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ORIGINAL PAPER

The indirect effects of habitat disturbance on the bird communities in a tropical African forest

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Abstract Tropical forests are increasingly threatened by anthropogenic activities often resulting in habitat and biodiversity loss. To effectively manage and protect these areas, it is important to have an understanding of the factors affecting their biodiversity. Previous research has shown that birds in tropical regions are severely affected by human-induced habitat conversion and disturbance. The effects, however, are often area and guild-specific and the underlying mechanisms are frequently unclear. In this study, we disentangle and quantify the direct and indirect effects of human population density, distance to forest edge, habitat disturbance, and vegetation structure and composition on the total abundance and species richness of birds in Kakamega Forest, Kenya. Specifically, we use structural equation modeling to develop and test path models, which reflect the potential causal relationships between the bird assemblages and the chosen explanatory factors. Relationships were tested on the overall bird community and on five different guilds, classified according to birds' forest specialization and feeding preferences (i.e. forest specialists,

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generalists and visitors, and frugivores and insectivores). Results showed that habitat disturbance, caused by logging, had a weak positive direct effect on the bird communities, but also had a strong detrimental indirect effect, particularly on the total abundance and species richness of forests specialists and insectivores. The negative effect was mediated through changes in the forest's vegetation structure and composition. Shorter distances to the forest edge also had a negative effect, on all bird categories except on forest visitors, which also benefited from higher levels of disturbance. Our study shows that although in some cases habitat disturbance may have no strong direct negative effects it can still negatively influence bird communities in an indirect way. In the case of Kakamega Forest, we suggest that to conserve bird communities it is important to maintain the forest's compositional and structural diversity by reducing human-induced habitat disturbance, such as illegal logging activities.

Keywords Bird conservation · Tropical forests · Structural equation modeling · Species richness · Anthropogenic habitat disturbance · Vegetation structure and composition

Introduction

Tropical forests are increasingly affected by anthropogenic activities, many of which result in habitat conversion (Booth et al. 2012). Consequently, only few undisturbed forest areas remain (Gibson et al. 2011; Kareiva et al. 2007; Sodhi et al. 2008). Growing human population size is likely to exert even stronger pressure on these ecosystems, causing further habitat and biodiversity loss (Cincotta et al. 2000). Tropical birds have been particularly affected by these human-induced changes with approximately 70 % of the birds threatened in the world found in tropical forests (Sodhi et al. 2008). The effective protection of these birds is imperative to the conservation of tropical ecosystems in general, as birds are known to perform essential ecological functions such as seed dispersal, pollination and pest control (Sekercioglu 2006).

The conservation of species in human-modified tropical areas is dependent on sound management practices (Gardner et al. 2009). Management needs to be based on a solid understanding of the underlying mechanisms influencing biodiversity. Although previous studies have shown that tropical bird species are particularly sensitive to habitat disturbance (Sodhi et al. 2008), the exact mechanisms by which disturbance affects the various bird guilds are often unclear (Schleuning et al. 2011a; Tscharntke et al. 2008). Birds' responses to habitat changes are not uniform and are influenced by species specific morphological and behavioural traits such as body size and foraging patterns (Sodhi et al. 2008; Mulwa et al. 2013; Newbold et al. 2013). Consequently, vulnerability to habitat disturbance varies depending on the specific species and guild (Sodhi et al. 2008; Schleuning et al. 2011a). For example, compared to frugivores and forest generalists, insectivores and forest specialists are considered to be more sensitive to disturbance as they often have more specialized feeding and habitat requirements (Sodhi et al. 2008).

The effects of disturbance also vary depending on the area examined and the type and levels of disturbance (Dranzoa 1998). While in some cases selective logging may benefit understory insectivorous birds, due to understory vegetation regrowth, in other cases it may affect insectivores negatively, due to changes in microclimate (Sodhi et al. 2008). Moreover, effects are often complex involving multiple interacting factors and mechanisms, which are not always easy to disentangle. Yet, understanding the mechanisms by which disturbance and other human-induced factors influence species and communities is important for developing and implementing targeted conservation measures to maintain diverse bird communities in tropical forests.

In this study, we use structural equation modeling (SEM) to study the mechanisms by which anthropogenic factors are affecting the species richness and total abundance of the bird communities in Kakamega Forest, Kenya, classified according to their forest specialization and feeding preferences (i.e. forest specialists, generalists and visitors, and frugivores and insectivores). Specifically, we test the following four hypotheses: (1) nearby human population density and distance to the forest edge determine habitat disturbance levels, (2) distance to the forest's edge has a direct impact on the species richness and total abundance of the overall bird communities and of the five bird guilds, (3) habitat disturbance has a *direct* effect on the species richness and total abundance of the overall bird communities and of the five bird guilds, (4) habitat disturbance has an *indirect* effect on the species richness and total abundance of the overall bird communities and of the five bird guilds, mediated through changes in vegetation structure and composition. We use SEM to test these hypotheses because although it is a correlative approach it allows for the simultaneous assessment of the direct and indirect effects of the explanatory variables on the response variables of interest (Grace 2006, 2008; Schumacker and Lomax 2004).

Methods and materials

Study area

Kakamega Forest is Kenya's only remaining tropical forest and the easternmost remnant of the Guineo-Congolian forest belt that once stretched across central Africa (Kokwaro 1988; Tsingalia 1990). Its elevation ranges from 1460 to 1765 m a.s.l. (Lung and Schaab 2006) and its average annual rainfall is 2007 mm (Bleher et al. 2006). It has a rich bird diversity, hosting more than 410 species (Mulwa et al. 2012), and it is one of Kenya's important bird areas (IBA) (Bennun and Njoroge 2000). Efforts to protect the forest date back to 1933 when it was first designated as Trust Forest and managed by the Forest Department (FD) (Bleher et al. 2006).

The forest is located in one of Kenya's most densely populated areas, with an average of 600 people/km^2 (Blackett 1994; Lung and Schaab 2006). It is considered highly fragmented and disturbed due to past and ongoing anthropogenic activities (Bleher et al. 2006). Although logging was officially banned since the mid-1990s (Mitchell 2004), continuing legal and illegal extraction of wood and non-timber forest products, driven by increasing human population and poverty, threatens the biodiversity of the forest (Rogo et al. 2001; Lung and Schaab 2010). Increasing need for agricultural land poses an additional threat resulting in further forest loss. Today, less than half of Kakamega Forest is covered by primary forest, and although in some areas the vegetation is regenerating (Lung and Schaab 2004; Lung et al. 2012; Mitchell 2004), it is in essence comprised of a mixture of primary and secondary forests, glades and clearings, and timber and tea plantations (Bleher et al. 2006).

For the purposes of this study, we used existing data from 2001/2002 and 2005/2006 (Farwig et al. 2006, 2008, 2009) and additional complementary data collected in 2009 at twenty-two sites located throughout the forest (Fig. 1). Study sites were located in five different types of forest: (1) near-primary forest, consisting mostly of indigenous climax plant species, (2) secondary forest, where forest's natural vegetation is regenerating (3) plantations of a mixture of indigenous species, (4) monocultures of indigenous *Maesopsis*

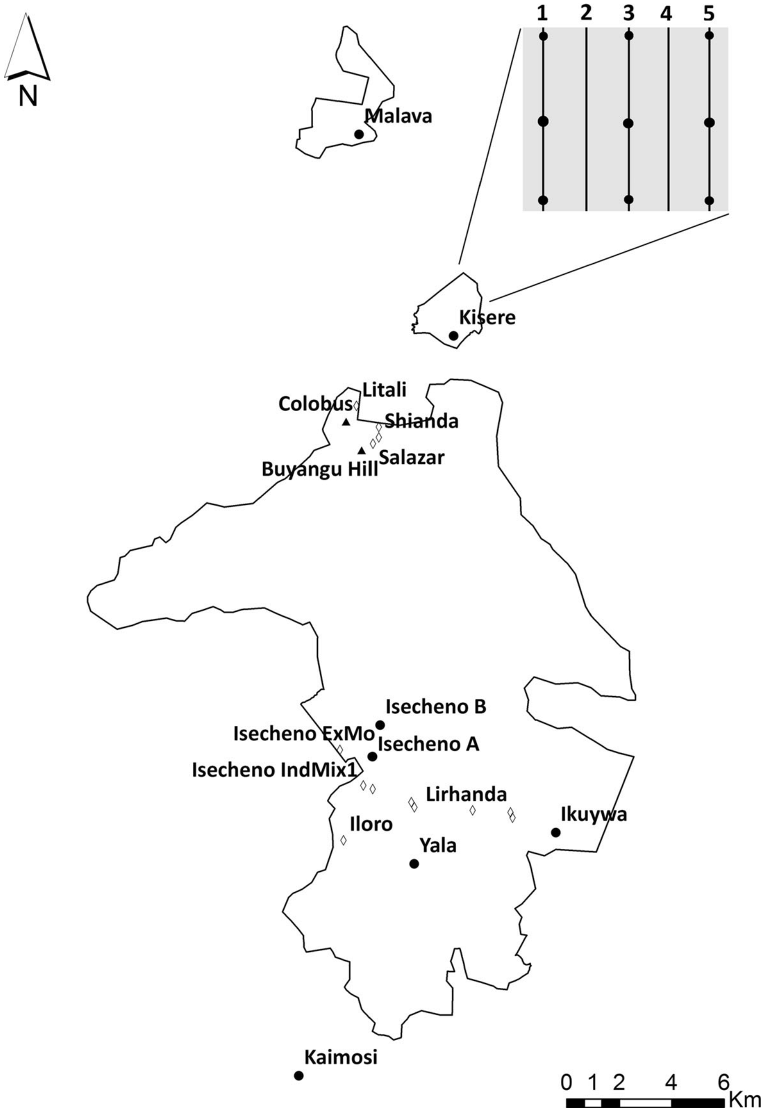

Fig. 1 Map of Kakamega Forest showing the forest's boundaries and the twenty-two study sites (*filled circle* Dataset 1, *open diamond* Dataset 2, *filled triangle* common sites). As an example, the 1 ha plot in one of the sites is shown along with the five transects, and the nine point-count locations used for the bird surveys

eminii, and (5) monocultures of exotic *Bischoffia javanica* (see Farwig et al. 2006, 2008 for a more detailed description of the sites).

Bird species richness and total abundance

Data on birds were collected in 2001/2002 and 2005/2006 (hereafter dataset 1 and dataset 2, respectively) using 10-minute point counts (Bibby et al. 1992), all conducted between

07:00 and 8:30 am at the 22 study sites. At each site, a 1 ha plot was established (100 m × 100 m), in which five 100 m long transects were run, separated by 20 m from each other (see diagram in Fig. 1). Bird surveys were carried out once a month, by Nixon Sajita a local field assistant, at nine different points (three on each odd numbered transects), all separated by 40 m (Fig. 1). During the surveys, all species seen or heard within a radius of 20 m were identified and recorded (see Farwig et al. 2006, 2008 for a more detailed description of the methods).

For dataset 1, 9 sites were sampled for 12 months (Fig. 1) while for dataset 2, 15 sites were sampled for 13 months (two sites were the same in both datasets; Fig. 1). For each site, the data from all nine points were combined and the monthly bird species richness and total abundances were calculated using the Biodiversity Calculator (Danoff-Burg and Xu 2006). Then, the monthly values were averaged to quantify an overall measure of bird species richness and abundance at each site. For the two sites present in both datasets the average of the overall values was taken.

The same procedure was followed to estimate species richness and total abundance of the five habitat and feeding guilds of birds used in the analysis. Birds were classified as forest specialists (FS), forest generalists (FG) and forest visitors (FV), according to their dependence on undisturbed forest, following the classification of Bennun et al. (1996). According to Bennun et al. (1996) forest specialists are species that typically prefer undisturbed forest, avoid edges and are likely to be the first affected by habitat disturbance. Forest generalists also depend on the forest for their survival but are more tolerant to disturbance and are often found in forest patches, gaps and near the edges. Forest visitors, on the other hand, are species which are commonly found in areas outside the forest and are likely to be affected the least by habitat disturbance. Birds were also classified as frugivores and insectivores based on the birds' major food items, using the database provided by Kissling et al. (2007). Species listed in the database as either obligate or partial frugivores and insectivores were assigned to the corresponding feeding guild.

Plant diversity

Plant diversity was estimated using data on trees collected in 2000/2001 and 2005/2006 (dataset 1 and 2 respectively) on the same 1 ha plots established for the bird counts. All trees within the plots, with a diameter at breast height (DBH) of more than 20 cm, were identified to species level and recorded. Using the Biodiversity Calculator (Danoff-Burg and Xu 2006), the Shannon-Wiener diversity index of tree diversity was calculated for each site (Magurran 1998).

Vegetation structure and habitat disturbance

Data on vegetation cover and structure and habitat disturbance were collected at each study site in 2009, using the same five 100 m long transects. Canopy cover was measured at five equidistant points, separated by 20 m, along each transect (i.e. a total of 25 points) using a digital camera (Nikon Coolpix 2400) and a hemispherical lens (Nikon FC-E9) (Danson et al. 2007). The Gap Light Analyzer Version 2.0 (Frazer et al. 2000) was used to calculate the percentage of canopy openness at each point, which was then averaged to obtain an overall value for each site.

At the same 25 points the foliage height diversity (FHD) was measured by visually estimating to the nearest 5 % the vegetation cover at seven different height levels (0, 1, 2, 4, 8, 16, 32), following the same method used in Farwig et al. (2008). Using the Shannon–

Wiener index (Magurran 1998), an estimate of FHD was obtained for each point, which was then averaged for each site (Farwig et al. 2008).

To assess human-induced habitat disturbance, the total number of tree stumps was measured. According to Bleher et al. (2006), this measure of logging intensity is the most appropriate disturbance index for Kakamega Forest. All tree stumps found along each transect and within 5 m to each side were recorded. To ensure that each site was sampled adequately, an additional 300 m of existing paths and trails, found adjacent to the transects, were also surveyed covering a total area of 0.8 ha (800 m × 10 m).

Data on human population densities were estimated using the 1999 national census data, made available by the Kenyan Central Bureau of Statistics, at the sublocation level, the smallest administrative unit in the census (Lung et al. 2013). Using GIS tools, each site's nearest access point to the forest was first identified and then its population density was estimated by dividing the population size of the corresponding sublocation by its total area. GIS tools were also used to estimate the distance to the nearest forest edge from each site.

Structural equation modeling

To explore the relationships between the explanatory variables and the bird communities we used structural equation modeling (SEM). SEM can be considered as a set of linear equations which when combined form a path model representing the hypothetical causal links between the chosen variables. SEM allows researchers to simultaneously test the direct and indirect effects of the independent variables on one or more response variables and on each other (Mitchell 1992; Wootton 1994).

To build the path models we first reviewed the available literature on Kakamega Forest to identify significant relationships between variables relevant to our research questions (e.g. Althof 2005; Bleher et al. 2006; Eshiamwata et al. 2006; Lung and Schaab 2006; Kirika et al. 2008a; Maina 2002; Mitchell and Schaab 2008). Then, using our previous research experience in the forest, we developed an initial path model, which represented the hypothesized mechanisms by which the selected variables were linked (Fig. 2).

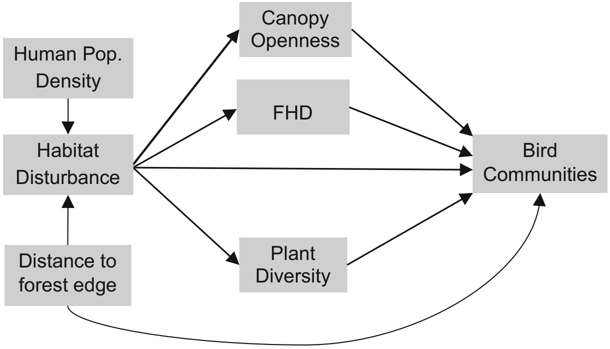

Fig. 2 Path model developed based on the literature and previous experience, illustrating the possible effects of human population density, distance to forest edge, habitat disturbance, canopy openness, foliage height diversity and plant diversity on the species richness and total abundance of the bird assemblages in Kakamega Forest. We assumed correlated errors between the three vegetation variables

Path models

We hypothesized that habitat disturbance, measured as number of tree stumps, was determined by nearby human population density (as measured at the nearest forest entry) and by distance to the forest edge. Sites in the vicinity of high population densities and closer to the forest edge were thought to be more likely to have higher disturbance levels. Distance to the forest edge was also hypothesized to have a direct impact on the bird communities. It was then hypothesized that habitat disturbance has a direct effect on the bird assemblages, but also an indirect effect by influencing the vegetation, i.e. canopy cover, FHD and plant diversity, which were hypothesized to directly affect bird species richness and total abundance (Fig. 2). Correlation links were added between the three vegetation variables in the model, as they are likely to be influenced by other common factors, not included in the model, such as climatic conditions and soil properties (Althof 2005; Fashing and Gathua 2004). Correlation links were allowed to vary during model selection.

To estimate the cumulative effects of habitat disturbance on each bird community we added all the averaged indirect and direct effects (Grace 2006; Schumacker and Lomax 2004). The size of an indirect effect was calculated by multiplying the averaged path coefficients along the paths that linked disturbance to the bird communities (Schumacker and Lomax 2004).

SEM analyses were conducted in AMOS 20.0, a statistical package developed by IBM particularly for structural equation modeling (Pugesek et al. 2003). For every bird category tested, we used multimodel inference (Burnham and Anderson 2002) on a model set which included the full model and all possible subset models (2^{10} paths = 1024 models). We ranked models in ascending order according to their AIC value (Burnham and Anderson 2002). We then selected all models with a ΔAIC of less than two. ΔAIC is the difference between a model's AIC and the AIC of the best performing model with the lowest value (Burnham and Anderson 2002). We averaged the path coefficients of the selected models using the zero method (Burnham and Anderson 2002), by adding the coefficients of each selected model after we have multiplied them by the model's Akaike weight (w_i). The zero method is the most appropriate in studies like ours, where model averaging is used to compare the importance of the effect of each predictor on the response variable (Nakagawa and Freckleton 2011). We used the same method to average the R^2 values and obtain an overall value for each bird category.

To check if any of our selected models ($n = 92$) were spatially autocorrelated we followed the approach of Kissling et al. (2008). For each endogenous variable in the selected path models, we ran a regression analysis with it as the dependent variable and the exogenous variables in the path models as predictors. We then tested the residuals of these models for spatial autocorrelation, using the Moran's I test in the package "ape" in R (Paradis et al. 2004, R Core Team 2015). For example, using the described approach, the full model in Fig. 2 would result in the five following regression equations:

$$\begin{aligned}\text{Habitat Disturbance} = \alpha 1 + \beta 1\ \text{Distance to the forest edge} \\ + \beta 2\ \text{Human Population Density} + \varepsilon 1\end{aligned} \tag{1}$$

$$\text{Canopy Openness} = \alpha 2 + \beta 3\ \text{Habitat Disturbance} + \varepsilon 2 \tag{2}$$

$$\text{Foliage Height Diversity} = \alpha 3 + \beta 4\ \text{Habitat Disturbance} + \varepsilon 3 \tag{3}$$

$$\text{Plant Diversity} = \alpha 4 + \beta 5 \text{ Habitat Disturbance} + \varepsilon 4 \tag{4}$$

$$\begin{aligned}\text{Bird Richness/Abundance} = {} & \alpha 5 + \beta 6 \text{ Canopy Openness} + \beta 7 \text{ Habitat Disturbance} \\ & + \beta 8 \text{ Foliage Height Diversity} + \beta 9 \text{ Plant Diversity} \\ & + \beta 10 \text{ Distance to the forest edge} + \varepsilon 5\end{aligned} \tag{5}$$

To check whether our variables were normally distributed we used the Shapiro–Wilk normality test in R. To achieve normality human population density, number of stumps, distance to the forest edge and canopy openness were log-transformed, while plant-diversity was transformed exponentially. We used the Shapiro–Wilk test to check whether the residuals of the regression models which included the specific variable were normally distributed. We followed the same procedure for three of the twelve response variables for which the p-value of the Shapiro–Wilk test was below 0.05.

Results

A total of 130 bird species were included in the analysis. Out of those, 45 species were forest specialists, 40 forest generalists, 31 forest visitors, as well as 104 insectivores and 34 frugivores. The overall monthly bird species richness at the twenty-two sites ranged from 14.7 to 23.9 species (mean 20.1). Total bird abundances ranged from 41.2 to 91.5 (mean 64.2). Table 1 provides the range and mean for each of the seven explanatory variables included in the original model.

No spatial autocorrelation was detected in the residuals of the selected models (Moran's I p-values for Eqs. 1–4 ranged from 0.14 to 0.77, and for the variants of Eq. 5 from 0.05 to 1 depending on the response variables and the predictors included; see Appendix in Table 4 for a complete list of the results). According to the results of the Shapiro–Wilk test, apart from human population density (p value ≤ 0.001), our independent variables were normally distributed ($0.08 \leq$ p values ≤ 0.86). When the residuals of the regression models which included human population density were tested, lack of normality was not found to be an issue (p value = 0.631 when distance to the forest edge was also in the model, i.e. Eq. 1, and 0.601 when human population density was the only independent

Table 1 Minimum, maximum, mean and standard deviation values for the six explanatory variables included in the path model, developed based on the literature

Explanatory Variable	Minimum	Maximum	Mean	SD
Human population density (inhabitants per km^2)	299	1845	778	494
Distance to forest edge (DFE) (meters)	11.80	1594.40	456	485
Number of tree stumps	78	1747	392	370
Canopy openness (CO)	5.93	13.07	7.89	1.52
Foliage height diversity (FHD)	1.23	1.58	1.43	0.10
Plant diversity	0.08	3.10	2.43	0.81

Foliage height diversity and plant diversity correspond to the Shannon–Wiener diversity index variable). When the response variables were tested, three out of the 12 had a p value of less than 0.05: Forests Specialists' total abundance (0.03), Forest Visitors' total abundance (0.02), and Insectivores' richness (0.02). The residuals of the regression models which included these variables were tested and found normality distributed (p value ranged from 0.17 to 0.95).

Overall, the models explained a higher percentage of variance in birds' total abundance than in species richness, with forest visitors as the only exception (Table 2). Human population density and distance to the forest edge had negligible effect on the levels of habitat disturbance (Figs. 3, 4). Disturbance had strong negative effects on the structure and composition of the vegetation in the forest. Higher levels of habitat disturbance resulted in larger canopy openness, lower foliage height diversity and lower plant diversity (Figs. 3, 4). The effects of the vegetation variables and of the distance to the forest on the bird communities varied depending on the guild examined.

Overall bird communities

Distance to the forest edge had a positive effect on total bird abundance (Fig. 3) and the overall species richness (Fig. 4). Habitat disturbance affected the bird communities in two ways. It had a positive direct effect, albeit weak for total abundance and negligible for species richness, but it also had a negative indirect effect, mediated through changes mostly in plant diversity (Figs. 3a and 4a). The overall path coefficient for the indirect effect of habitat disturbance on the total bird abundance was −0.22 and on species richness −0.12. The total effects after accounting for the positive direct effects were −0.12 and −0.11 respectively (Table 3).

Habitat guilds

Forest specialists and generalists benefited from larger distances to the forest edge and higher plant diversity. Canopy openness had a negligible negative effect on forest specialists and a positive effect on forest generalists (Figs. 3b, c and 4b, c). Foliage height diversity positively affected forest specialists. The direct effects of habitat disturbance on the specialists were negative, albeit very weak, and positive but also weak on the

Table 2 Averaged R^2 values of the selected models, predicting the effects of human population density, distance to forest edge, human disturbance, canopy openness, foliage height diversity and plant diversity on bird species richness and total abundance

Bird assemblages	R^2
Overall bird richness	0.19
Overall bird abundance	0.57
FS richness	0.54
FS abundance	0.74
FG richness	0.53
FG abundance	0.69
FV richness	0.81
FV abundance	0.79
Frugivores richness	0.28
Frugivores abundance	0.69
Insectivores richness	0.30
Insectivores abundance	0.59

Response variables are overall bird communities, *FS* forest specialists, *FG* forest generalists, *FV* forest visitors, frugivores and insectivores

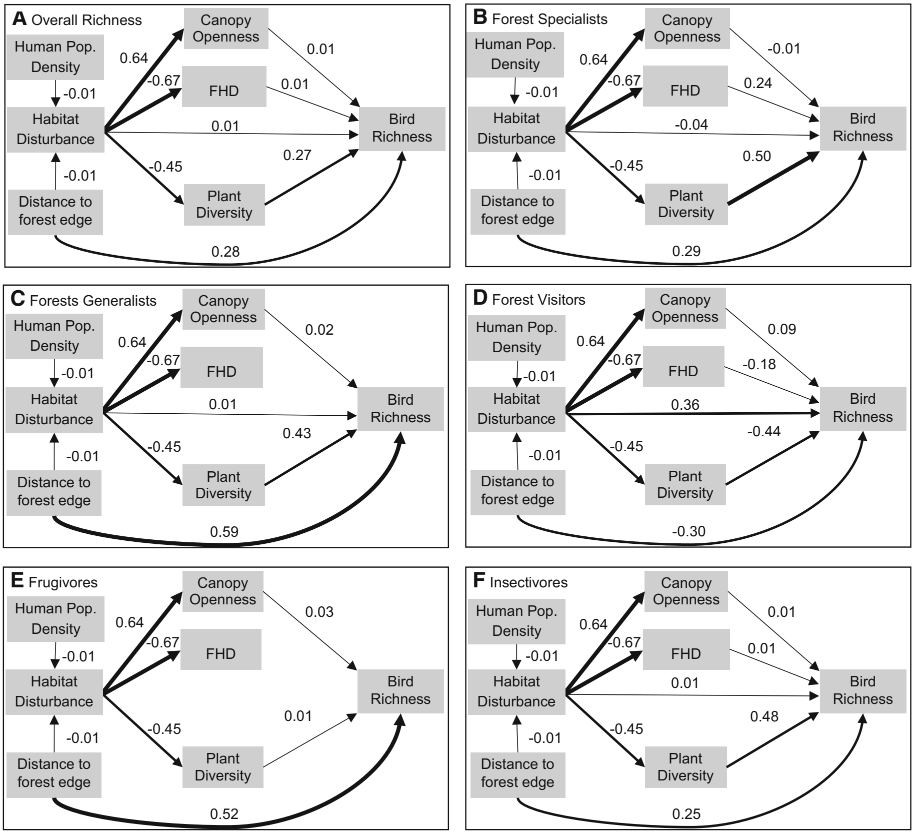

Fig. 3 The final path models showing the causal relationships, and the corresponding standardized path coefficients, between the explanatory variables and the species richness of the bird guilds tested (i.e. overall bird communities, forest specialists (FS), forest generalists (FG), forest visitors (FV), frugivores and insectivores). We assumed correlated errors between the three vegetation variables

generalists. The cumulative effects, however, were negative with the specialists being affected the most (Table 3).

Forest visitors' total abundance and species richness were negatively affected by higher plant diversity, higher foliage height diversity, and larger distances to the forest edge (Figs. 3d and 4d). They were positively affected by more open canopies and higher levels of disturbance, which had strong positive direct and indirect effects on visitors' total abundance and species richness (Table 3).

Feeding guilds

Frugivores' richness was affected positively by distance to the forest edge and positively but very weakly by canopy openness and plant diversity (Fig. 3e). Habitat disturbance had no direct effect on frugivores' richness and only a negligible indirect effect. The effects of distance to the forest edge, canopy openness and plant diversity were also positive on frugivores' total abundance. Their total abundance was also influenced positively (both indirectly and directly) by habitat disturbance. Insectivores' total abundance was

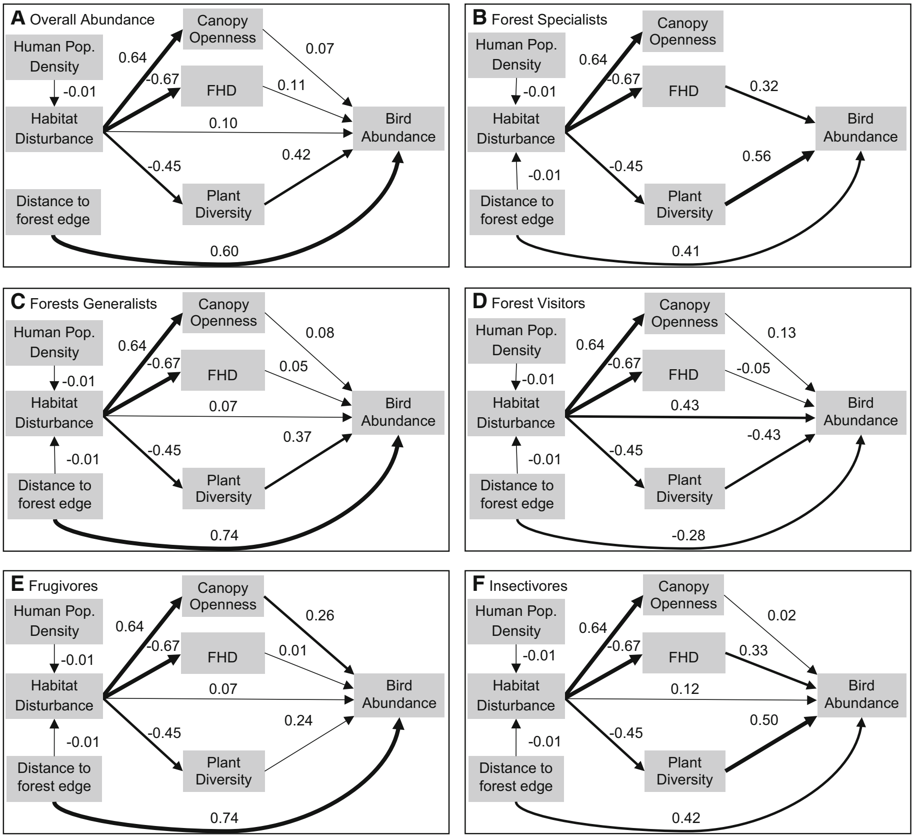

Fig. 4 The final path models showing the causal relationships, and the corresponding standardized path coefficients, between the explanatory variables and the species total abundance of the bird guilds tested (i.e. overall bird communities, forest specialists (FS), forest generalists (FG), forest visitors (FV), frugivores and insectivores). We assumed correlated errors between the three vegetation variables

influenced negatively by habitat disturbance mainly due to the strong negative effects which canceled out the weak direct positive effect (Table 3). Insectivores' abundance was positively influenced by foliage height diversity, plant diversity and distance to the forest edge (Fig. 4f). Their species richness was mostly affected, positively, by plant diversity and distance to the forest edge (Table 3; Fig. 3f). The effects of disturbance on insectivores' richness were largely indirect and highly negative (Table 3).

Discussion

Using structural equation modeling, we were able to link and quantify the factors influencing the bird communities in Kakamega Forest, showing the underlying mechanism by which habitat disturbance affects the bird communities in the area. An important finding of our study is that the overall negative effects of habitat disturbance on the bird communities are mostly expressed through indirect effects mediated by changes in vegetation structure

Table 3 Standardized path coefficients representing the direct, indirect and total effects of habitat disturbance on each bird guild examined

Bird assemblages	Total indirect effects	Direct effects	Total effects of habitat disturbance
Overall richness	−0.12	0.01	−0.11
Overall abundance	−0.22	0.10	−0.12
Forest specialists richness	−0.39	−0.04	−0.43
Forest specialists abundance	−0.47	–	−0.47
Forest generalists richness	−0.18	0.01	−0.18
Forest generalists abundance	−0.15	0.07	−0.08
Forest visitors richness	0.37	0.36	0.73
Forest visitors abundance	0.31	0.43	0.74
Frugivores richness	0.01	–	0.01
Frugivores abundance	0.05	0.07	0.12
Insectivores richness	−0.22	0.01	−0.21
Insectivores abundance	−0.43	0.12	−0.31

and composition. The strength and direction of these effects, however, varied between the different avian habitat and feeding guilds examined in this study.

We acknowledge that a potential limitation to our approach is that we used data from different time periods to parameterize the correlative path models. Yet, we are confident that the results are valid since the temporal variation of the factors included in the models is unlikely to be large enough to have confounded our results. Another potential source of error may be the 40 m distance between the transects used for the bird surveys. Although it is plausible for a bird to cover that distance during the surveys and be double-counted, we believe that the chance of that happening was too small and consistent across all sites to have affected our conclusions.

Reduced plant diversities and foliage height diversities, partly caused by habitat disturbance, correlated with fewer bird species and lower number of bird individuals, especially of forest specialists and insectivores. This pattern is most likely caused by reduced structural complexity in sites with lower plant and foliage height diversities. Sites with lower structural complexity can only provide a narrower range of ecological niches supporting fewer species with specialized habitat requirements (Kissling et al. 2008; Hewson et al. 2011; Mulwa et al. 2012). It is probably for that reason that specialists and insectivores were affected the most, as they are known to often have narrower and more specialized habitat requirements and thus be the most sensitive to disturbance (Kirika et al. 2008a; Sodhi et al. 2008; Tscharntke et al. 2008; Waltert et al. 2005, Watson et al. 2004).

Frugivores were less affected by these floristic changes possibly because they often have larger home ranges (Farwig et al. 2006; Schleuning et al. 2011b) and can track food resources even in less suitable habitats (Saracco et al. 2004; Mulwa et al. 2013). For frugivores, local plant diversities may not be as important, especially if key food resources can be located nearby. On the other hand, frugivores were found to be more sensitive to the distance to the edge than insectivores. Previous studies have found the opposite to be true (Lindell et al. 2007; Menke et al. 2012). In previous work, the increase of frugivores at forest edges was mostly driven by non-forest species visiting fruiting trees at forest-farmland margins (Menke et al. 2012). Because our study plots were all located inside the forest, we hardly detected non-forest species that avoid to enter forest habitats. Due to the high visitation rates of non-forest species at forest margins and potential competition with other species, forest frugivores may have been pushed towards forest interior habitats in the area. Forest visitors were the only guild that was positively affected from shorter distances to the forest edge and higher levels of habitat disturbance (both directly and indirectly). This effect was not surprising as these species are known to depend on non-forest habitats for their survival (Bennun et al. 1996) and therefore favour structurally simple, disturbed habitats, especially close to their preferred non-forest habitats.

The mechanism we propose, by which disturbance influences the bird communities in Kakamega Forest complements well previous findings from the area. These studies showed that disturbance negatively affects plant communities (Tsingalia 1990; Fashing et al. 2004; Althof 2005) and that the presence of avian frugivores, forests specialists and generalists is lower in more disturbed sites (Kirika et al. 2008a). Based on our results, the effects of habitat disturbance are mostly indirect, through changes in the forest's vegetation. Addressing this threat of habitat simplification will be important for the long-term persistence of the forest's biodiversity, as the negative effect of habitat disturbance on birds can potentially disrupt important ecological functions (Sekercioglu 2006) and result in further loss of plant species, possibly establishing a negative feedback loop.

It has been shown in Kakamega Forest and other areas that changes in species richness and total abundance of frugivores can result in reduced seed dispersal (Kirika et al. 2008b; García and Martínez 2012). This can have important implications on the persistence of tree species in the forest (Bleher and Böhning-Gaese 2006), considering that the majority of tropical trees depend on frugivorous animals for their dispersal (Farwig and Berens 2012; Howe and Smallwood 1982). Similarly, changes in insectivorous species can have negative cascading effects on plants if insect pests increase as a response to birds' lower abundances and species richness (Sekercioglu et al. 2004). To prevent further biodiversity loss in Kakamega Forest, it is important that the structural and compositional diversity of the forest is maintained by taking appropriate conservation actions to reduce current disturbance levels, especially the intensity of illegal logging activities.

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Appendix

See Table 4.

Table 4 List of all models with a ΔAIC of less than two, for each bird category tested

Model	k	df	AIC	ΔAIC	w(*i*)	R^2	Moran's I	PopD → HD	DE → HD
Overall bird richness									
1	22	13	63.71	0.00	0.22	0.24	0.27		
2	21	14	64.74	1.03	0.13	0.12	0.26		
3	21	14	64.92	1.20	0.12	0.12	0.36		
4	23	12	65.40	1.68	0.09	0.25	0.20		
5	23	12	65.50	1.78	0.09	0.26	0.24		
6	20	15	65.50	1.79	0.09	0.00	NA		
7	23	12	65.54	1.83	0.09	0.25	0.27		−0.09
8	23	12	65.55	1.84	0.09	0.24	0.27	−0.09	
9	23	12	65.62	1.91	0.08	0.24	0.35		
Overall bird abundance									
1	22	13	68.58	0.00	0.18	0.54	0.20		
2	24	11	68.89	0.31	0.15	0.60	0.36		
3	23	12	69.13	0.55	0.14	0.57	0.08		
4	23	12	69.35	0.77	0.12	0.58	0.15		
5	24	11	69.49	0.91	0.11	0.58	0.22		
6	25	10	70.15	1.57	0.08	0.61	0.30		
7	23	12	70.28	1.70	0.08	0.54	0.30		
8	23	12	70.41	1.83	0.07	0.55	0.20		
9	23	12	70.42	1.84	0.07	0.54	0.20	−0.09	
Forest specialists richness									
1	23	12	64.32	0.00	0.25	0.56	0.88		
2	23	12	65.74	1.42	0.12	0.54	0.28		
3	22	13	65.81	1.49	0.12	0.50	0.20		
4	24	11	66.11	1.79	0.10	0.56	0.82		
5	24	11	66.13	1.81	0.10	0.56	0.87		

Table 4 continued

Model	k	df	AIC	ΔAIC	w(*i*)	R^2	Moran's I	PopD → HD	DE → HD
6	24	11	66.15	1.83	0.10	0.57	0.88		−0.09
7	24	11	66.16	1.84	0.10	0.56	0.88	−0.09	
8	22	13	66.30	1.98	0.09	0.49	0.82		
Forest specialists abundance									
1	23	12	64.18	0.00	0.39	0.74	0.99		
2	24	11	66.01	1.83	0.16	0.75	0.99		−0.09
3	24	11	66.02	1.84	0.16	0.74	0.99	−0.09	
4	24	11	66.16	1.98	0.15	0.74	0.98		
5	24	11	66.17	1.98	0.15	0.74	1.00		
Forest generalists richness									
1	22	13	67.11	0.00	0.33	0.53	0.36		
2	23	12	68.58	1.48	0.16	0.54	0.25		
3	23	12	68.94	1.83	0.13	0.54	0.36		−0.09
4	23	12	68.95	1.84	0.13	0.53	0.36	−0.09	
5	23	12	68.99	1.88	0.13	0.54	0.36		
6	23	12	69.09	1.98	0.12	0.53	0.39		
Forest generalists abundance									
1	22	13	73.60	0.00	0.15	0.67	0.14		
2	23	12	73.64	0.05	0.14	0.70	0.06		
3	23	12	73.90	0.30	0.13	0.70	0.13		
4	24	11	74.38	0.79	0.10	0.71	0.20		
5	24	11	74.74	1.14	0.08	0.70	0.09		
6	24	11	75.36	1.77	0.06	0.71	0.20		
7	23	12	75.42	1.83	0.06	0.68	0.14		−0.09
8	23	12	75.43	1.84	0.06	0.67	0.14	−0.09	
9	24	11	75.47	1.87	0.06	0.70	0.06		−0.09

Table 4 continued

Model	k	df	AIC	ΔAIC	w(*i*)	R^2	Moran's I	PopD → HD	DE → HD
10	24	11	75.48	1.88	0.06	0.70	0.06	−0.09	
11	25	10	75.56	1.97	0.05	0.72	0.14		
12	23	12	75.57	1.97	0.05	0.67	0.15		
Forest visitors richness									
1	24	11	68.05	0.00	0.23	0.81	0.57		
2	25	10	68.32	0.27	0.20	0.83	0.38		
3	23	12	69.04	0.99	0.14	0.79	0.94		
4	24	11	69.07	1.02	0.14	0.81	0.57		
5	24	11	69.73	1.68	0.10	0.80	0.41		
6	25	10	69.88	1.83	0.09	0.82	0.57		−0.09
7	25	10	69.89	1.84	0.09	0.81	0.57	−0.09	
Forest visitors abundance									
1	24	11	67.18	0.00	0.26	0.79	0.86		
2	23	12	67.52	0.34	0.22	0.76	0.72		
3	25	10	68.06	0.88	0.17	0.80	0.71		
4	24	11	68.17	0.99	0.16	0.78	0.96		
5	25	10	69.00	1.83	0.10	0.80	0.86		−0.09
6	25	10	69.02	1.84	0.10	0.79	0.86	−0.09	
Frugivores richness									
1	21	14	62.24	0.00	0.28	0.27	0.92		
2	22	13	63.25	1.01	0.17	0.30	0.88		
3	22	13	63.98	1.73	0.12	0.28	1.00		
4	22	13	64.07	1.83	0.11	0.27	0.92		−0.09
5	22	13	64.08	1.84	0.11	0.27	0.92	−0.09	
6	22	13	64.20	1.96	0.11	0.26	0.89		
7	22	13	64.23	1.99	0.10	0.27	0.90		

Table 4 continued

Model	k	df	AIC	ΔAIC	w(*i*)	R^2	Moran's I	PopD → HD	DE → HD
Frugivores abundances									
1	23	12	68.39	0.00	0.27	0.69	0.92		
2	24	11	69.67	1.28	0.14	0.71	0.81		
3	23	12	69.68	1.29	0.14	0.69	0.92		
4	24	11	70.21	1.82	0.11	0.69	0.94		
5	22	13	70.21	1.82	0.11	0.63	0.92		
6	24	11	70.22	1.83	0.11	0.69	0.92		−0.09
7	24	11	70.23	1.84	0.11	0.69	0.92	−0.09	
Insectivores richness									
1	22	13	64.23	0.00	0.27	0.32	0.08		
2	21	14	64.93	0.70	0.19	0.23	0.13		
3	23	12	66.00	1.77	0.11	0.32	0.14		
4	23	12	66.05	1.83	0.11	0.33	0.08		−0.09
5	23	12	66.06	1.84	0.11	0.32	0.08	−0.09	
6	23	12	66.16	1.93	0.10	0.33	0.08		
7	23	12	66.16	1.94	0.10	0.32	0.07		
Insectivores abundance									
1	24	11	66.86	0.00	0.20	0.62	0.51		
2	23	12	67.00	0.15	0.19	0.58	0.28		
3	22	13	67.92	1.06	0.12	0.54	0.05		
4	24	11	68.09	1.24	0.11	0.59	0.27		
5	25	10	68.68	1.83	0.08	0.62	0.51		
6	25	10	68.69	1.84	0.08	0.62	0.51	−0.09	
7	25	10	68.81	1.95	0.08	0.62	0.48		
8	24	11	68.83	1.97	0.07	0.59	0.28		−0.09
9	24	11	68.84	1.98	0.07	0.58	0.28	−0.09	

Table 4 continued

Model	HD → CO	HD → FHD	HD → PD	HD → Birds	CO → Birds	FHD → Birds	PD → Birds	DE → Birds
Overall bird richness								
1	0.64	−0.67	−0.45				0.34	0.35
2	0.64	−0.67	−0.45					0.35
3	0.64	−0.67	−0.45				0.34	
4	0.64	−0.67	−0.45		0.11		0.36	0.35
5	0.64	−0.67	−0.45	0.10			0.39	0.36
6	0.64	−0.67	−0.45					
7	0.64	−0.67	−0.45				0.34	0.35
8	0.64	−0.67	−0.45				0.34	0.35
9	0.64	−0.67	−0.45			0.06	0.32	0.34
Overall bird abundance								
1	0.64	−0.67	−0.45				0.41	0.61
2	0.64	−0.67	−0.45	0.37		0.31	0.46	0.59
3	0.64	−0.67	−0.45		0.18		0.43	0.61
4	0.64	−0.67	−0.45	0.18			0.48	0.62
5	0.64	−0.67	−0.45		0.28	0.23	0.36	0.58
6	0.64	−0.67	−0.45	0.27	0.16	0.33	0.42	0.59
7	0.64	−0.67	−0.45			0.09	0.37	0.60
8	0.64	−0.67	−0.45				0.40	0.61
9	0.64	−0.67	−0.45				0.41	0.61
Forest specialists richness								
1	0.64	−0.67	−0.45			0.32	0.49	0.31
2	0.64	−0.67	−0.45	−0.25			0.50	0.35
3	0.64	−0.67	−0.45				0.60	0.37
4	0.64	−0.67	−0.45	−0.09		0.26	0.47	0.31
5	0.64	−0.67	−0.45		−0.07	0.28	0.49	0.32

Table 4 continued

Model	HD → CO	HD → FHD	HD → PD	HD → Birds	CO → Birds	FHD → Birds	PD → Birds	DE → Birds
6	0.64	−0.67	−0.45			0.31	0.48	0.31
7	0.64	−0.67	−0.45			0.32	0.49	0.31
8	0.64	−0.67	−0.45			0.39	0.44	
Forest specialists abundance								
1	0.64	−0.67	−0.45			0.33	0.56	0.41
2	0.64	−0.67	−0.45			0.32	0.55	0.41
3	0.64	−0.67	−0.45			0.33	0.56	0.41
4	0.64	−0.67	−0.45		−0.02	0.32	0.56	0.42
5	0.64	−0.67	−0.45	−0.02		0.31	0.56	0.41
Forest generalists richness								
1	0.64	−0.67	−0.45				0.43	0.59
2	0.64	−0.67	−0.45		0.11		0.44	0.59
3	0.64	−0.67	−0.45				0.42	0.58
4	0.64	−0.67	−0.45				0.43	0.59
5	0.64	−0.67	−0.45	0.06			0.45	0.59
6	0.64	−0.67	−0.45			0.02	0.42	0.59
Forest generalists abundance								
1	0.64	−0.67	−0.45				0.35	0.74
2	0.64	−0.67	−0.45		0.17		0.37	0.74
3	0.64	−0.67	−0.45	0.18			0.43	0.75
4	0.64	−0.67	−0.45	0.30		0.20	0.41	0.73
5	0.64	−0.67	−0.45		0.24	0.14	0.33	0.73
6	0.64	−0.67	−0.45	0.09	0.12		0.41	0.74
7	0.64	−0.67	−0.45				0.35	0.73
8	0.64	−0.67	−0.45				0.35	0.74
9	0.64	−0.67	−0.45		0.17		0.37	0.74

Table 4 continued

Model	HD → CO	HD → FHD	HD → PD	HD → Birds	CO → Birds	FHD → Birds	PD → Birds	DE → Birds
10	0.64	−0.67	−0.45		0.17		0.37	0.74
11	0.64	−0.67	−0.45	0.21	0.14	0.22	0.38	0.73
12	0.64	−0.67	−0.45			0.03	0.34	0.74
Forest visitors richness								
1	0.64	−0.67	−0.45	0.40		−0.24	−0.41	−0.29
2	0.64	−0.67	−0.45	0.29	0.16	−0.22	−0.44	−0.30
3	0.64	−0.67	−0.45	0.53			−0.44	−0.32
4	0.64	−0.67	−0.45	0.40	0.18		−0.47	−0.33
5	0.64	−0.67	−0.45		0.29	−0.32	−0.51	−0.31
6	0.64	−0.67	−0.45	0.39		−0.23	−0.40	−0.28
7	0.64	−0.67	−0.45	0.40		−0.24	−0.41	−0.29
Forest visitors abundance								
1	0.64	−0.67	−0.45	0.40	0.21		−0.45	−0.29
2	0.64	−0.67	−0.45	0.55			−0.41	−0.28
3	0.64	−0.67	−0.45	0.32	0.20	−0.15	−0.43	−0.27
4	0.64	−0.67	−0.45	0.46		−0.17	−0.39	−0.26
5	0.64	−0.67	−0.45	0.39	0.21		−0.45	−0.29
6	0.64	−0.67	−0.45	0.40	0.21		−0.45	−0.29
Frugivores richness								
1	0.64	−0.67	−0.45					0.52
2	0.64	−0.67	−0.45		0.18			0.52
3	0.64	−0.67	−0.45				0.10	0.52
4	0.64	−0.67	−0.45					0.52
5	0.64	−0.67	−0.45					0.52
6	0.64	−0.67	−0.45			0.04		0.51
7	0.64	−0.67	−0.45	−0.02				0.52

Table 4 continued

Model	HD → CO	HD → FHD	HD → PD	HD → Birds	CO → Birds	FHD → Birds	PD → Birds	DE → Birds
Frugivores abundances								
1	0.64	−0.67	−0.45		0.32		0.25	0.74
2	0.64	−0.67	−0.45	0.15	0.23		0.30	0.75
3	0.64	−0.67	−0.45	0.31			0.34	0.75
4	0.64	−0.67	−0.45		0.35	0.06	0.23	0.74
5	0.64	−0.67	−0.45		0.29			0.74
6	0.64	−0.67	−0.45		0.32		0.25	0.75
7	0.64	−0.67	−0.45		0.32		0.25	0.74
Insectivores richness								
1	0.64	−0.67	−0.45				0.48	0.31
2	0.64	−0.67	−0.45				0.48	
3	0.64	−0.67	−0.45			0.10	0.44	0.29
4	0.64	−0.67	−0.45				0.48	0.30
5	0.64	−0.67	−0.45				0.48	0.31
6	0.64	−0.67	−0.45	0.05			0.50	0.31
7	0.64	−0.67	−0.45		0.05		0.48	0.31
Insectivores abundance								
1	0.64	−0.67	−0.45	0.28		0.45	0.53	0.42
2	0.64	−0.67	−0.45			0.28	0.46	0.42
3	0.64	−0.67	−0.45				0.56	0.47
4	0.64	−0.67	−0.45		0.15	0.36	0.46	0.41
5	0.64	−0.67	−0.45	0.28		0.45	0.52	0.41
6	0.64	−0.67	−0.45	0.28		0.45	0.53	0.42
7	0.64	−0.67	−0.45	0.26	0.04	0.45	0.52	0.41

Table 4 continued

Model	HD → CO	HD → FHD	HD → PD	HD → Birds	CO → Birds	FHD → Birds	PD → Birds	DE → Birds
8	0.64	−0.67	−0.45			0.28	0.46	0.42
9	0.64	−0.67	−0.45			0.28	0.46	0.42

Assumed correlated errors were also allowed to vary during model selection. Number of parameters (k), degrees of freedom (df), Akaike Information Criterion (AIC), ΔAIC, and Akaike weights (*w(i)*) are also presented in the table, along with each model's R^2 value, the result of the Moran's I spatial autocorrelation test and the standardized path coefficients

PopD human population density; *DE* distance to the forest edge; Hd habitat disturbance; *CO* canopy openness; *FHD* foliage height diversity, *PD* plant diversity

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