistrata live fences (6% and 1% respectively) facilitates the movement of all assessed species (low but existing net movement probabilities). Among the tested alternative on-farm conservation strategies we found that *worst case* scenario limited species mobility for almost all assessed species, whereas both conservation scenarios contributed differently to species mobility. For instance, the *trees around* scenario is likely more effective for increasing the *farmscape* area used by birds to move across habitats whereas *trees within* eases species' movement between habitats through the same passage area (the non-habitat area through which movement is possible for each species).

The proposed approach can provide much-needed guidance for targeting conservation efforts for restoring, retaining, protecting and diversifying tree cover in a fragmented world. The contribution of agricultural landscapes' management to conservation objectives is often undervalued, nonetheless here we demonstrate the contribution from multistrata live fences despite a conservative modeling approach. In particular, multistrata live fences improve *farmscape* connectivity for bird species with different levels of forest-dependency and, life history characteristics that persist in agriculture-dominated landscapes. Attaining conservation objectives requires revisiting the often perceived rivalry between agriculture and conservation. This demands new strategies for planning biodiversity conservation efforts with farmers without compromising productivity while contributing to conservation goals beyond the farm level.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2019.109504.

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