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Active restoration facilitates bird community recovery in an Afrotropical rainforest

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ABSTRACT

Active restoration of rainforests is essential in enhancing the recovery of biodiversity in many tropical regions suffering from deforestation. However, the value of actively restored rainforests for birds is still relatively poorly understood because of the short history of active restoration programs. Here, we studied the recovery of bird communities in Kibale National Park, Uganda. We sampled birds along a restoration gradient consisting of six restoration areas (3–16 years old) and used five primary forests as reference areas. We found that bird community compositions changed in an orderly fashion along the restoration gradient. The abundance of arboreal insectivore frugivores and forest specialists increased, while that of foliage-gleaning insectivores, granivores and forest visitors decreased towards older sites. The similarity of the bird communities of the restored forests to those of the nearby primary forests increased linearly with time. If this recovery rate is extrapolated to the future, the bird communities could reach a pre-disturbance state after only approximately 20 years of active restoration. However, previous studies have shown that recovery is typically a non-linear process, and the time needed for bird communities to recover is more likely longer than this. Nevertheless, our study provides evidence that bird communities benefit from active rainforest restoration after human-induced deforestation.

1. Introduction

Ongoing deforestation and degradation of tropical rainforests are among the most important threats to the world's biodiversity. It is unlikely that natural recovery could reestablish the ecological functioning and diversity of all deforested tropical areas; this is due to the vast scale and rapid rate of deforestation in the tropics, recurrent disturbances in deforested areas (e.g., fires) or long colonisation distances which prevent species from returning (Lamb, 1998; Dirzo and Raven, 2003; Wright, 2005; Achard et al., 2014). In some cases, the natural recovery of a rainforest becomes slow or halted, e.g., due to dominance of grasses, herbs or shrubs ("arrested succession"; Chapman and Chapman, 1997). In these areas, human intervention in a form of passive or active restoration is needed to enhance the recovery and long-term conservation of tropical rainforests. In passive restoration, the natural regeneration of a forest is allowed by protecting the remnant vegetation or by removing human disturbances. Active restoration, on the other hand, includes assisted natural recovery (e.g., weeding or cutting climbers), planting trees or spreading seedlings in restored areas (Lamb et al., 2005; Shono et al., 2007; Chazdon, 2008; Holl and Aide, 2011). When successful, active restoration can speed up the recovery in ecosystems where natural recovery could take decades (Dobson et al., 1997). However, the rate of the recovery of tropical forests, both natural and assisted, depends on a number of factors, including the land use history, the surrounding land use matrix and distance to remnant primary forests, as well as soil type, temperature and rainfall in the recovering forest areas (Chazdon, 2008; Holl and Aide, 2011).

Forest restoration is aimed at accelerating the recovery of forest structure, ecological functioning and biodiversity towards those found in climax forest; yet, it is still poorly understood how effectively the overall biodiversity can be restored, including that of birds (Catterall et al., 2012; Smith et al., 2015). Birds are frequently used as indicators of change when studying the effects of anthropogenic disturbances to biodiversity and should therefore serve as a valuable indicator group when studying the recovery of biodiversity during forest restoration. The taxonomy of birds is well-known, which makes them more easily identified in the field than some other groups. Species vary widely in their ecological requirements (e.g., level of forest dependence), determining their ability to reoccupy sites after disturbances and making them ideal for studying environmental change (Bennun et al., 1996; Gray et al., 2007). Further, classifying birds into functional groups according to their forest dependence (habitat categories) or into feeding guilds aids understanding of the functional relationship between a

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(group of) species and an ecosystem (Ghazoul and Hellier, 2000; Gray et al., 2007). This is because the disturbances to tropical forests affect the feeding guilds differently; frugivores and insectivores are particularly vulnerable to disturbance while granivores benefit from it (Gray et al., 2007), and this has great implications for ecosystem processes (Sodhi et al., 2008). The presence of the species belonging to the most sensitive guilds could represent ecosystem functions returning to restored sites, as they provide important ecosystem services such as seed dispersal, pollination and pest control (Sekercioglu, 2006; Kirika et al., 2008; Morrison and Lindell, 2012; Karp and Daily, 2014). On the contrary, the failure of these bird guilds to recover in restored forests could result in a diminished rate of return by avian-dispersed rainforest plants and limited recovery of ecosystem services (Sekercioglu, 2011; Caves et al., 2013; Moran and Catterall, 2014). This, in turn, may result in a further delay of recovery among species in other bird feeding guilds. Yet, the guilds' responses to restoration are largely to be uncovered (but see Edwards et al., 2009; Reid et al., 2014).

Although restoration of rainforests is currently of great interest, due to the short history of active restoration actions, its value for bird communities is still poorly understood (but see Edwards et al., 2009; Freeman et al., 2015), and practically unknown in the Afrotropics (Farwig et al., 2008). In their pioneering work, Catterall et al. (2012) modelled the recovery trajectories of bird species composition (measuring the presence/absence of species) in different aged restored forests in tropical Australia. However, to our knowledge, no studies have modelled the recovery trajectories of bird community compositions (measuring the relative abundances of species in communities), focusing on the ecologically important differences in species frequencies among communities (Jost et al., 2011). Such information is greatly needed in order to determine whether restoration efforts can bring back the community compositions of birds in primary forests, and which species groups could be used as indicators of recovery in the future monitoring and management of restoration projects.

In this study, we examined how bird community compositions and bird functional groups, including categories of forest dependence and feeding guilds, have recovered following active forest restoration in Kibale National Park, Uganda. We studied bird communities along a restoration gradient consisting of six restoration sites, ranging from 3 to 16 years of age, and used five adjacent undisturbed primary forests as reference areas. Our specific study questions were: 1) Do bird community compositions differ among differently aged restored forests? 2) Is there a directional recovery pattern in the community composition of birds, or 3) in the abundances (or proportions) of different feeding guilds, or habitat categories, along the restoration gradient (from the youngest to the oldest restoration sites)? and 4) If the bird communities of restored forests are becoming increasingly similar to the primary forest communities as a function of time since restoration started, how long is it estimated that bird communities will take to recover following restoration?

2. Methods

2.1. Study area

We performed our study in western Uganda in Kibale National Park (795 km^2; 0°13′ to 0°41′ N and 30°19′ to 30°32′ E), which is a mid-altitude tropical rainforest, consisting of mature natural forests (59.7%), secondary forests, grasslands, woodlands and wetlands (Struhsaker, 1997). The mean annual precipitation in the park is 1547 mm (1903–2001), with March–May and September–November being the rainy seasons (Chapman et al., 2005).

Our study area in Kibale was located in the Uganda Wildlife Authority – Forests Absorbing Carbon Dioxide Emissions (UWA-FACE) project area, which covers approximately 10,000 ha (UWA-FACE, 2006). Agricultural encroachers illegally occupied these forests in the 1970s, leading to forest destruction (van Orsdol, 1986); however, by 1992, the encroachers were evicted. Following this, the former encroached areas became largely dominated by elephant grass (*Pennisetum purpureum*) that suppressed naturally regenerating tree seedlings, and halted or greatly slowed down the natural succession in these areas (UWA-FACE, 2006). In 1993, Kibale became a National Park, and in 1994, the Ugandan government and the Face the Future Foundation (previously The Face Foundation) initiated a reforestation program to reestablish carbon sinks to offset carbon dioxide emissions and to restore the deforested areas to their natural condition, with active tree plantings commencing in 1995 (UWA-FACE, 2006). Our study area included six restoration sites, ranging from 3 to 16 years of age (RS3–RS16), and three adjacent undisturbed primary forests (MPF1–MPF3) (Fig. 1, Table 1). The primary forests have never experienced commercial harvesting or large-scale or mechanized logging (Struhsaker, 1997; Chapman et al., 2005; Kasenene, 2007).

2.2. Bird data

We sampled birds by point counts in the six restoration sites and three adjacent primary forests, in September and October 2013 during the bird breeding season in Kibale (Dranzoa, 2001). We carried out point counts of 10 min duration at a total of 166 points (Fig. 1), whose locations were randomised with a grid system in each study site (11–20 points in each).

Upon arriving at the point, the observer (PL) waited 2 min to allow birds to recover from any disturbance. All the birds seen or heard within a 100-m radius were recorded, and the movement of individuals was carefully mapped to avoid double counts. Overflying birds were excluded from the analysis. All counts were made between 07:00 and 10:30 h when the bird activity was highest and only in the mornings with no rain or heavy wind that could decrease the activity of birds or the number of birds detected. The visit order of the study sites (and the points in them) was randomised on a daily basis on each sampling morning.

Bird nomenclature follows Clements et al. (2015). We assigned the bird species to 12 feeding guilds (following Johns, 1989; Dranzoa, 1995; and Waltert et al., 2005), while eight species remained uncategorised (online Appendix, Table A.1). Birds were also categorised into three habitat categories according to their forest-dependence: forest specialists, forest generalists and forest visitors (Bennun et al., 1996). Forest specialists occur primarily in the interior of undisturbed forests whereas forest generalists occupy both undisturbed and disturbed forest habitats like forest gaps and edges, and are also frequently found in secondary forests. Forest visitors mainly occupy non-forest habitats and only occasionally visit forest habitats (Bennun et al., 1996).

In addition, data from two primary forest areas (K30 and K31 with 20 and 18 points respectively; see map and details in Latja et al., 2015; the minimum distance between these and the study sites sampled in this study is 5 km) from the northern part of Kibale National Park were included in some analyses to better represent the bird communities in primary forests. This data were collected in September and October 2011, and are composed of 571 individuals representing 73 species.

2.3. Data analyses

To visualise the patterns in the community composition of birds across sampling points, we used non-metric multi-dimensional scaling (MDS) in PRIMER-E (with 50 restarts) (Clarke and Gorley, 2006). We conducted MDS separately for the six restoration sites alone, and for the restoration sites and primary forests. For clarity, distances between centroids of forest areas are shown (Anderson et al., 2008). To test if the bird community composition differed among the differently aged restored study sites, we conducted analysis of similarity (ANOSIM; a non-parametric permutation test) in PRIMER-E (Clarke, 1993). Prior to these multivariate analyses, species abundances at each sampling point were square root transformed (to slightly lessen the influence of

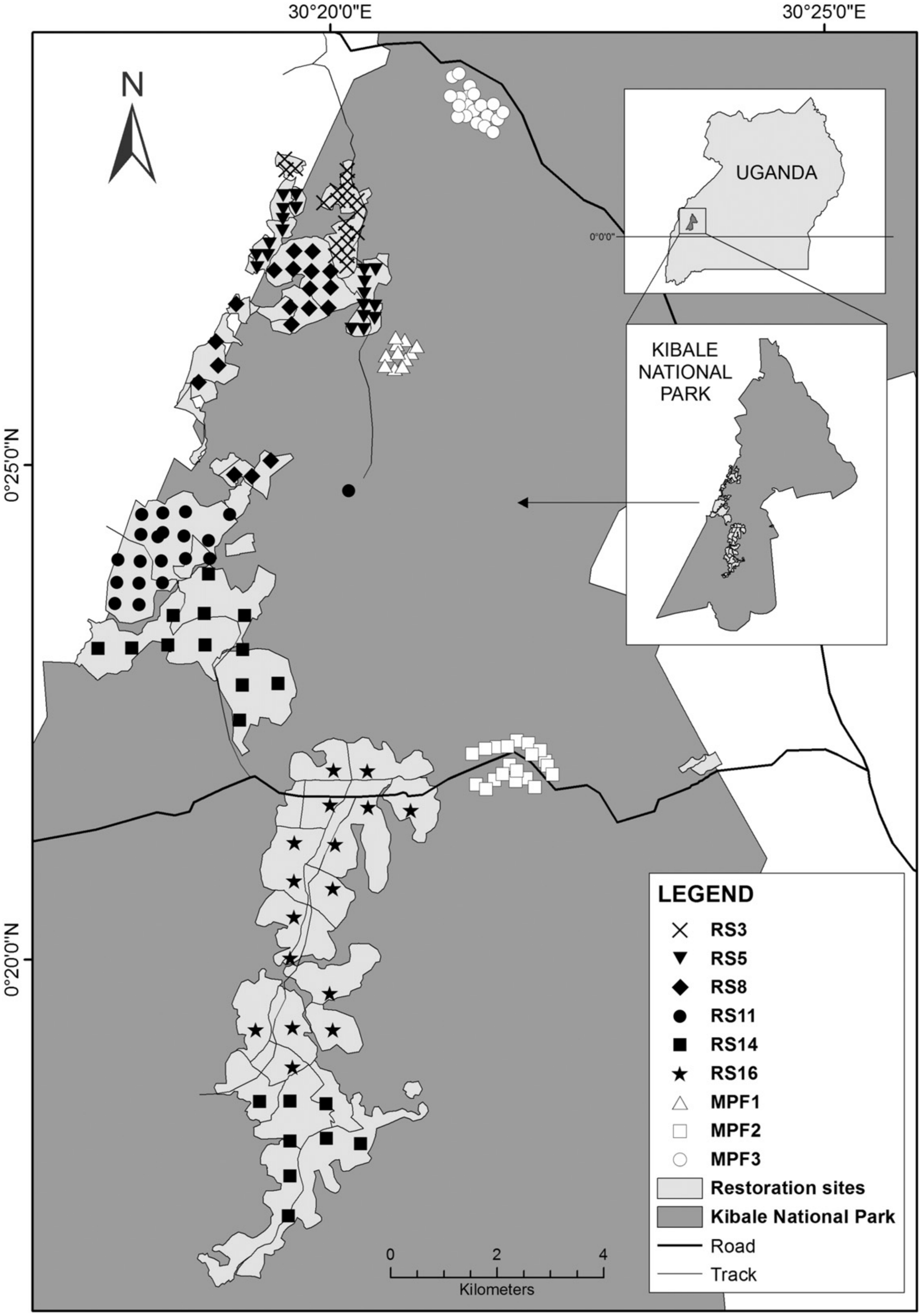

Fig. 1. Map of the study area in Kibale National Park, Uganda.

the most abundant species), and similarities in community composition between sampling points were calculated with a zero adjusted Bray-Curtis metric.

To test for a directional age gradient in bird community compositions in the restoration sites, and to account for spatial autocorrelation in our data, we used variance partitioning and canonical correspondence analysis (CCA; ter Braak, 1986), and principal coordinates of neighbouring matrices analysis in program CANOCO 5 (ter Braak and Smilauer, 2012). With variance partitioning, we identified if the age of the sampling points (years since restoration planting) independently accounted for variation in the bird community compositions, apart from the spatial variation (the east-west location of the sampling points). We could not include

Table 1
The study area in Kibale National Park, Uganda included eleven study sites: six restoration sites (RS3–RS16) and five primary forests (MPF1–MPF3 and K30–K31). Mean age of restoration (years since planting), area (ha) and the number of point counts performed in each study site and the mean distance between points (m), are shown.

Study site	Mean age of restoration	Point counts	Mean distance between points (m)	Area (ha)
RS3	3	20	210	467
RS5	5	20	240	310
RS8	8	19	360	469
RS11	11	20	420	354
RS14	14	20	660	979
RS16	16	16	720	1410
MPF1	Primary forest	11	200	–
MPF2	Primary forest	20	200	–
MPF3	Primary forest	20	200	–
K30	Primary forest	20	197	–
K31	Primary forest	18	201	–

the north-south axis in this analysis because the restoration planting in Kibale National Park was commenced in order to offset carbon dioxide emissions, not designed for scientific purposes, and therefore it was carried out as practically as possible by starting restoration from the south and continuing towards north, creating an age gradient parallel to north-south axis (visible in Fig. 1). Subsequently, the (possible) age gradient and the north-south axis correlate strongly with each other, and their independent roles in explaining the variation in bird community compositions cannot be tested separately. This is fortunately counteracted with similar distances to the contiguous primary forests (in the east) from each restoration area (minimum distance ranging from 1 to 4 km).

CCA was used to illustrate the relationship between bird community composition and the explanatory variables, and to show how species optima (the peak abundance of a species) are located along the age gradient. CCA is a multivariate ordination technique that relates community composition to environmental variables (here, the age and east-west location of the sampling points) using nonlinear, unimodal responses (ter Braak, 1986). Prior to analysis, the bird data were square root transformed to slightly lessen the influence of the most abundant species. We used the default procedures in CANOCO 5 and tested for significance of age and the east-west axis using the conditional effects and Monte Carlo permutations (499 permutations).

To ensure that the age gradient in community compositions in the restoration sites was not confounded by finer-scale spatial variation, we used principal coordinates of neighbouring matrices analysis (PCNM; Borcard and Legendre, 2002; Dray et al., 2006) in CANOCO 5. PCNM is able to detect and quantify spatial patterns in community composition over a wide range of scales (Borcard and Legendre, 2002). In this method, first, a matrix of truncated Euclidean distances among the sampling points is constructed. Then, principal coordinate analysis (PCO) of the truncated distance matrix is computed, and the eigenvectors corresponding to positive eigenvalues obtained by it are used as explanatory variables in CCA (Borcard and Legendre, 2002). We used the standard CCA method and default truncation settings in CANOCO 5, and included the most important PCO axes identified by the PCNM analysis and age of the sampling points as the explanatory variables.

We also tested for a directional change in the abundance and in the mean proportion of birds in each feeding guild and habitat category along the restoration gradient in the restoration sites. For each restoration study site, we calculated the mean number of individuals and the mean proportion of individuals in each feeding guild and habitat category (across the sampling points), and conducted Pearson correlations (in SPSS version 21) between these and the age of restoration planting ($RS3 = 3$, $RS5 = 5$, $RS8 = 8$, $RS11 = 11$, $RS14 = 14$, $RS16 = 16$). In addition, we tested for differences in species richness (rarefied total species richness, calculated for the largest number of shared individuals, 143) among the study sites (including the primary forests), and for a directional change in the average species density (number of species/point), Shannon diversity index and Berger-Parker dominance index of birds, as well as in the total abundance of birds, along the restoration gradient (Pearson correlations; details in online Appendix). We applied Bonferroni correction to account for the increased risk of Type I error associated with multiple tests.

To estimate the time needed for bird community compositions to recover, we modelled the change in similarity of bird communities of each of the six restoration sites to the five primary forests as a response to the number of years since restoration started. We fitted two competing models: 1) linear change and 2) non-linear change following negative exponent function, which is ecologically more realistic because it allows the similarity to slowly approach an asymptote (Matthews et al., 2009; Woodcock et al., 2012). Similarities were calculated from the zero adjusted Bray-Curtis similarity matrix between sampled points. For each restoration site, the average similarity of its sampling points to sampling points in the five primary forests was calculated and used as a response variable in the models. The models were fitted with SPSS and program R (R Development Core Team, 2008). The fit of the competing models was compared with corrected Akaike's Information Criterion (AICc; Burnham and Anderson, 2002), calculated from model predicted values.

3. Results

We recorded a total of 118 bird species with 2113 individuals during the bird sampling at 166 points in nine study sites (online Appendix, Table A.1).

3.1. Shift in community compositions along the restoration gradient

Bird community composition changed in a rather orderly fashion from the youngest to the three oldest restoration sites, and towards the primary forests (MDS; Fig. 2A–B). The community composition of birds differed among the restoration study sites (ANOSIM, Global $R = 0.15$, $p = 0.001$). The pairwise comparisons revealed that bird community compositions of the youngest restoration sites RS3 and RS5 differed the most from the restoration site RS14 ($R = 0.37$ and 0.30, $p < 0.05$; see details in Online Appendix Table A.2).

The age gradient in the restoration sites explained variation in bird communities independently of the east-west location of the sampling points. The age of the sampling points (years since restoration planting) independently explained 74.2% of the observed variation in the bird community composition (variance partitioning; Monte-Carlo permutation test, pseudo-$F = 2.7$, $p = 0.002$) while the east-west axis explained 19.8% (pseudo-$F = 1.5$, $p = 0.002$), and their interaction explained 6.1% of the variation (pseudo-$F = 2.2$, $p = 0.002$). The CCA ordination diagram shows that the age of the sampling points correlated most strongly with the first canonical axis (eigenvalues, Axis $1 = 0.21$, Axis $2 = 0.11$), which represents the most important variation in the bird community composition (Fig. 3). Most forest specialist species, such as yellow-throated tinkerbird (*Pogoniulus subsulphureus*), scaly-breasted illadopsis (*Illadopsis albipectus*) and buff-throated apalis (*Apalis rufogularis*), were primarily found at the older sampling sites, while forest visitor species, such as weavers (*Ploceus* sp.) and green-backed camaroptera (*Camaroptera brachyura*), were clearly more frequently found at the younger sampling sites. Generalist bird species showed no preference among the differently aged restoration sites (Fig. 3).

PCNM and variance partitioning revealed that the age of the sampling points (years since restoration planting) explained variation in bird communities independently of spatial variation also when the finer-scale spatial variation was taken into account. Age accounted independently for 14.9% of variation in bird communities while spatial variation accounted for 17.7% (Fig. A.1). PCNM forward selection procedure (499 permutations) identified one significant PCO axis: PCO1 (pseudo-$F = 2.9$, $p = 0.002$, eigenvalue = 0.2). In PCNM, the first few

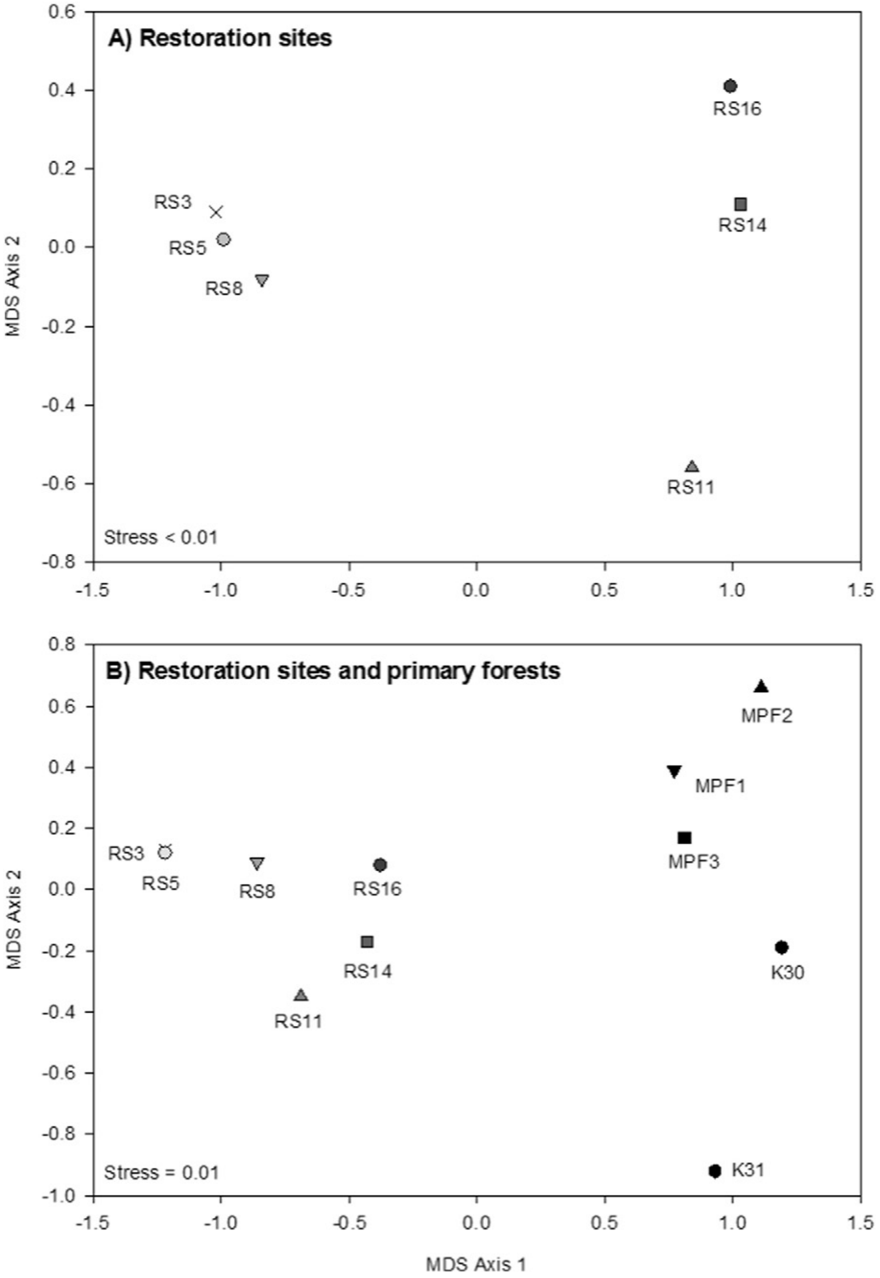

Fig. 2. MDS ordination showing A) the change of community compositions of birds of younger restoration sites (RS3–RS8) towards the older restoration sites (RS11–RS16), and B) the relationship between bird community compositions of restoration sites and primary forests (MPF1–MPF3 and K30–K31) in Kibale National Park, Uganda. Study sites that are located closer to each other have more similar bird community composition. Symbols represent centroids of forest areas.

PCO axes correspond to global trends (ter Braak and Smilauer, 2012), and therefore our results show that finer-scale spatial variation was not significant in explaining the variation in bird community compositions. Although with CANOCO it is not possible to statistically test the independent proportion of variation explained by age or PCO axes, the CCA ordination shows that age does not largely explain the same variation as the most important spatial trends in the data (the significant PCO1 axis; Fig. A.2).

3.2. Responses of functional groups and bird species richness and diversity along the restoration gradient

Three feeding guilds showed significant increasing or decreasing patterns along the restoration gradient. The proportion (of all individuals) of arboreal insectivore frugivores increased with the site age, while those of foliage-gleaning insectivores and granivores decreased (Fig. 4A, Bonferroni-corrected significance level is 0.008). For all other guilds, the patterns along the restoration gradient were non-significant ($p > 0.008$).

Also, the bird habitat categories, classified by their forest-dependence, showed distinct patterns along the restoration gradient. The abundance and the proportion (of all individuals) of forest specialists increased while those of forest visitors decreased significantly towards older sites (Fig. 4B–C). Forest generalists did not show directional changes along the restoration gradient ($p > 0.008$). 67.5% of all forest specialist species and 38.4% of all forest specialist individuals were seen in the restoration areas, outside of primary forests.

We found no significant differences in the total species richness of birds among the study sites, and the species density, diversity, dominance and the total abundance of birds did not show directional changes along the restoration gradient in the restoration sites (Fig A.3–4; online Appendix).

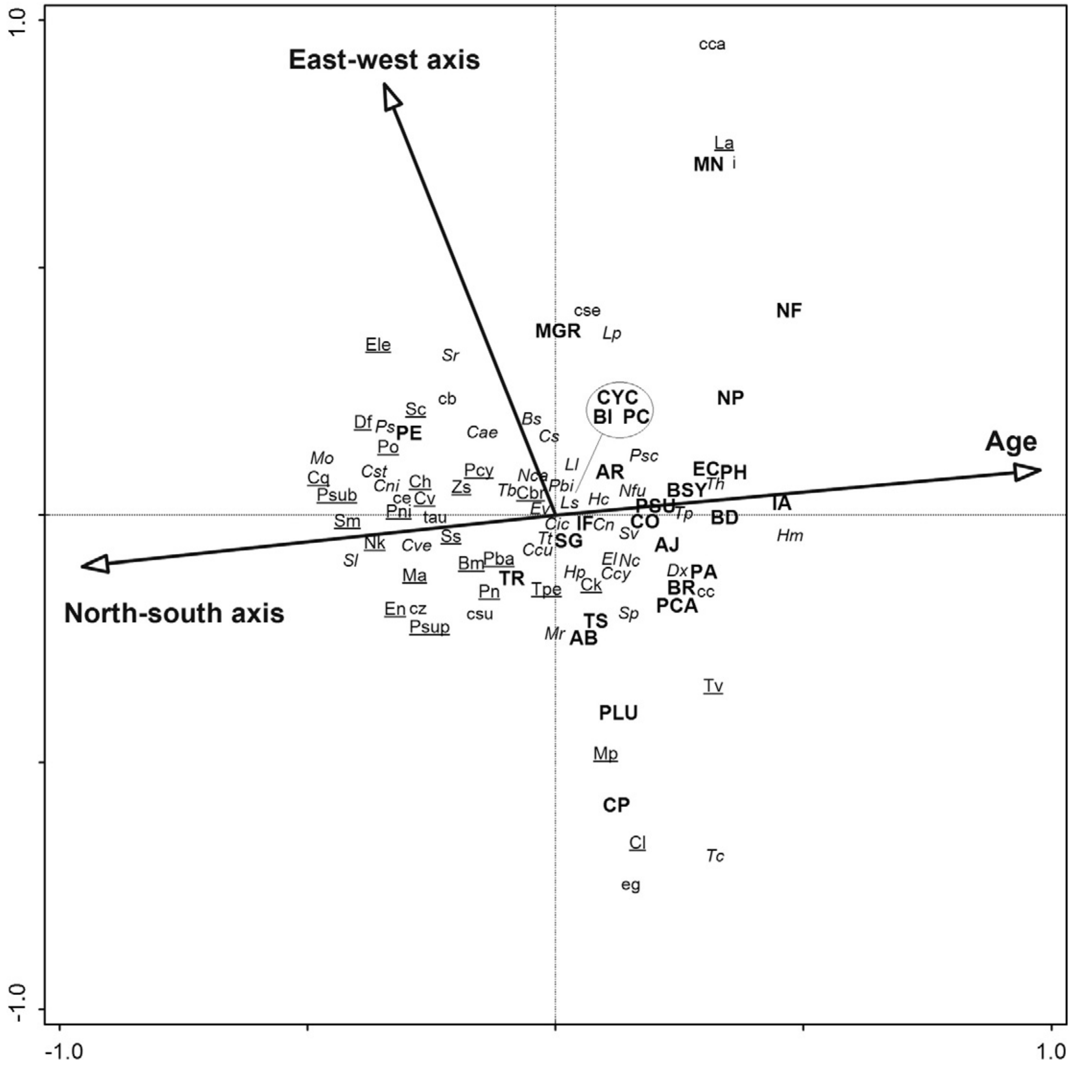

Fig. 3. CCA ordination diagram showing the association of bird community composition (see species codes in online Appendix, Table A.1) and age, east-west location of the sampling points and north-south axis (arrows) in Kibale National Park, Uganda. The ordination shows that the age of the sampling points explains variation in bird community composition independently of east-west location of sampling points. Species codes indicate the optima of species along the age gradient. The length of the arrow indicates the importance of the variable in explaining the variation in bird communities. Altogether 102 (out of 118 observed) best fitting species are shown and optima of some species are moved slightly to improve the figure clarity. Forest dependence of bird species is shown: upper case and bold = forest specialist, italic = forest generalist, underlined = forest visitor, lower case = uncategorized.

3.3. Estimated recovery time of bird community compositions

The similarity of bird communities between the six restoration sites and the five primary forests increased approximately linearly along with the years since restoration started, without reaching an asymptote (Fig. 5). The linear recovery model ($R^2 = 0.95$, $p = 0.001$) fitted best to the data (ΔAICc between linear and non-linear model >2; AICc linear = 27.0, non-linear = 30.3). The mean similarity of bird communities between differently aged restoration sites and primary forests was 28–56% and the range among the five primary forests was 51–70%. Extrapolating the linear model to the future, bird communities could become similar to those in primary forests in approximately 20 years after restoration started.

4. Discussion

Our results show that bird communities can start to recover rapidly following active restoration of rainforests. Following restoration, the community composition of birds started to change so that the proportion of arboreal insectivore frugivores and forest specialists increased, while foliage-gleaning insectivores, granivores and forest visitors decreased towards the older restoration areas. Previously, Catterall et al. (2012) showed that the species composition of birds started recovering following active restoration of rainforests in tropical Australia; however, the studies examining how bird communities recover following active forest restoration are still limited. The opposite phenomenon, on the other hand, showing the effect of human-induced disturbances to bird communities in rainforests, has been studied extensively. Logging has been found to have significant long-term effects on the community and functional composition of birds in the tropics (Latja et al., 2015; Owiunji, 2000; Sekercioglu, 2002; Gray et al., 2007; Edwards et al., 2009). These include an influx of forest generalist species, replacing forest specialists, in areas of more intensive logging (Burivalova et al., 2014), as well as a decrease in the abundance of frugivorous and insectivorous species (Gray et al., 2007; Powell et al., 2015a). Based on our results, it seems likely that community disassembly (due to human-induced disturbances) and reassembly (due to active restoration) are reversible processes, since those functional groups that have been shown to be adversely affected by disturbance benefitted from active restoration of rainforest, and those found to favor disturbed forests declined in older restoration areas. This gradual change in community composition from the youngest to older restoration sites offers hope that the recovery of bird communities can be aided with active restoration of rainforests. A comparison between bird community compositions in early restoration

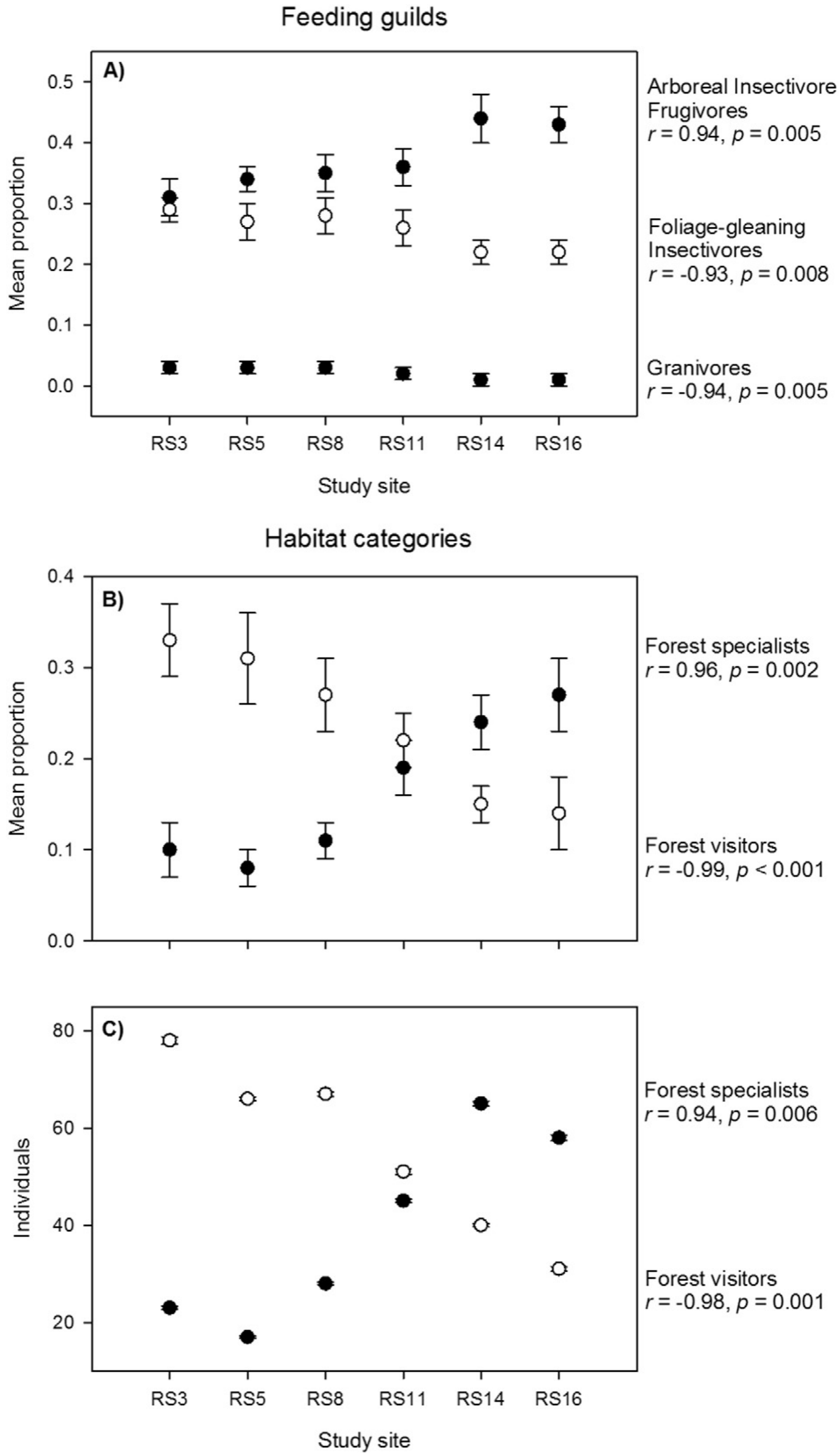

Fig. 4. Significant relationships after Pearson correlations between the age of restoration planting and feeding guilds and habitat categories: A) The mean proportion (of all individuals) of arboreal insectivore frugivores, foliage-gleaning insectivores and granivores, B) the mean proportion (of all individuals) of forest specialists and forest visitors, and C) the mean number of individuals (per study site) of forest specialists and forest visitors along the restoration gradient in Kibale National Park, Uganda. Pearson correlation coefficient and *p*-value are shown. Values are averages (± SE).

areas and in primary forests further demonstrates the development that has been achieved only in 16 years of active restoration.

Our study provides evidence that active restoration of deforested areas in the tropics can mitigate the loss of biodiversity, which could have significant consequences for ecosystem recovery and ecosystem services. Birds assist the recovery of other biota in restored areas via seed dispersal, pollination and pest control (Sekercioglu, 2006; Kirika et al., 2008; Morrison and Lindell, 2012; Karp and Daily, 2014).

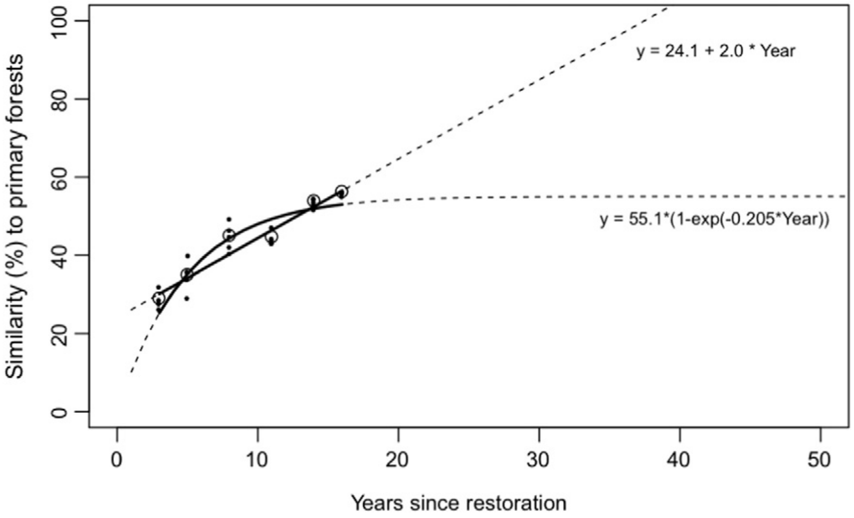

Fig. 5. Bray-Curtis similarity of bird communities between restoration sites and primary forests as a function of years since restoration started in Kibale National Park, Uganda. White circles represent the average similarity of bird communities of each restored study site to the five primary forests (black dots representing the similarities to the five primary forests from which the average was calculated). The two competing models (linear and non-linear recovery) are overlaid, extrapolated years shown with slashed line.

Specifically, frugivores have been found to be able to improve the functional connectivity of fruit plants across fragmented forest landscapes (Müller et al., 2014), and foliage-gleaning insectivores could help regulate herbivore populations on planted trees (Reid et al., 2012). Frugivores that in our study increased in abundance towards the older restoration areas were arboreal insectivore frugivores, such as tinkerbirds (*Pogoniulus* sp.) and greenbuls (*Eurillas* sp., *Phyllastrephus* sp.), many of which are forest specialists and therefore require intact primary forest as a breeding habitat; this makes them highly sensitive to forest disturbance (Thiollay, 1997; Gray et al., 2007). However, for frugivorous birds, physical connectivity between primary and regenerating forests may not be necessary for their movement between the areas (Moran and Catterall, 2014). Most of the foliage-gleaning insectivores that were more abundant in younger restoration sites were generalists or visitor species, such as white-chinned prinia (*Schistolais leucopogon*) and gray-headed nigrita (*Nigrita canicapillus*) or black-necked weaver (*Ploceus nigricollis*) and yellow white-eye (*Zosterops senegalensis*), that were probably more able to exploit the feeding resources provided in these areas. Although we did not study the movements of birds among habitats, it has been shown elsewhere that birds bringing seeds to restored areas could enhance or be crucial to the recruitment and regeneration of rainforest plants, thus initiating a subsequent self-organised regrowth with a positive feed-back loop between birds and rainforest plants (Neilan et al., 2006; Caves et al., 2013; Moran and Catterall, 2014), which could increase both plant and bird diversity in the long term.

On the other hand, although our results indicate a partial recovery of bird communities during the first 16 years of active restoration, we did not find any patterns in the responses of the most disturbance-sensitive feeling guilds, i.e. terrestrial insectivores and terrestrial insectivore frugivores, in the restoration gradient. This suggests that the species belonging to these guilds have not yet returned even to the oldest restoration areas. Previous studies have shown that major factors contributing to the recovery of bird communities after disturbances are a short distance to the source populations in undisturbed primary forests that provide possibilities for the natural colonisation of recovering areas, and well-connected matrix quality between the source and the recovering habitat patches (Sekercioglu et al., 2002; Deikumah et al., 2014); the same phenomena should also apply to restoration sites. It has been established that especially for forest-dependent (usually understory insectivore) species, their low mobility and limited dispersal ability through high contrast matrix most likely slow down or prevent the colonisation to regenerating or restored areas (Sekercioglu et al., 2002; Jansen, 2005; Catterall et al., 2012; Deikumah et al., 2014). Usually, the high contrast matrix habitat generally includes pastures, roads and other non-forest land uses, which may prevent their dispersal between forest patches (Sekercioglu, 2006). This was not the case in our study, however, where the matrix between primary forests and restoration sites is recovering secondary forest. But for some forest-dependent species, such as the terrestrial rufous-capped antthrush (*Formicarius colma*) in the Amazon, even thirty-year-old regenerating forests have been revealed to be unsuitable for dispersal (Powell et al., 2015b). Permitting second growth or, as in our study, actively restoring forest areas, may be the only ways to reconnect forest fragments back to continuous forest in order to enable the persistence of understory bird species in the long term (Stouffer et al., 2006).

Our results suggest that bird communities could reach a similar state present in primary forests after only approximately 20 years of active rainforest restoration, which seems to be an overly optimistic estimation. Extrapolation of our results from the linear model shows that, in approximately 20 years, the restoration areas could reach 51–70% similarity with primary forests, representing the mean similarity among the three primary forests in our study. Comparable recovery times (18 to 40 years) were estimated for fruit-feeding butterfly communities in the same restoration areas of Kibale National Park (Nyafwono et al., 2014). However, extrapolation from the linear model is likely to be too optimistic since natural succession processes are not typically linear; for example, the post-disturbance recovery of bird communities in naturally regenerating secondary rainforest fragments in India slowed down after approximately 25 years (Raman et al., 1998). Perhaps the slow recovery of certain characteristics of the forest (e.g., tree species composition and/or the number of large trees) could result in even slower recovery of the most specialised primary forest animals (DeWalt et al., 2003; Smith et al., 2015). Also, although the recovery time for species richness of many tropical animal taxa during tropical forest regeneration has been estimated to be 20 to 40 years, the species composition of birds appears to recover more slowly, with estimates ranging from 30 to 150 years (Raman et al., 1998; Dunn, 2004; Catterall et al., 2012; Thinh et al., 2012). Furthermore, the recovery time for naturally regenerating forests of Kibale National Park was estimated to be up to 74 to 158 years (Bonnell et al., 2011). Therefore, our estimate of recovery time of 20 years is most likely a very best-case scenario, however, showing the rapid change in bird communities towards those of primary forests already in early stages of active restoration.

In conclusion, our results show that bird communities start to recover from human-induced disturbances rapidly following active restoration of rainforests. We found that, during early active restoration, forest specialists, including some forest-dependent frugivores, start to return, and forest visitor species, including disturbance-tolerant insectivores and granivores, decline as the restoration areas age, and bird communities become increasingly similar to those of primary forests. However, although our and other studies show that the results of active restoration actions are promising in compensating biodiversity loss, we have covered here only the early phases of active restoration, and the most disturbance-sensitive functional groups, i.e., understory insectivores, have not yet returned even to the oldest restoration areas. Indeed, long-term studies are needed to fully understand how restoration activities help bring back the biodiversity values to deforested and degraded tropical forests. Regardless of this uncertainty, our study provides evidence that bird communities benefit from active rainforest restoration after human-induced deforestation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.05.035.

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