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The Effects of Restoring Logged Tropical Forests on Avian Phylogenetic and Functional Diversity

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Abstract

Selective logging is the most prevalent land-use change in the tropics. Despite the resulting degradation of forest structure, selectively logged forests still harbour a substantial amount of biodiversity leading to suggestions that their protection is the next best alternative to conserving primary, old-growth forests. Restoring carbon stocks under Reducing Emissions from Deforestation and Forest Degradation (REDD+) schemes is a potential method for obtaining funding to protect logged forests, via enrichment planting and liberation cutting of vines. This study investigates the impacts of restoring logged forests in Borneo on avian phylogenetic diversity—the total evolutionary history shared across all species within a community—and on functional diversity, with important implications for the protection of evolutionarily unique species and the provision of many ecosystem services. Overall and understorey avifaunal communities were studied using point count and mist-netting surveys, respectively. Restoration caused a significant loss in phylogenetic diversity and MPD (mean pairwise distance) leaving an overall bird community of less total evolutionary history and more closely related species compared to unlogged forests, while the understorey bird community had MNTD (mean nearest taxon distance) that returned towards the lower levels found in a primary forest, indicating more closely related species pairs. The overall bird community experienced a significant loss of functional strategies and species with more specialized traits in restored forests compared to that of unlogged forests, which led to functional clustering in the community. Restoration also led to a reduction in functional richness and thus niches occupied in the understorey bird community compared to unlogged forests. While there are additional benefits of restoration for forest regeneration, carbon sequestration, future timber harvests, and potentially reduced threat of forest conversion, this must be weighed against the apparent loss of phylogenetic and functional diversity from unlogged forest levels, making the biodiversity-friendliness of carbon sequestration schemes questionable under future REDD+ agreements. To reduce perverse biodiversity outcomes, it is important to focus restoration only on the most degraded areas or at reduced intensity where breaks between regimes are incorporated.

Keywords: Biodiversity, Birds, Liana cutting, Payments for Ecosystem Services, REDD+, Restoration, Selective logging, Silviculture, Southeast Asia, Sustainable forest management

INTRODUCTION

Selective logging is the most extensive land-use change in tropical ecosystems (Edwards *et al.* 2014b, Asner *et al.* 2009), causing structural damage and short-term changes in climatic conditions (Holdsworth and Uhl 1997, Laporte *et al.* 2007). Climbing vines and bamboos often over run the forest following logging, which impedes the ability of trees to regenerate (Putz *et al.* 2008, Osazuwa-Peters *et al.* 2015) and reduces the survival of disturbance sensitive-species that require dark, humid understorey conditions (Baraloto *et al.* 2012, Edwards *et al.* 2014b). Because tropical forests harbour the highest amounts of biodiversity globally, the expansion of selectively logged forest to dominate forest cover instead of primary old-growth forest is a major conservation concern.

Selective logging activities degraded 20% of tropical forests worldwide from 2000 – 2005 and, presently, more than 400 million hectares of forests in the tropics are in permanent timber estates and are expected to remain under forest cover (Asner *et al.* 2009, Blaser *et al.* 2011). Forests that have been degraded by selective logging activities are more prone to hunting, invasion by alien species and fires, and those that fall outside of permanent concessions are threatened by conversion to agriculture (Sheil and Meijaard 2005, Peres *et al.* 2006, Padmanaba and Sheil 2014, Abood *et al.* 2015) – with agricultural conversion up to 400% more likely than primary forests in the Brazilian Amazon (Asner *et al.* 2006). In combination, habitat degradation causes biodiversity to drastically decline (Wilcove *et al.* 2013), with losses to degradation in the Brazilian Amazon as large as conservation losses from deforestation and particularly detrimental to species that are functionally valuable (Barlow *et al.* 2016).

Protecting logged forests from conversion to agriculture and other risks associated with selective logging has been proposed as the next best alternative to protecting primary forests for biodiversity conservation (Meijaard and Sheil 2007, Chazdon *et al.* 2009, Edwards *et al.*

2011). This is because: (1) despite the altered conditions in the forest, selectively logged forests can retain high biodiversity levels, with the degree of retention in part dependent upon the logging regime used (Edwards *et al*. 2011, Putz *et al*. 2012, Bicknell *et al*. 2014, Martin *et al*. 2015); (2) it can be more cost-effective to protect logged forests than primary forests due to the reduced opportunity costs of foregone timber revenues (Fisher *et al*. 2011b); and (3) these logged forests could be used to connect or enlarge current protected areas (Edwards *et al*. 2014b). Obtaining funding and political will to protect these logged forests from conversion to agriculture is thus a critical issue. Enhancing carbon stocks via restoring degraded forests under payment for ecosystem service schemes such as the Reducing Emissions from Deforestation and Forest Degradation (REDD+) program is a potential mechanism to acquire such funding (Chazdon 2008). In the context of logging, restoration activities would enhance the background rate of carbon sequestration to yield carbon payments (Edwards *et al*. 2010).

Some suggest that restoring logged forests has potential benefits to reverse biodiversity loss, accelerate forest regeneration, and improve timber harvests (Kobayashi 2007, Bekessy and Wintle 2008, Edwards *et al*. 2010, Gourlet-Fleury *et al*. 2013). However, others suggest there is a danger that these techniques cause further damage to logged-over forests, and are destructive carbon-farming that will erode biological value (Putz and Redford 2009, Sasaki and Putz 2009). There are two key types of restoration methods, which can be applied individually or together: (1) enrichment planting of native trees, and (2) liberation cutting of competing vines, bamboos, herbaceous plants, or early successional trees (Putz *et al*. 2001a, Kobayashi 2007). Previous studies have shown that these two methods make logged forests better carbon sinks and encourage more rapid forest regeneration (Gourlet-Fleury *et al*. 2013, Wheeler *et al.* 2016). Research also suggests some positive effects on the diversity and community composition of tree (Wheeler *et al.* 2016), understorey avian (Edwards *et al.*

2009, Ansell *et al.* 2011) and invertebrate (Edwards *et al.* 2012) communities. However, before restoration can be accepted as an effective conservation strategy, we need to understand its impacts on species that are evolutionarily distinct or functionally important and which are vital for ecosystem processes.

Species that are locally evolutionarily distinct are important for local ecosystem functions as they possess unique traits and occupy unique niches (Jetz *et al.* 2014). Evolutionary distinctiveness metrics – the amount of unique evolutionary history a species represents – can be included into biodiversity conservation strategies to preserve these unique traits and resulting ecosystem functions (Redding and Mooers 2006, Jetz *et al.* 2014). Phylogenetic diversity metrics (measures of evolutionary history and patterns of evolutionary relationships in a community) and functional diversity metrics (measures of species or community functional uniqueness and patterns of functional trait distribution in communities) are also important for conservation planning (Cadotte *et al.* 2011, Rolland *et al.* 2012, Gossner *et al.* 2013). These metrics can inform us on community assembly processes (Pavoine and Bonsall 2011), ecosystem functioning (Petchey *et al.* 2004, Cadotte, *et al.* 2009, 2011, Bässler *et al.* 2014), intrinsic conservation value (Mace *et al.* 2003, Winter *et al.* 2013) and community resilience (Díaz *et al.* 2007, Cadotte *et al.* 2012).

Incorporating phylogenetic and functional diversity metrics provides us with important insights into community responses to environmental change. Phylogenetic diversity metrics are less affected by taxonomic revisions and more sensitive to inclusions of non-native species to an ecological community compared to species richness (Isaac *et al.* 2004, Meiri and Mace 2009). Functional diversity assessments can better reveal the state and resilience of a community's functioning than does species richness or community composition (Petchey *et al.* 2004, Cadotte *et al.* 2009, Mouillot *et al.* 2013).

This study investigates the effects of restoring logged forests in the global biodiversity hotspot of Borneo (Myers *et al.* 2000), where extensive habitat degradation from selective logging has been responsible for many local species extinctions (Wilcove *et al*. 2013). We examine whether restoration management to improve forest structure and carbon stocks in selectively logged forests that are unhunted and unburned can also aid the recovery of biodiversity towards primary forest levels. This study focuses on phylogenetic and functional diversity impacts for both the entire (overall) and understorey avian communities. Birds are well-known taxonomically, have a global phylogeny (Jetz *et al*. 2012), are good indicators of responses to logging in other taxa (Edwards *et al*. 2014a) and play important roles for ecosystem functioning (Sekercioglu 2006). Restored logged forests were enrichment planted with native tree species and liberation cutting was performed on vines and climbing bamboos. The impacts of restoring logged forests were then compared to unlogged primary forests and naturally regenerating logged forests as controls. The aims were thus to: (1) determine how logged forest restoration affects the phylogenetic diversity of avian communities; and (2) determine how logged forest restoration affects the functional diversity of avian communities. Given the emerging forest restoration agenda globally (Pistorius and Freiberg 2014), the results will help to determine if restoration can aid biodiversity conservation and, if so, would lend further support for using carbon enhancement funding to protect selectively logged forests.

MATERIALS AND METHODS

STUDY SITE

The study was conducted in the global biodiversity hotspot of the island of Borneo (Myers *et al*. 2000). Three habitat types (unlogged primary forests, naturally regenerating logged forests and restored forests that were previously logged at the same time as sampled naturally regenerating logged forests) were surveyed in the lowland dry dipterocarp forests of the one million hectare Yayasan Sabah (YS) logging concession in Sabah, Malaysian Borneo. Within the YS concession is 45,200 ha of unlogged primary forests in the Danum Valley Conservation Area and adjacent Palum Tambun Watershed reserves, which are dominated by large dipterocarp trees (Dipterocarpaceae) valuable for timber (Fisher *et al*. 2011a) and represented our unlogged primary forests, and 238,000 ha naturally regenerating and restored logged forest in the adjacent Ulu Segama-Malua Forest Reserve (US-MFR).

The US-MFR was selectively logged between 1976 and 1991 using a modified uniform system in which all commercially valuable trees of more than 60 cm diameter at breast height (DBH) were harvested using high lead cable extraction and tractor techniques, with ~113 m^3 of timber removed per hectare (Fisher *et al*. 2011b). Although some areas of the US-MFR were re-logged between 2001 and 2007 (Edwards *et al*. 2011), we focus on the once-logged forests. As a result of selective logging, the structure of logged forests is very different to that of unlogged forests. For instance, logged forest canopies have more gaps, a higher density of understorey vegetation and climbing bamboos (Berry *et al*. 2008, Ansell *et al*. 2011), as well as roads, logging dumps and skid trails that fragment the forest landscape (Pinard *et al*. 2000, Laporte *et al*. 2007).

About 11,000 hectares of once-logged forests in the US-MFR were restored between 1993 and 2011 by the Innoprise-FACE Foundation Rainforest Rehabilitation Project (INFAPRO), with another 14,000 hectares designated for future restoration (Ansell *et al*. 2011). Restoration involved enrichment planting with a variety of native dipterocarp (95%) and wild fruit (5%) species along planting lines at densities of 200 seedlings per ha or lower and liberation cutting of all climbing bamboos and vines, 6 months before and 3 years after enrichment planting. Non-commercial understorey plants were also removed along the planting lines immediately before and 3 months after enrichment planting (see Ansell *et al*.

2011 for further details). Additionally, 500 ha of once-logged forest in the US-MFR were restored between 2002 and 2003 in the Sabah Biodiversity Experiment (SBE; Hector *et al.* 2011), with liberation cutting and enrichment planting at densities of about 60 seedlings per ha.

AVIFAUNAL SAMPLING

Two avian communities were sampled during the drier seasons (Walsh and Newberry 1999): the overall (i.e. whole) bird community and the understorey bird community. Data for both communities were extracted from Ansell *et al*. (2011) and Edwards *et al*. (2013, 2014a). Sampled logged forests (naturally regenerating logged forests and restored forests that were previously logged) were harvested between 1987 and 1991, with restored forests enrichment planted between 1993 and 1995 (2002 and 2003 in SBE), and thus sampled 16-22 years post logging, with restored forests sampled 14-16 years (5-6 years in SBE) post restoration treatment.

Overall bird community: Point count surveys with unlimited-radius were conducted from May – September 2008 and May – June 2009. At sites created within each habitat type, we sampled 12 point-count stations per site with each station separated by 250 m (48 point-count stations in unlogged forests, 24 in naturally regenerating forests, and 36 (24 INFAPRO; 12 SBE) in restored forests) (Appendix S1: Fig S1a). Studies in tropical forests have shown that bird census points or mist-net transects separated by more than 200 m are statistically independent (Hill and Hamer 2004). Point-count surveys occurred for 15 minutes on three consecutive days from 0545 – 1000 h. Each site was only sampled in one year, and any temporal effects (within or between years) were minimized by rotating sampling between the different habitat types. The highest number of individual birds recorded for a certain species on any of the three days was taken as our estimate of maximum abundance but not the species' true abundance, which is unknown. All point counts were conducted by a single experienced observer (D. P. Edwards) to minimise the potential for observer bias. The point count surveys resulted in 167 species across all habitat types.

Understorey bird community: Mist netting was conducted from June – October 2007, May – September 2008 and May – July 2009 to survey the cryptic lower-storey birds that can be undersampled using point counts (Blake and Loiselle 2001). Fifty-four transects were created (18 transects in unlogged primary forests, 18 in naturally regenerating logged forests and 18 (16 INFAPRO; 2 SBE) in restored logged forests) with transects within each habitat placed at least 500 m apart to ensure statistical independence (Appendix S1: Fig S1b). Each transect contained 15 mist nets (12 x 2.7 m; mesh size 25 mm) placed end to end. Sampling occurred for three consecutive days from 0600 – 1200 h. Each site was only sampled in one year, and any temporal effects (i.e., within or between years) were minimized by rotating sampling between the different habitat types. To ensure that individual birds were sampled only once, each bird was marked with a uniquely numbered metal leg ring. Totalling the unique individuals of each species across the three sampling days gave an estimate of maximum abundance, but not a species' true abundance, which is unknown. A total of 100 species were recorded in the mist net surveys across all habitat types.

PHYLOGENETIC DIVERSITY & EVOLUTIONARY DISTINCTIVENESS MEASURES

The following methods were conducted for the overall and understorey bird datasets. For each dataset, five hundred phylogenetic trees were downloaded from http://birdtree.org/ (Jetz *et al*. 2012) of which 250 trees were based on the Hackett *et al*. (2008) backbone and 250 trees on the Ericson *et al*. (2006) backbone. Each phylogenetic tree represents a hypothesis of species evolutionary relationships that is different from the other. Six abundance-weighted phylogenetic diversity metrics and one metric of local evolutionary distinctiveness were calculated for each of the 500 phylogenetic trees. These were:

1. *Phylogenetic Diversity (PD)* – the total amount of evolutionary history in a community;
2. *Standard effect size of PD (sesPD)* – PD taking into account species richness, as PD is correlated with species richness (Swenson 2014, Li *et al*. 2015). SesPD is calculated by comparing the PD of the observed community with the PD of null communities of equal species richness, which are created by drawing species at random from the regional species pool. Positive values of sesPD suggest that communities have higher PD values than expected for that given species richness and the opposite is true for negative values;
3. *Mean Pairwise Distance (MPD)* – the average distance on a phylogenetic tree between all individuals of a community. High MPD values indicate that species are widely distributed across clades, while low MPD values indicate that species are phylogenetically clustered;
4. *Standard effect size of MPD (sesMPD)* – MPD taking into account species richness. Positive values of sesMPD imply that communities have higher MPD than expected for that given species richness and the opposite is true for negative sesMPD values;
5. *Mean Nearest Taxon Distance (MNTD)* – the average distance on a phylogenetic tree between individuals and their closest non-conspecific relative. High MNTD values suggest that individuals that are closely related do not co-occur in the community, while low MNTD values suggest that they occur in the community;
6. *Standard effect size of MNTD (sesMNTD)* – MNTD taking into account species richness. Positive values of sesMNTD imply that communities have higher MNTD than expected for that given species richness and the opposite is true for negative sesMNTD values;
7. *Evolutionary Distinctiveness (ED)* – the amount of unique evolutionary history represented by a species in a phylogenetic tree. A species with a high ED value indicates that it has no extant close relatives and vice versa.

A full description and equations of the phylogenetic metrics are given in the Supplementary Materials (see Appendix S1: Section S1). All seven metrics were calculated using the *picante* package (Kembel *et al.* 2010) in R (R Core Team 2016). To calculate the standard effect size (ses) for PD, MPD and MNTD, the observed community was compared against 999 null communities. These null communities were generated using null models with an independent swap algorithm which draws species at random from the regional species pool whilst maintaining species richness (Gotelli 2000). Local ED was used instead of global ED because species that are locally evolutionarily distinct are important for maintaining local ecosystem function (Crozier 1997, Hidasi-Neto *et al.* 2015). ED was calculated using the fair proportions method (Isaac *et al.* 2007) (Appendix S1: Table S3). To account for phylogenetic uncertainty, the mean values of each of the six phylogenetic diversity metrics and the median ED value were calculated from all 500 trees for each point count sample and each mist-net transect.

FUNCTIONAL DIVERSITY MEASURES

The following methods were conducted for the overall and understorey bird datasets. Functional diversity was evaluated using resource-use traits, which studies have shown to be functionally important (Flynn *et al.* 2009). Traits from four categories (Diet, Foraging substrate, Foraging strategy, Morphological) were used – the diet category determined the types of food eaten (e.g. fruit); foraging substrate determined where foraging takes place (e.g. ground); foraging strategy determined how the food item was obtained (e.g. sallying); and the morphological category determined the physical attributes of the species (e.g. body size) (see Appendix S1: Table S2 for more information on traits used). Data for the trait matrix was extracted from Smythies (1960) and Handbook of the Birds of the World Alive (http://www.hbw.com/), following Edwards *et al.* (2013).

Using the trait data, five complementary measures of functional diversity were measured:

1. *Functional Diversity (FD)* – the total length of branches on a functional dendrogram (Petchey and Gaston 2002);
2. *Functional Richness (FRic)* – the amount of functional space occupied by species in a community. High FRic values suggest that lots of niches are occupied by species in the community while the opposite is true for low values;
3. *Functional Evenness (FEve)* – describes the distribution of species abundances in a community across functional space. High FEve values indicate that niches are evenly occupied and utilised, while low FEve values indicate that niches may be under-occupied and under-utilised;
4. *Functional Divergence (FDiv)* – describes patterns of niche differentiation in a community. High FDiv implies that there is high niche differentiation within a community; low FDiv that there is low niche differentiation;
5. *Functional Specialization (FSpe)* – measures the functional uniqueness of a community compared to the regional species pool. High FSpe values indicate that a community is more specialized, while communities with low FSpe values are less specialized.

A full description and equations of the functional metrics are given in the Supplementary Materials (see Appendix S1: Section S1). FD was calculated starting with a trait matrix converted into a distance matrix and then into a functional dendrogram. The functional dendrogram was created using the extended Gower distance measure (Pavoine *et al.* 2009) using the *vegan* package (Oksanen *et al.* 2016) and an unweighted pair-group arithmetic average (UPGMA) clustering (Blackburn *et al.* 2005). The extended Gower distance measure is suitable for measuring a combination of variable types including binary, categorical, continuous and multi-choice nominal variables (Podani and Schmera 2006). The

UPGMA clustering method produced the highest cophenetic coefficient (overall bird community: 0.77; understorey bird community: 0.81), which suggests that the dendrogram accurately preserves the pairwise distances of the original data points (Petchey and Gaston 2006). The functional dendrogram was then used to calculate FD using the *picante* package in R (Kembel *et al.* 2010) for each point count sample and each mist-net transect.

FRic, FEve, FDiv and FSpe were calculated using Villéger *et al.*'s (2008, 2010) formulae and convex hull methodology (*FD* package in R: Laliberté *et al.* 2014). Using this method, traits are coordinates in multidimensional functional niche space which determines a species' functional niche. Traits were weighted equally and species abundance was taken into account when calculating these metrics. The trait matrix was first converted to a distance matrix using the extended Gower distance measure (Pavoine *et al.* 2009) and then a principal coordinate analysis (PCoA) was carried out to produce a matrix of transformed coordinates (Villéger *et al.* 2008). The PCoA axes (overall bird community: n=6; understorey bird community: n=8) were then used to calculate the functional metrics for each point count sample and each mist-net transect.

STATISTICAL ANALYSES

All analyses were conducted separately for the overall bird and understorey bird communities. To study the effects of habitat type (unlogged, naturally regenerating logged, restored logged forests) on phylogenetic and functional diversity metrics for the overall bird community, we used linear mixed-effects models (LMMs). Analysis is at the point count level, which is unaffected by the imbalanced total number of point counts between habitats. Habitat type was included in the model as a fixed effect, while sampling site and the year sampled were included as random effects. LMMs were estimated using maximum likelihood from the *lme4* package in R (Bates *et al.* 2015). Model residuals were checked for homoscedasticity and normality. FRic was the only metric that was log-transformed. Model fit was compared using Akaike Information Criterion (AIC) (Anderson 2008) where the best models had the lowest AIC values. The amount of variation explained by each model's fixed and random effects was calculated using Nagakawa and Schielzeth's R^2 (Nakagawa and Schielzeth 2013) from the *MuMIn* package in R (Barton 2016). Pairwise comparisons were conducted using Tukey post hoc tests in the *multcomp* package in R (Hothorn *et al.* 2008). Inclusion of data from SBE did not affect our results, and so we present only the full analysis.

To study the effects of habitat type on phylogenetic and functional diversity metrics for the understorey community, ANOVA models were used; since mist-net transects were not aggregated into sites, no nested random effects were included. The ANOVA models were built using the *lm* function in R (R Core Team 2016). Model residuals were checked for homoscedasticity and normality. FRic was the only metric that was log-transformed. Model fit was tested using the *AICcmodavg* package in R (Mazerolle 2016). The best models were selected based on their AIC values of which the lowest values indicated the best models. Pairwise comparisons were then conducted using Tukey post hoc tests in the *multcomp* package (Hothorn *et al.* 2008). Inclusion of data from SBE did not affect our results, and so we present only the full analysis.

Correlation plots between the different phylogenetic metrics and between the different functional metrics for both the overall bird and understorey bird community are included in the Supplementary Materials (Appendix S1: Fig S2). To check whether spatial autocorrelation influenced any results at the point or transect levels, the Moran's I statistic was used from the *spdep* package in R (Bivand and Piras 2015) using model residuals with 1000 repetitions. All analyses were done on RStudio (R Core Team 2016).

RESULTS

A total of 87 species were shared between the point count and mist net datasets, with both datasets sampling unique components of the avian community (point counts = 80 species; mist nets = 13 species) (Appendix S1: Table S1).

PHYLOGENETIC DIVERSITY & EVOLUTIONARY DISTINCTIVENESS

The phylogenetic metrics of both the overall bird and the understorey bird community tended to be significantly correlated (Appendix S1: Fig S2). Spatial autocorrelation was not detected for any of the residuals for phylogenetic diversity and evolutionary distinctiveness models (Moran's I test: all p>0.4).

Overall Bird Community

Including habitat type as a fixed effect improved model fit for all metrics except MNTD (Table 1). Pairwise comparisons showed that restored forests had significantly lower PD than unlogged (p=0.003) and naturally regenerating forests (p=0.020), which did not differ significantly (p=0.989, Fig 1a). Restored forests had significantly lower sesPD than unlogged forests (p=0.014, Fig 1b), while naturally regenerating forests did not significantly differ with restored (p=0.394) or unlogged forests (p=0.518). MPD and sesMPD in restored forests was significantly lower compared to naturally regenerating (MPD: p=0.003; sesMPD: p=0.012) and unlogged forests (MPD: p<0.001; sesMPD: p<0.001) (MPD: Fig 1c; sesMPD: Fig 1d), which did not differ significantly (MPD: p=0.178; sesMPD: p=0.111). There was no significant difference between habitat pairs for MNTD (p>0.3, Appendix S1: Fig S3a), sesMNTD (p>0.054, Appendix S1: Fig S3b) and ED (p>0.1, Appendix S1: Fig S4a).

Understorey Bird Community

Including habitat type as a fixed effect improved model fit for PD, MPD, MNTD and sesMNTD, but not for sesPD, sesMPD and ED (Table 2). Naturally regenerating forests had significantly higher MNTD and sesMNTD than restored (MNTD: p=0.0436; sesMNTD: p=0.008) and unlogged forests (MNTD: p=0.011; sesMNTD: p=0.036) (MNTD: Fig 1e; sesMNTD: Fig 1f), which did not differ significantly (MNTD: p=0.844; sesMNTD: p=0.841. Pairwise comparisons revealed that all habitat pairs were not significantly different for PD (p>0.08, Appendix S1: Fig S3c), sesPD (p>0.4, Appendix S1: Fig S3d), MPD (p>0.08, Appendix S1: Fig S3e), sesMPD (p>0.1, Appendix S1: Fig S3f) and ED (p>0.8, Appendix S1: Fig S4b).

FUNCTIONAL DIVERSITY

The functional metrics of both the overall bird and the understorey bird community were less strongly correlated than the phylogenetic metrics (Appendix S1: Fig S2), with no or only weak correlations between FD and FRic versus FEve and FDiv. Spatial autocorrelation was not detected for any of the residuals for functional diversity models (Moran's I test: all p>0.09).

Overall Bird Community

Models with habitat type included as a fixed effect improved model fit for all metrics (Table 1). Pairwise comparisons reveal that FD was significantly lower in restored forests than in naturally regenerating (p=0.023) and unlogged (p<0.001) forests, which did not differ significantly (p=0.880; Fig 2a). Restored forests had significantly lower FRic (p<0.001, Fig 2b) and FEve (p=0.043, Fig 2c) than unlogged forests, while naturally regenerating forests did not significantly differ with restored (FRic: p=0.147; FEve: p=0.743) or unlogged forests (FRic: p=0.441; FEve: p=0.369). Logging significantly reduced FDiv (p=0.039; Appendix S1: Fig S5a) and FSpe (p<0.001; Appendix S1: Fig S5b), which were unaffected by restoration (FDiv: p=0.964; FSpe: p=0.432).

Understorey Bird Community

Including habitat type as a fixed effect improved model fit for FD and FRic, but not for FEve and FDiv (Table 2). FRic in restored forests was significantly lower than in naturally regenerating (p=0.031) and unlogged forests (p=0.018) (Fig 2d), which did not differ significantly (p=0.975, Fig 2d). Pairwise comparisons showed no significant differences for FD (p>0.07), FEve (p>0.4), FDiv (p>0.9) and FSpe (p>0.1) (Appendix S1: Fig S5c-f).

DISCUSSION

It has become increasingly urgent to find ways of ensuring the retention of conservation values within selectively logged forests, and to protect these forests from conversion to agricultural lands. Funding via carbon enhancements under REDD+ could increase the economic value of these degraded forests (Edwards *et al.* 2010). Here we investigated the impacts of forest restoration on the phylogenetic and functional diversity of birds where restoration is a management technique applied to selectively logged forests that have not been burned. The interpretation of these metrics only applies to our sampled communities and we thus caution against extrapolating these inferences to species occurring in our sample areas that we did not detect or to communities living in ecosystems with different habitat structures. We found that restoration caused a loss in evolutionary history, functional strategies and species with more specialized traits in our sampled overall bird community compared to those of unlogged and naturally regenerating forests, leaving behind a community with more closely related species and more functional clustering. For most metrics, our sampled understorey bird community was robust to restoration, with restoration returning MNTD (mean nearest taxon distance) levels towards unlogged forest levels, perhaps indicating the return of forest specialist species, but with reduced functional strategies (FRic). On balance, therefore, the biodiversity-friendliness of carbon sequestration schemes under future REDD+ agreements is questionable.

PHYLOGENETIC DIVERSITY

Restoration significantly decreased PD, MPD and sesMPD of the overall bird community compared to that of unlogged forests and naturally regenerating forests, and restoration resulted in lower sesPD compared to unlogged forest, which did not differ to naturally regenerating forest. These reductions suggest a loss of evolutionary history which leaves behind a community with more closely related species as different environmental conditions would alter the likeliness of different clades to survive in that environment (i.e. environmental filtering) (Webb *et al.* 2002). Other studies have shown decreases in PD and MPD with land-use change, especially those that involve more drastic habitat change such as forest conversion to agriculture (Frishkoff *et al.* 2014, Prescott *et al.* 2016).

The loss of phylogenetic diversity could result from restoration altering the structure of the forest understorey, with a more open understorey with fewer shrubs and lianas (Ansell *et al.* 2011). Many generalists and understorey frugivores depend on the fruits produced by these understorey shrubs and vines while insectivores rely on vine tangles which trap leaf-litter to provide them with a foraging substrate. The vines are also an important nesting site and refuge for many bird species (Putz *et al.* 2001a). Furthermore, birds that forage by sallying prefer undisturbed forests with clear understorey (Thiollay 1992, Ansell *et al*. 2011). A decrease in MPD and the maintenance of MNTD in the overall bird community after restoration suggests that species that replaced those lost after restoration were similarly closely related to those that were lost.

The phylogenetic diversity (PD, sesPD, MPD, sesMPD) of the understorey bird community was largely unaffected by logging and subsequent restoration. Restoration returned MNTD and sesMNTD of the understorey bird community from elevated levels in naturally regenerating forest to those found in unlogged forest. This implies that there is a coexistence of closely related species, most likely returning forest specialists (Ansell *et al*. 2011, Prescott *et al*. 2016), in restored and unlogged forests compared to that of naturally regenerating forests. ED of both the overall bird and understorey bird community did not differ between habitats indicating a similar amount of unique genes and traits across the habitat types. This is not surprising considering that these habitat types would tend to harbour species that have been adapted to forested lands. In the context of understorey birds and all evolutionary distinct species, these results represent positives or at least no negative impacts of restoration.

FUNCTIONAL DIVERSITY

The functional diversity of the overall bird community experienced some negative effects from restoration, with a decline in FD relative to unlogged and naturally regenerating forest, and restoration resulted in lower FRic and FEve compared to unlogged forest, which did not differ to naturally regenerating forest. These suggest a loss of species and functional strategies (Duffy 2002, Laliberté *et al*. 2010), which could be attributable to environmental filtering effects. Changes in the resources, structure and microclimate of restored forests

(Ansell *et al*. 2011, Berry *et al*. 2008) could reduce the ability of sensitive species to inhabit these forests (Belmaker *et al*. 2012, Edwards *et al*. 2014b). Loss of FD after habitat change also occurs in anurans (Ernst *et al*. 2006), birds (Devictor *et al*. 2008, Edwards *et al*. 2013), mammals (Flynn *et al*. 2009), and dung beetles (Edwards *et al*. 2014c). The loss of functional groups from ecosystems has the potential to have negative implications on food web stability, invasion resistance and ultimately ecosystem functioning (Mason *et al*. 2005, Flynn *et al*. 2009, Cadotte *et al.* 2011), with some available resources in the habitat likely unused.

Lower FEve implies that there is a less even distribution of abundance of functionally different species and their distances in functional space are less regular (Villéger *et al*. 2008). This indicates functional clustering, where several species with similar traits occupy the same resource-use niches (Edwards *et al*. 2013), which could increase the functional redundancy of species niches, making the community more robust to future disturbances (Schleuning *et al*. 2012).

Restoration had very few impacts on the functional diversity of the understorey bird community, although FRic declined below both unlogged and naturally regenerating forest levels. This indicates lower resource-use efficiency in the community, as some niches remain unoccupied (Mason *et al*. 2005). This is to be expected since dense vegetation species would tend to be most affected by the removal of vines and understorey shrubs (Putz *et al*. 2001a). The maintenance of FEve, FDiv and FSpe in the understorey bird community across habitats implies that any loss of FD from logging is offset by species with similar functional traits occupying the vacant niches and that resource utilisation is robust to logging and restoration activities (Edwards *et al*. 2013, 2014c).

SAMPLING LIMITATIONS

Our study only observed the impacts of restoration on one taxa; however, birds have been shown to be a good indicator group for biodiversity responses as a whole (Edwards *et al*. 2014a, Barlow *et al*. 2007). Previous studies on restoration impacts have also used birds (Edwards *et al*. 2009, Ansell *et al*. 2011) and invertebrates (Edwards *et al*. 2012), suggesting that studying impacts on trees and plants—some of which are directly subjected to cutting or planting—is an important research direction. This study was also only conducted in one region and there is a need to assess restoration impacts in other regions where logging intensities are frequently lower (Putz *et al*. 2001b).

Detection biases can result from numerous sources such as the cryptic nature of species, the observer's ability to detect species, and variation in vegetation densities between habitats, and failure to account for these biases in detection can lead to erroneous conclusions (Banks-Leite *et al*. 2014). Because we focused on spatial replication, we did not have enough repeats at each point count or mist-net transect to statistically partition habitat-specific occupancy and detection probabilities in an occupancy modelling framework (Welsh *et al.* 2013). If some species are in fact easier to detect in one forest type, apparent diversity metrics in our analyses might therefore be biased relative to other habitats (but see Banks-Leite *et al.* 2014 who show that using unadjusted data gave similar results on the impacts of tropical land-use change in the Brazilian Atlantic Forest to detection adjusted data). However, all surveyed habitat types were in dense forest with similar vegetative structure, and we controlled for potential temporal variation in detection by rotating sampling amongst habitat types within and between years and by including the year sampled as a random term in our analyses. Our broadly similar results using two very different sample methods (point counts and mist-nets) provide strong support for the validity of our conclusions (Barlow *et al*. 2007).

Nevertheless, we recommend that future studies use more robust methods of estimating species abundance that account for detection probability, which is important when deriving measures of functional and phylogenetic diversity (Jarzyna and Jetz 2016). Methods to account for detection probability in point count data include distance sampling (Buckland *et al.* 2001), multiple observer methods (Nichols *et al.* 2000) and N-mixture models (Royle 2004). Another method by Clement *et al.* (2015) utilises the assumption that populations have a fission-fusion grouping, where a population is made up of individual groups that change composition and size depending on individual movements around groups. Finally, for mist-net sampled data, estimates of abundance that have accounted for detection biases can be obtained from closed population capture-mark-recapture models (Otis *et al.* 1978), provided that enough recaptures are acquired within years. It is also possible to obtain these abundance estimates for studies across years using Jolly-Seber models (Jolly 1965, Seber 1965, Schwarz and Arnason 1996) or Robust Design methods (Pollock 1982).

CONSERVATION AND MANAGEMENT IMPLICATIONS

There are both positives and negatives of these results for conservation, which must be considered within the context of restoration of logged over forests offering forest regeneration, carbon sequestration, and improved future timber harvests benefits, plus potentially reduced threat of forest conversion to agriculture (which if true is an enormous benefit). On the positive side, phylogenetic and most functional diversity metrics of the understorey bird community were not adversely affected by restoration, while MNTD returned to pre-logging levels after restoration. Thus, restoration management of logged forests evidently retains important evolutionary history, evolutionarily distinct species, and ecosystem functions within the understorey. On the negative side, however, phylogenetic and functional diversity of the overall bird community was lower in restored forests than in unlogged forests, probably indicating that the main drivers of change are those species living above understorey level. These reductions likely underscore losses of evolutionary history, evolutionarily distinct species, and ecosystem functions. Future research should also determine whether other taxa respond in a same way to the avian communities.

Since liberation cutting in logged forests reduces the abundance of species dependent on dense vegetation, it has been proposed that breaks be incorporated into the liberation cutting regime so as to retain critical dense tangle microhabitats similar to those of unlogged forests (Ansell *et al.* 2011), which could benefit biodiversity (Levey 1988, Schnitzer and Carson 2001). However, these breaks could cause a decline in the rate of tree recovery and thus carbon sequestration, which could reduce the overall ecosystem service benefits of restoration. Research is urgently needed into the precise impacts of liberation cutting as the most economically viable tool for forest restoration, given that seedlings are expensive to cultivate.

The use of restoration as a tool for obtaining carbon enhancement funding under REDD+ should only be conducted on logged-over forests that will not be subjected to future logging activities. Restoring logged forests under REDD+ when a core aim is to increase future timber yields is unlikely to provide long-term benefits for carbon stocking, and may instead be detrimental to long-term biodiversity and carbon sequestration potential. Furthermore, restoring degraded forests should depend on the state of the forest since less degraded forests would not benefit much in terms of carbon sequestration (Kobayashi 2007) and our results suggest would likely suffer negative impacts on phylogenetic and functional diversity. On the flip side, in heavily degraded areas, the added ecosystem service benefits of restoration may well outweigh any biodiversity costs, especially if a less intensive liberation-cutting regime is used. This trade-off in forest management strategy has been demonstrated in temperate and boreal ecosystems, which highlights the need for new procedures to reconcile this paradox (Thom and Seidl 2016). Enhancing carbon via restoring degraded forests still represents an important aspect in the future REDD+ agreement, but this must be applied with care to ensure that these are biodiversity-friendly schemes.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/suppinfo

Data Availability

Data available from Figshare: http://dx.doi.org/10.15131/shef.data.5017328

TABLE 1. Model selection of linear mixed-effects models for the overall bird community. Models were selected for all phylogenetic diversity, evolutionary distinctiveness and functional diversity metrics in relation to habitat type based on their AIC values. The null models include only point and site as nested random effects. Best models are highlighted in bold. AIC = Akaike Information Criterion; ΔAIC = the AIC difference between the best model and the stated model; Marginal R^2 = variation explained by fixed effects (Habitat); Conditional R^2 = variation explained by the model.

Phylogenetic Diversity & Evolutionary Distinctiveness

Response variable	**Model**	**AIC**	**ΔAIC**	**Marginal R^2**	**Conditional R^2**
PD	**Habitat**	1453.60	0.00	0.16	0.25
	Null	1459.30	5.70	0.00	0.32
sesPD	**Habitat**	241.90	0.00	0.07	0.07
	Null	244.83	2.93	0.00	0.06
MPD	**Habitat**	841.63	0.00	0.25	0.25
	Null	855.88	14.25	0.00	0.24
sesMPD	**Habitat**	252.75	0.00	0.25	0.33
	Null	262.32	9.57	0.00	0.24
MNTD	**Null**	760.83	0.00	0.00	2.59e^{-15}
	Habitat	761.94	1.11	0.03	0.03
sesMNTD	**Habitat**	256.44	0.00	0.05	0.05
	Null	257.88	1.44	0.00	0.02
ED	**Habitat**	459.49	0.00	0.04	0.04
	Null	460.24	0.75	0.00	2.75e^{-20}

Functional Diversity

Response variable	**Model**	**AIC**	**ΔAIC**	**Marginal R^2**	**Conditional R^2**
FD	**Habitat**	16.72	0.00	0.14	0.27
	Null	25.27	8.55	0.00	0.36
FRic	**Habitat**	219.84	0.00	0.15	0.33
	Null	226.30	6.46	0.00	0.42
FEve	**Habitat**	-297.22	0.00	0.05	0.05
	Null	-295.47	1.75	0.00	0.03
FDiv	**Habitat**	-404.39	0.00	0.07	0.07
	Null	-399.93	4.46	0.00	0.02
FSpe	**Habitat**	114.79	0.00	0.22	0.27
	Null	126.18	11.39	0.00	0.30

TABLE 2. Model selection of ANOVA models for the understorey bird community. Models were selected for all phylogenetic diversity, evolutionary distinctiveness and functional diversity metrics in relation to habitat type based on their AIC values. Best models are highlighted in bold. K = number of parameters; AIC = Akaike Information Criterion; ΔAIC = the AIC difference between the best model and the stated model; AICWt = AIC weights; Cum.Wt = Cumulative Akaike weights; LL = maximum likelihood.

Phylogenetic Diversity & Evolutionary Distinctiveness

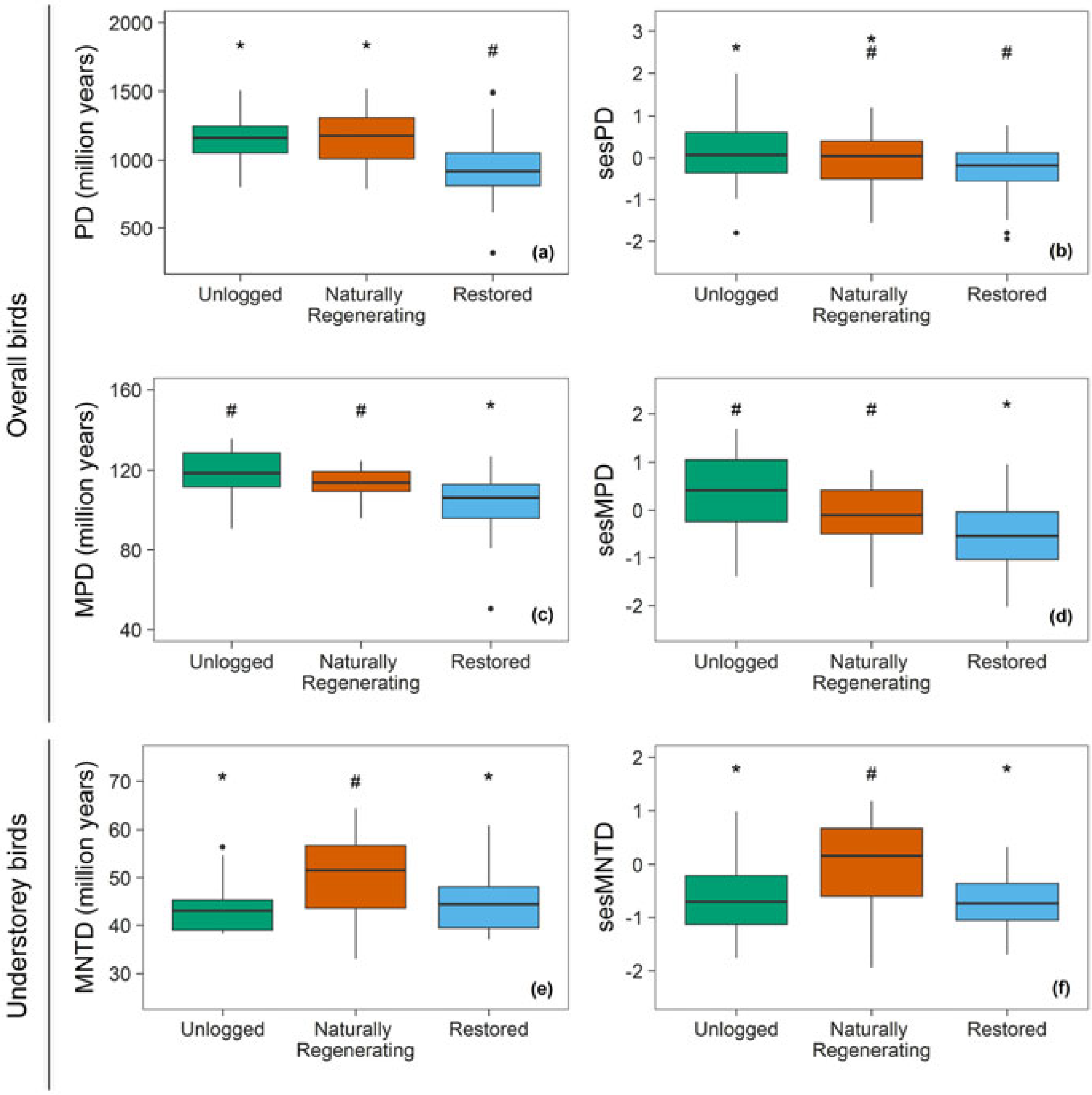
Response variable	**Model**	**K**	**AIC**	**ΔAIC**	**AICWt**	**Cum.Wt**	**LL**
PD	**Habitat**	4	702.43	0.00	0.68	0.68	-347.22
	Null	2	703.90	1.47	0.32	1.00	-349.95
sesPD	**Null**	2	151.39	0.00	0.76	0.76	-73.70
	Habitat	4	153.73	2.34	0.24	1.00	-72.87
MPD	**Habitat**	4	398.06	0.00	0.61	0.61	-195.03
	Null	2	398.91	0.86	0.39	1.00	-197.46
sesMPD	**Null**	2	129.64	0.00	0.55	0.55	-62.82
	Habitat	4	130.07	0.43	0.45	1.00	-61.03
MNTD	**Habitat**	4	368.37	0.00	0.95	0.95	-180.18
	Null	2	374.38	6.02	0.05	1.00	-185.19
sesMNTD	**Habitat**	4	127.40	0.00	0.96	0.96	-59.70
	Null	2	133.95	6.55	0.04	1.00	-64.98
ED	**Null**	2	264.92	0.00	0.86	0.86	-130.46
	Habitat	4	268.60	3.69	0.14	1.00	-130.30

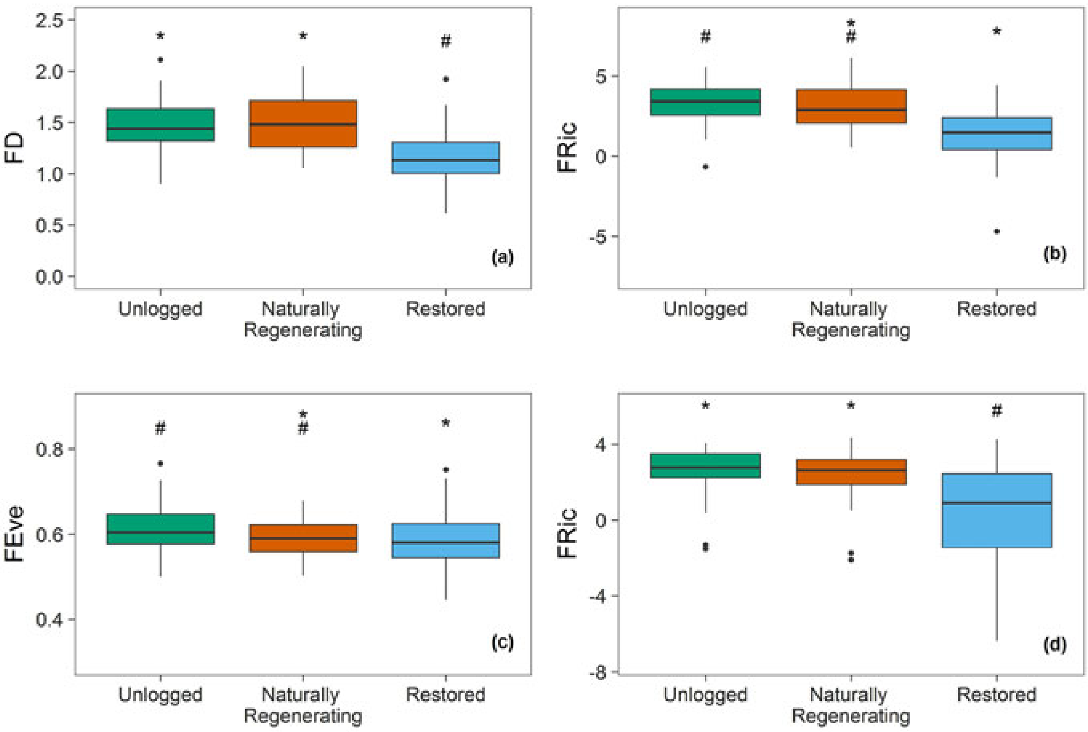
Functional Diversity

Response variable	**Model**	**K**	**AIC**	**ΔAIC**	**AICWt**	**Cum.Wt**	**LL**
FD	**Habitat**	4	-23.38	0.00	0.7	0.7	15.69
	Null	2	-21.66	1.72	0.3	1.0	12.83
FRic	**Habitat**	4	244.10	0.00	0.94	0.94	-118.05
	Null	2	249.73	5.64	0.06	1.00	-122.87
FEve	**Null**	2	-152.86	0.00	0.79	0.79	78.43
	Habitat	4	-150.25	2.61	0.21	1.00	79.12
FDiv	**Null**	2	-185.65	0.00	0.87	0.87	94.82
	Habitat	4	-181.82	3.82	0.13	1.00	94.91
FSpe	**Null**	4	33.23	0.00	0.56	0.56	-12.62
	Habitat	2	33.67	0.44	0.44	1.00	-14.84

FIG 1. Habitat effects on the phylogenetic diversity of the overall bird (**a – d**) and understorey bird (**e**, **f**) communities. (**a**) Phylogenetic diversity (PD); (**b**) Standard effect size of PD (sesPD); (**c**) Mean pairwise distance (MPD); (**d**) Standard effect size of MPD (sesMPD); (**e**) Mean nearest taxon distance (MNTD); (**f**) Standard effect size of MNTD (sesMNTD). The bottom and top of the boxplots represent the first and third quartiles, respectively, the bold line represents the median, and the points represent outliers. Different symbols indicate that there is a significant difference between the habitat types ($p<0.05$); similar symbols indicate no significant difference.

FIG 2. Habitat effects on the functional diversity of the overall bird (**a** – **c**) and understorey bird (**d**) communities. (**a**) Functional diversity (FD); (**b**) Functional richness (FRic); (**c**) Functional evenness (FEve); (**d**) Functional richness, understorey (FRic). FRic is logarithmic for visual clarity. The bottom and top of the boxplots represent the first and third quartiles, respectively, the bold line represents the median, and the points represent outliers. Different symbols indicate that there is a significant difference between the habitat types ($p<0.05$); similar symbols indicate no significant difference.


Overall birds
Understorey birds
PD (million years)
2000
1500
1000
500
*
*
#
(a)
sesPD
3
2
1
0
-1
-2
*
*
#
#
(b)
MPD (million years)
160
120
80
40
#
#
*
(c)
sesMPD
2
1
0
-1
-2
#
#
*
(d)
MNTD (million years)
70
60
50
40
30
*
#
*
(e)
sesMNTD
2
1
0
-1
-2
*
#
*
(f)
Unlogged
Naturally Regenerating
Restored



2.5
2.0
1.5
1.0
0.5
0.0
FD
*
*
#
(a)
Unlogged
Naturally Regenerating
Restored
5
0
-5
FRic
#
*
#
*
(b)
Unlogged
Naturally Regenerating
Restored
0.8
0.6
0.4
FEve
#
*
#
*
(c)
Unlogged
Naturally Regenerating
Restored
4
0
-4
-8
FRic
*
*
#
(d)
Unlogged
Naturally Regenerating
Restored