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Selective logging intensity in an East African rain forest predicts reductions in ant diversity

Samuel R. P.-J. Ross[1,2,3], **Francisco Hita Garcia**[1,4,6], **Georg Fischer**[1,4], and **Marcell K. Peters**[4,5]

[1] Okinawa Institute of Science and Technology, Onna-son, Kunigami, Okinawa 904-0495, Japan

[2] School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK

[3] Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland

[4] Zoological Research Museum Alexander Koenig, Adenauerallee 160, Bonn 53113, Germany

[5] Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am Hubland, Würzburg 97074, Germany

ABSTRACT

As natural forest ecosystems increasingly face pressure from deforestation, it is ever more important to understand the impacts of habitat fragmentation and degradation on biodiversity. Most studies of anthropogenic change in the tropics come from Southeast Asia and South America, and impacts of habitat modification are often taxon-specific. Here we empirically assessed the impact of habitat fragmentation and recent (within 25 yr) and historic (>25 yr ago) selective logging on the diversity of ants in the Kakamega rain forest in western Kenya, and asked whether these forms of degradation interact as multiple stressors. We found that the severity of recent selective logging was negatively related to overall species richness and abundance as well as the richness and abundance of forest specialists, but found no detrimental effect of past selective logging or habitat fragmentation on ant diversity, although habitat fragment size was correlated with estimated species richness. There was also no effect of any form of habitat degradation on the richness or abundance of open habitat specialists, even though these species often exploit niches created in disturbed environments. Ultimately, this study reveals the detrimental impact of even moderate forms of habitat degradation on insect biodiversity in the understudied African rain forests.

Key words: biodiversity; disturbance specialists; forest specialists; habitat degradation; habitat fragmentation; Kakamega forest; Kenya; multiple stressors.

THE LARGEST DRIVER OF BIODIVERSITY LOSS across the globe is habitat loss due to anthropogenic activity (Morris 2010, Laurance *et al.* 2014, Barlow *et al.* 2016). Understanding the consequences of this loss is a critical goal of conservation ecology, particularly in light of the important role that biodiversity plays in the stability and functioning of ecosystems (Hooper *et al.* 2005). Habitat fragmentation occurs when continuous habitats are split by roads, the expansion of settlements, agricultural land or similar dispersal barriers (Edwards *et al.* 2017). Within habitats, human modification of the abiotic or biotic environment can also reduce habitat quality, leading to changes in the structure and composition of biological communities (Morris 2010, Tylianakis *et al.* 2010, Gibson *et al.* 2011, Koerner *et al.* 2017). Selective logging is one such form of habitat degradation, whereby specific trees are targeted for extraction based on some pre-defined condition, resulting in a patchy removal of trees within habitats (Broadbent *et al.* 2008, Woodcock *et al.* 2011).

Habitat fragmentation and selective logging have frequently been shown to reduce biodiversity across a range of taxa (Heydon & Bulloh 1997, Ewers *et al.* 2015, Hamer *et al.* 2015, Ross *et al.* 2017). Yet these relationships may not be so one-dimensional; in some cases, habitat fragmentation and selective logging have been found to have neutral or even positive relationships with certain components of biodiversity, particularly after a recovery time of several decades (Azevedo-Ramos *et al.* 2006, Gunawardene *et al.* 2010, Edwards *et al.* 2013). This might be because ecosystems rarely face just one source of disturbance, and are often subject to multiple stressors that compound the effect of individual drivers on biodiversity (Laurance & Useche 2009, Barlow *et al.* 2016). Indeed, historic pressures may leave a footprint on biodiversity, even long after they cease (Dunn 2004, Gunawardene *et al.* 2010), but current conditions may be more critical in the structuring of ecological communities than such legacy effects (Edwards *et al.* 2012). Determining the degree to which these kinds of pressures interact as multiple stressors can help further elucidate the complex relationships between biodiversity and anthropogenic activity in an increasingly degraded world (Piggott *et al.* 2015).

These complex relationships may be better understood when breaking down communities into groups of species. For example, the response of habitat specialists may be different to that of generalist species, especially in cases of forest clearance, where forest specialists may lose niche space which can subsequently be exploited by generalists or open habitat specialists, often from outside the regional species pool (Farwig *et al.* 2008, Edwards *et al.* 2013, Morante-Filho *et al.* 2016). Discerning the degree to which different components of biodiversity are equally affected

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[6] Corresponding author; e-mail: fhitagarcia@gmail.com

TABLE 1. *List of 12 study sites and environmental variables in Kakamega forest. Sites are listed by name and have been assigned a Site ID (in brackets) which corresponds to the data in Fig. 1. Main/Fragment indicates whether a study site is part of the main forest patch or a smaller forest fragment. Fragment size represents the area of each forest fragment in ha. Minimum, mean and maximum distances to the main forest represent the distance of each fragment to the main forest in km (see Fig. S1—Online Supplementary Material); hence, there are no data for the sites which are part of the main forest patch. Past and recent selective logging indicate the number of trees logged/ha over 25 yr before the start of the study (past logging) or within 25 yr prior to the study (recent logging). For corresponding biodiversity variables, see Table S1—Online Supplementary Material.*

Site name (Site ID)	Main/Fragment	Fragment size (ha)	Minimum distance to main forest (km)	Mean distance to main forest (km)	Maximum distance to main forest (km)	Past Selective logging (trees/ha)	Recent Selective logging (trees/ha)
Buyangu (A)	Main	8245	–	–	–	5	4.1
Colobus (B)	Main	8245	–	–	–	2.9	2.3
Isecheno I (C)	Main	8245	–	–	–	0	12.5
Isecheno II (D)	Main	8245	–	–	–	0	9
Mwanzu (E)	Main	8245	–	–	–	2.9	2.3
Salazar (F)	Main	8245	–	–	–	2	0
Ikyuwa (G)	Fragment	1370	0.9	0.9	1.1	3.5	33.5
Kaimosi (H)	Fragment	65	6.3	6.7	7.1	0	30
Kisere (I)	Fragment	420	0.7	1.6	2.1	1.9	8.5
Malava East (J)	Fragment	113	5.1	5.4	6.6	3.8	5.4
Malava West (K)	Fragment	77	5.3	5.7	6.7	2.6	3.7
Yala (L)	Fragment	1178	1.8	2.1	2.7	1.3	1.5

by anthropogenic disturbance is therefore of interest when inferring community- or ecosystem-level responses to such disturbance (McIntyre & Lavorel 1994).

In this study, we empirically assessed patterns of ant diversity and abundance in an East African rain forest facing different levels of habitat fragmentation and degradation by past and recent selective logging. Ants (Hymenoptera: *Formicidae*) are a vital component of many terrestrial ecosystems, often comprising a large proportion of the total biomass of a system, and they are key indicators of ecosystem processing and functioning (Folgarait 1998, Andersen & Majer 2004, Dunn 2004). They also often make an important contribution to the establishment and structure of ecological communities through their role as ecosystem engineers (Philpott & Armbrecht 2006, Peters *et al.* 2013). Here we assess how habitat fragmentation and selective logging influence the taxonomic diversity and abundance of ants, as well as the diversity and abundance of forest versus open habitat specialists, to discern the degree to which compounded pressures may influence different elements of ant communities (Edwards *et al.* 2012).

METHODS

STUDY SITE.—Sampling took place in the Kakamega forest, a mid-altitudinal rain forest in western Kenya (Fig. S1—Online Supplementary Material), from May 2007 to August 2008. Forest fragments are surrounded by a densely populated agricultural matrix consisting mainly of structurally diverse subsistence farmland supporting maize, sugarcane and tea crops, as well as grassland, bush vegetation and young regrowth forest in some areas (Peters *et al.* 2009, Schleuning *et al.* 2011). The Kakamega forest has been intensively exploited by local communities, predominantly for firewood and timber, as well as through industrial logging operations, resulting in a reduction of forest area from ~25,000 ha at the end of the nineteenth century to ~12,000 ha in 2001 (Brooks *et al.* 1999, Mitchell *et al.* 2004, Mitchell & Schaab 2008). This exploitation has consisted mainly of illegal logging and timber extraction by a variety of groups, without any specific silvicultural techniques being used to reduce damage to surrounding vegetation (Bleher *et al.* 2006), and has persisted despite varying levels of protection since the 1930s (Blackett 1994, Espira 2001). All parts of the forest have been either historically logged (>25 yr before our study), or have been selectively logged in recent years (Mitchell *et al.* 2004). So Kakamega forest consists of a mix of disturbed primary forest and secondary forest which is either currently being exploited or not. At the time of sampling, the forest was highly fragmented, with a main forest patch of ~8245 ha and six surrounding forest fragments of varying size (see Table 1). All forest fragments are thought to have been isolated from the main forest patch for at least 35 yr (Mitchell & Schaab 2008) and are situated at elevations ~1550–1680 m above sea level.

SAMPLING METHODS.—At each site, one 200-m sampling transect was established, resulting in six transects within the main forest patch, and one each in the remaining six forest fragments (Fig. S1—Online Supplementary Material; Table 1). Each transect included 20 sampling positions separated by 10 m, and all started at least 50 m away from any trail, road or other contiguous habitat to minimize the influence of edge effects (Broadbent *et al.* 2008), although we note that the impact of edge effects is expected to be further reaching in smaller habitat fragments (Bradshaw 1992). To sample ant communities, a combination of pitfall trapping and leaf litter extraction techniques was applied since these methods together have been shown to effectively produce an unbiased sample of leaf litter and ground ant communities (Fisher 1999). Pitfall traps were placed on all sampling positions 5 m away from the transect. Pitfall traps were filled with 99 percent ethanol and after 7 d of operation all captured ants were collected. At every second sampling position, on the other side of the transect line, a 1 m² leaf litter sample was collected, sifted and transported for Winkler extraction following Bestelmeyer *et al.* (2000). Winkler samples were left to dry for 7 d in storeroom conditions.

Sampled ant material was processed following Lattke (2000). Identification effort was substantial in order to provide high taxonomic resolution for analysis. All mounted worker specimens were identified to genus level using Bolton (1994). Species-level identifications were performed using taxonomic literature for genera that had received a modern revision (see Hita Garcia *et al.* 2009, 2013, Fischer *et al.* 2012). For genera without an updated taxonomy, the sampled material was compared with reference and type material from the collections in natural history museums in London, Geneva, Los Angeles and San Francisco. If species identification was not possible, then specimens were sorted to morphospecies on the basis of external morphology. Additional hand-collected material allowed better assessment of intraspecific variation, such as polymorphisms and minor color variations, to avoid an artificially high number of poorly sorted morphospecies. Voucher specimens of all species listed in this study are deposited in the Hymenoptera collection of the Zoological Research Museum Alexander Koenig, Bonn, Germany.

ENVIRONMENTAL VARIABLES.—The environmental variables included in this study were forest fragment size and past and recent logging activity. Forest fragment sizes are taken from Peters *et al.* (2009) and were derived from on-screen visual interpretation of a Landsat-ETM7 satellite image, with digitizing and subsequent area calculations for the gained polygons all being performed in ArcGIS 8 (Esri, Redlands, California, U.S.A.). For the best distinction of forest types, a combination of the spectral bands 5/4/3 was used and contrast enhancement was included to improve the distinction between diverse forest formations. Mature forest was separated from the background that comprised of agricultural land, grassland and younger forest formations and plantations. Fragment size was included as a log-transformed continuous variable, but note that fragment size was identical for all six sites within the main forest patch. Yet these main forest sites are reasonable replicates considering the main forest patch is heterogeneous in structure, consisting of a mix of primary and secondary forest and because distances among sites within the main forest were rather large (see also Schleuning *et al.* 2011).

Both historic and recent selective logging activity were considered here to determine the extent to which biodiversity changes result from current or legacy effects (Vanderwoude *et al.* 2000, Gunawardene *et al.* 2010, Edwards *et al.* 2012). First, we used data on the past extent of selective logging in each site obtained from Bleher *et al.* (2006); disturbance surveys from 2002 to 2003 distinguished historic versus recent logging activity based on decomposition and shape of remaining stumps (see also Mutangah 1996). This allowed for measures of past logging, *i.e.*, logging activity which occurred more than 25 yr prior to our study, and recent logging, *i.e.*, logging activity occurring within 25 yr of our study. Hence, we used data on past extent of selective logging as the number of trees per hectare that had been logged more than 25 yr before our study. Second, we used data on recent logging activity as the number of trees that had been logged within 25 yr of the beginning of our study (Bleher *et al.* 2006). The extent of historic selective logging varied among sites, but was generally small (mean = 2.2 trees/ha ± 1.6 S.D.), whereas recent logging activity appears more intense in many cases, although there are considerable differences between sites (mean = 9.4 trees/ha ± 11.1 S.D.). Indeed, these between-site differences have been shown to reflect differences in the management regimes of sites (Bleher *et al.* 2006), with many of the well-protected sites having lower logging intensity in recent years than historically. All environmental variables are provided in Table 1.

BIODIVERSITY MEASUREMENT.—Patterns of ant taxonomic diversity were analyzed using empirically observed species richness, calculated expected species richness and total abundance across all species in the study, as well as the observed richness and abundance of forest habitat specialists, and of open habitat specialist species found across our sites (see Table S1—Online Supplementary Material for a list of biodiversity values across sites). We measured observed species richness as the total number of species sampled for a given site (transect) after processing 20 pitfall traps and 10 Winkler samples per site. As empirically observed species richness often represents only a biased subsample of the real community composition found in nature (Longino 2000), we calculated expected species richness for each site using the Chao2 method in EstimateS (Colwell 2009, Table S1—Online Supplementary Material) since this is an incidence-based estimator—*i.e.*, capable of handling presence/absence data—which has on several occasions been shown to have low bias compared to other species richness estimators through empirical comparisons (*e.g.*, Colwell & Coddington 1994, Walther & Morand 1998).

Measuring ant abundance is often problematic because in the wild, strong spatial aggregation due to the eusocial nature of ant species results in sampling methods often collecting colonies or colony parts (Gotelli *et al.* 2011). This can lead to a misrepresentation of community composition and relative abundance (Longino 2000). To avoid this problem, we calculated ‘abundance’ as the frequency of species occurrence at the 20 sampling locations per transect, such that species can have abundance values between 0 and 20. The abundances—*i.e.*, occurrence frequencies (0–20) along the transect—of all species found at each site were summed to produce overall ant abundance per site, with a presence of a species in a pitfall and/or Winkler sample counting as a single occurrence for those sampling points measured by both techniques. These biodiversity measures were taken first for all ant species identified in the study ($N = 106$), then for two subsets of data.

The species data for this study represent a subset of a significantly larger dataset based on an intensive sampling inventory of the local ant community undertaken from 2001 to 2010. Ants were collected from all habitats and microhabitats by different leaf litter sifting (1000+ Winkler samples), pitfall trapping (2000+ traps), canopy fogging (200+ trees), above-ground baiting (tuna, honey, insects), subterranean baiting (oil and fat) and numerous hand collections events. Using these data (see Table S2—Online Supplementary Material), we were confidently able to classify species as either habitat generalists or specialists—primarily being associated with either forest or open habitats. The first subset we considered included only species which occurred predominantly or solely in forest habitat, herein termed 'forest specialists' ($N = 90$). Second, we measured the richness and abundance of 'open habitat specialists' ($N = 12$)—defined here as species which had been previously sampled mainly or exclusively in agricultural sites or open habitats—since open habitat specialism is in some cases synonymous with disturbance exploitation specialism (*e.g.*, Hoffmann & Andersen 2003). We then tested the effect of our environmental variables on biodiversity measures of these three groups: all species, forest specialists and open habitat specialists (see below).

STATISTICAL ANALYSIS.—All analyses were performed in R v. 3.3.2 (R Core Team, 2016) using the packages MASS (v. 7.3-45; Venables & Ripley 2002) and Vegan (v. 2.4-2; Oksanen *et al.* 2017). We fit generalized linear models (GLMs) to evaluate which factors best predicted the following response variables: observed species richness (S), expected species richness (E), total ant abundance (N), forest specialist species richness (S_F), forest specialist species abundance (N_F), open habitat specialist species richness (S_O) and open habitat specialist species abundance (N_O). As data values were generally high, model residuals were normally distributed and variances appeared to be homogeneous, so a Gaussian rather than a Poisson error distribution was used in all GLMs to model the data. For each of our diversity estimates, we tested GLMs with combinations of the predictor variables habitat fragmentation and intensity of past and recent selective logging. Stepwise model selection was performed by dropping terms from an initial model with a three-way interaction between habitat fragmentation and the two measures of logging activity. Minimum adequate models (MAMs) were identified using Akaike's information criterion with small sample correction (AICc). AICc is based in information theory and evaluates models based on model fit and model complexity; when comparing a series of models, the one with the lowest AIC value is considered the best (Burnham & Anderson 2004). Significance of model terms included in the MAM was assessed using likelihood ratio tests (LRTs) when terms were dropped from the model. Significance of all other terms was assessed by adding terms to the MAM. Spearman's rank correlation coefficients, chosen for conservativeness, were calculated for all combinations of predictor variables to test for covariation. If correlation coefficients were between -0.5 and 0.5 for two predictor variables, these variables were treated as uncorrelated in models.

To test whether spatial autocorrelation was affecting model results, we calculated Moran's *I* values from residuals of models and the geographic coordinates of study sites (Bjørnstad *et al.* 1999). Moran's *I* significance was determined through the use of a permutation test with 1,000 permutations. Tests of spatial autocorrelation indicated no signs of spatial autocorrelation for all tested models (Moran's I mean $= -0.024$, $P > 0.05$ for distance classes up to 4.35 km). We thus concluded that spatial processes were not significantly influencing our results.

To assess the degree to which habitat fragmentation and selective logging influence ant community composition, we performed 1000 nonmetric multidimensional scaling analyses (NMDS) based on Bray-Curtis dissimilarity (Faith *et al.* 1987) to maximize the likelihood of model convergence and reduce minimum stress values. NMDS is an ordination technique which represents a multidimensional distance matrix in reduced-dimension space. Here, the distance matrix being displayed is that of community dissimilarity among sites, as described above. We then took the output with the lowest stress value and fit and tested the environmental predictor variables: habitat fragment size, recent intensity of selective logging and past intensity of selective logging, in combination and alone, on the ordination by performing 10,000 permutations of a permutational multivariate analysis of variance (PERMANOVA) test, implemented in the *adonis* function of the R package *vegan*, using distance measures to determine significance (Clarke 1993). Significant values would suggest that sites support significantly different ant communities.

Nestedness analyses were used to determine the degree to which communities with lower species richness contained a nested subset of those species found in more species-rich sites. We tested for community nestedness of species occurrence using the checkerboard approach, a commonly used metric of community nestedness based on a 'checkerboard' of 2 × 2 community submatrices (see Stone & Roberts 1990). The significance of nestedness was then tested using a null model approach—the 'quasiswap' method (Miklós & Podani 2004). This method involves randomly filling matrices ($N = 100$) whilst honoring row and column totals, and performing quasiswaps on 2 × 2 submatrices. We chose to preserve marginal totals by not allowing the production of values greater >1 during swapping, as this considerably reduces the chance of type I error and increases the conservativeness of the model (Miklós & Podani 2004).

RESULTS

A total of 70,711 ant specimens from 240 pitfall traps and 120 Winkler bags were processed and identified to 106 species from 31 genera and 7 subfamilies (see Table S2—Online Supplementary Material for list of all species identified in the study). Due to the sampling methodology, the vast majority of species yielded in this study were ground and/or leaf litter ants, whereas arboreal and strictly subterranean ants were seldom collected. Most of the ants sampled live in relatively small colonies, nest in leaf litter, rotten sticks or logs or in the soil, and forage in or above the leaf litter stratum (F. Hita Garcia & G. Fischer, pers. obs.). A few

TABLE 2. *Relationships between environmental predictors and biodiversity variables. The minimum adequate model (MAM) when testing the effects of three environmental variables (habitat fragment size, recent logging intensity and past logging intensity) on biodiversity values is given. MAMs were identified based on AICc values via stepwise removal of nonsignificant terms from the full three-way interactive model and Likelihood ratio tests were used to assess the significance of dropped terms. In all cases, MAMs had δ AICc values of 0, and we did not identify any closely competing models (*i.e. *those with δ AICc < 2). Results show L Ratio values when removing significant terms from the model. MAM and* P *values are given for significant models only; nonsignificant results are marked with 'N.S.' Significance level is represented with * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.005$). Sample level represents the subsample of the data used: all species = the biodiversity of all species in the study, forest specialists = only those species found primarily in forests and open habitat specialists = those species found primarily in agriculture or open habitats (identified as part of a larger study, see above). Fragment size represents the size in hectares of the forest fragment in which each site was situated (see Peters* et al. *2009). Recent logging intensity represents the number of trees logged/ha in the 25 yr immediately prior to our study. All environmental variables were $\log_{10}$ transformed for use in models.*

Sample level	Biodiversity measure	Minimum adequate model term(s)	Minimum adequate model significance
All species	Observed species richness	Recent Logging Intensity	L.Ratio = 8.84, $P < 0.005$***
	Expected species richness	Habitat Fragment Size	L.Ratio = 7.50, $P = 0.006$**
	Total species abundance	Recent Logging Intensity	L.Ratio = 4.99, $P = 0.026$*
Forest specialists	Observed species richness	Recent Logging Intensity	L.Ratio = 8.43, $P < 0.005$***
	Total species abundance	Recent Logging Intensity	L.Ratio = 6.27, $P = 0.012$*
Open habitat specialists	Observed species richness	None	N.S.
	Total species abundance	None	N.S.

species such as some *Pheidole* Westwood, *Tetramorium* Mayr, or the army ants of the genus *Dorylus* Fabricius are very abundant and may be ecologically dominant, but this remains somewhat speculative. On the basis of preliminary stable isotope analyses, it appears that most species have a predominantly predatory diet (S.R.P-J. Ross, pers. obs.).

The highest observed species richness ($S = 63$) and total abundance ($N = 356$) were observed in the main forest Salazar site, which has the lowest overall past + recent logging intensity (see Table 1), whilst the lowest observed species richness ($S = 47$) and total abundance ($N = 187$) were recorded in the smallest forest fragment, Kaimosi, which has the second highest overall logging intensity, driven entirely by recent logging within the 25 yr prior to our study. Kaimosi also had the lowest recorded richness ($S = 42$) and total abundance ($N = 177$) of forest specialist species, but only ten individuals of five species made up the remaining ant diversity at this site. Open habitat specialists were much less common across all sites, and where present were often found as singletons or at very low abundance (see Table S2—Online Supplementary Material).

Spearman's rank correlations found no significant correlations between any combinations of predictor variable. That is, habitat fragment size was not correlated with either recent intensity of selective logging (Spearman's $\rho_{12} = -0.28$, $P = 0.38$) or past selective logging intensity (Spearman's $\rho_{12} = -0.09$, $P = 0.77$), and past and recent intensities of selective logging were also suitably independent of each other in models (Spearman's $\rho_{12} = -0.21$, $P = 0.52$). When modeling environmental variables against biodiversity measures, we found that most biodiversity measures were best explained by recent selective logging intensity alone (see Table 2). The minimum-adequate model selected by AICc only included recent selective logging intensity as a predictor variable to explain observed species richness of all species (GLM: L.Ratio = 8.84, $P < 0.005$), the species richness of forest specialists (GLM: L.Ratio = 8.43, $P < 0.005$; Fig. 1B), as well as the total abundance of all species (GLM: L.Ratio = 4.99, $P = 0.025$) and the abundance of forest specialists (GLM: L.Ratio = 6.27, $P < 0.005$; Fig. 1D). Habitat fragment size alone predicted the expected richness of all species in our study (GLM: L.Ratio = 7.5, $P = 0.006$). Conversely, there were no significant effects of our tested environmental variables on the richness (GLM: L.Ratio = 1.27, $P = 0.26$; Fig. 1A, B) or abundance (GLM: L.Ratio = 0.86, $P = 0.35$; Fig. 1C, D) of open habitat specialist ant species.

COMMUNITY COMPOSITION.—The permutational multivariate analysis of variance using distance measures (PERMANOVA) employed to discern the degree to which our environmental variables explained any observed differences in ant community composition found no significant results when testing environmental variables in isolation. There was no significant effect of forest fragment size on community composition based on this method (PERMANOVA: $F = 0.803$, $P = 0.675$) and little separation between intact and fragmented forest communities when visualized in reduced dimension space based on NMDS analysis (see Fig. 2). It should be noted that with a relatively low stress value of 0.14, we can be confident that the observed ordination was a fair representation of the community dissimilarity matrix. Similarly, we found no significant influence of the past extent of selective logging (PERMANOVA: $F = 1.09$, $P = 0.373$) or the recent extent of selective logging on community composition (PERMANOVA: $F = 1.3$, $P = 0.206$; see point sizes in Fig. 2). The observed (albeit marginal) differences in community composition were however significantly explained more clearly by an

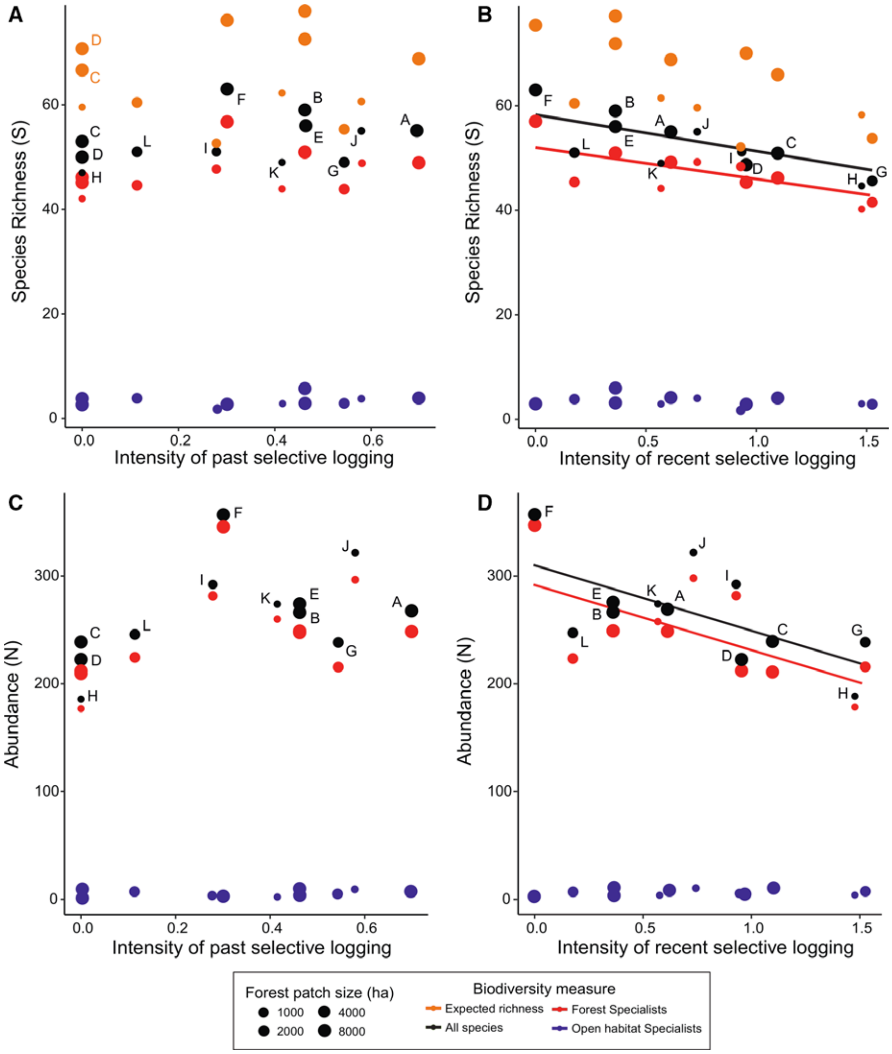

FIGURE 1. (A) Relationship between species richness and the intensity of past selective logging across each of 12 sites. (B) Relationship between species richness and the intensity of recent selective logging across each of 12 sites. (C) Relationship between observed ant abundance and the intensity of past selective logging across each of 12 sites. (D) Relationship between observed ant abundance and the intensity of recent selective logging across each of 12 sites. In all panels, point size represents the untransformed habitat fragment size in hectares. Trend lines are linear trend lines highlighting significant results based on the minimum adequate model for each biodiversity measure (see above). The intensity of past logging is measured as the number of trees logged/ha over 25 yr before the start of this study, whereas intensity of recent logging is the number of trees logged/ha within the 25 yr prior to the start of this study. In all cases, letters correspond to site IDs (see Table 1) and logging intensities (*x*-axis values) are $\log_{10}$ transformed; see Table 1 for raw values of past and recent logging intensity.

interactive model incorporating both historic logging activity (>25 yr prior to our study) and habitat fragment size (PERMANOVA: $F = 2.23$, $P = 0.017$; Fig. 2), suggesting that multiple stressors may be interacting to shape ant community composition in minor ways, despite these stressors not interacting to influence ant taxonomic diversity. Our nestedness analysis based on quasiswapping submatrices of 100 null models revealed possible evidence for nestedness of our communities (Nestedness Test_{100}: C-score = 2.564, $P = 0.069$). This would suggest that the species poor communities in our study are indeed likely to be a nested subset of those found in sites with higher taxonomic richness, which clarifies our finding that community composition largely did not differ among sites.

DISCUSSION

This study compares ant communities and patterns of habitat fragmentation and historic and recent selective logging in Kakamega forest, western Kenya. Studies often address similar questions for taxa in Southeast Asia (see for example Ewers *et al.* 2015, Edwards *et al.* 2017) but less frequently assess the impacts of global change in the African tropics (but see Peters *et al.* 2008, Schleuning *et al.* 2011), and rarely do studies investigate the combined effect of both habitat fragmentation and degradation on biodiversity as possible multiple stressors (Barlow *et al.* 2016). We found that various components of ant taxonomic diversity were lower in recently logged areas, and that this effect outweighed

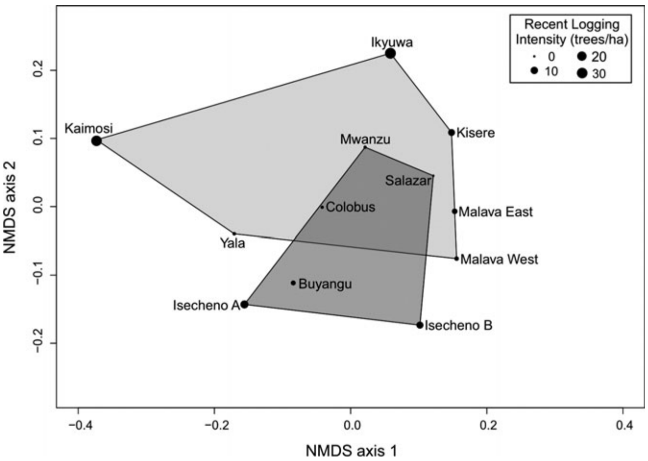

FIGURE 2. Nonmetric multidimensional scaling ordination plot (stress = 0.141) of ant community composition across 12 study sites based on Bray-Curtis dissimilarities. Polygons are fit around all six communities in the main, unfragmented forest habitats (dark grey polygon) and the six fragmented habitats of varying fragment size (light grey polygon, see Table 1 for details). Data point size indicates the recent intensity of selective logging based on the log-transformed number of trees logged/ha in the last 25 yr, such that larger data points represent greater past logging pressure (see legend for details).

that of habitat fragmentation and any legacy effects of past logging activity, except in the case of expected richness. Critically, we found that more intensive recent selective logging was related to communities with lower abundance and diversity of ants—particularly in the case of forest specialists—but that there were no differences among open habitat specialist ants under different disturbance regimes (Table 2, Fig. 1).

With logging pressure increasingly threatening natural forest ecosystems globally, unraveling the impacts of selective logging and habitat fragmentation on biodiversity is more important than ever before (Asner *et al.* 2005). Our study adds to the growing body of literature evidencing a negative effect of selective logging on taxonomic diversity and abundance in the understudied tropical region of East Africa (Peters *et al.* 2008, 2011, Schleuning *et al.* 2011). We found that ant communities in sites with a higher extent of selective logging had lower taxonomic diversity in most cases. Specifically, these communities had lower observed species richness and abundance of all species in our study, as well as lower observed richness and abundance of the forest specialists identified here. These findings align well with similar studies on selective logging and diversity of ants (*e.g.*, Peters *et al.* 2011, Edwards *et al.* 2012), mammals (*e.g.*, Heydon & Bulloh 1997, Chapman *et al.* 2000) and birds (*e.g.*, Peters *et al.* 2008, Edwards *et al.* 2013) across Africa, South America and Southeast Asia (see also Gibson *et al.* 2011, Newbold *et al.* 2015). Interestingly, however, we found no relationship between selective logging and habitat fragmentation on the richness or abundance of open habitat specialist ants in our samples. In accordance with a range of empirical work, this points to a high sensitivity of forest specialists to even moderate forms of habitat degradation (see Thiollay 1999, Farwig *et al.* 2008, Edwards *et al.* 2013, Morante-Filho *et al.* 2016). Ultimately, this suggests that in degraded forests, habitat generalists or invading open habitat specialists cannot compensate for a loss of forest specialists.

Since both habitat fragmentation and selective logging alone have been shown to impact biodiversity in a range of systems, it could be expected *a priori* that in systems where selective logging and habitat fragmentation both occur, these pressures combine to further influence biodiversity (Laurance & Useche 2009). We found little evidence that ant community diversity was shaped additively or interactively by selective logging and habitat fragmentation (see also Vanderwoude *et al.* 2000). We did not reveal an influence of habitat fragmentation in this system, with many species—including forest habitat specialists—occurring in even the smallest of these forest fragments. This is perhaps unsurprising because even the smallest fragments of this study were still quite large (>65 ha), *i.e.*, considerably larger than the smallest size classes tested in most other studies finding negative effects of habitat fragmentation on insects (see for example Nichols *et al.* 2007).

Our finding that the marginal differences among communities in their composition were best explained by an interaction between historic logging intensity and habitat fragment size is perhaps unsurprising considering that many studies report a strong negative effect of forest fragmentation on habitat specialists (*e.g.*, Farwig *et al.* 2008, Edwards *et al.* 2013). Yet community composition did not differ significantly among the main forest and forest fragments (Fig. 2). Indeed, we largely found no difference in community composition even among sites with differing species richness. This is because the species-poor sites within Kakamega were likely composed of a nested subset of those species from sites with higher ant diversity, suggesting that any effects of disturbance on ant communities in Kakamega occur by limiting the persistence of species already present in the community, rather than through changes to community composition. The fact that our main forest patch communities did not differ significantly in community composition to our forest fragments contrasts previous work finding that environmental filtering results in forest specialists being systematically replaced by more open habitat species, with studies often reporting permanent changes to community composition following logging (*e.g.*, Vasconcelos *et al.* 2000, Gunawardene *et al.* 2010). Nonetheless, we found that the diversity and abundance of forest specialists were more likely to be related to habitat degradation than open habitat specialists, a finding supported by past studies on the vulnerability of forest specialists (Farwig *et al.* 2008, Morante-Filho *et al.* 2016, see also Miranda *et al.* 2017).

Our study is limited by its size; with 12 transects, we cannot exclude the possibility that several extreme values may be driving observed patterns of biodiversity. Yet, when testing the effect of recent logging with the six most extreme abundance values removed, we still revealed a significant relationship between recent logging activity and total species abundance (results not shown), suggesting that extreme values are likely not the main drivers of the patterns observed here. Our categorization of habitat specialism also leaves a few widely distributed habitat generalist species explicitly unaccounted for ($N = 4$), except for within 'total' species richness and abundance. Further, our communities contained many fewer open habitat specialists than forest specialists, potentially reducing our ability to detect differences among open habitat specialists. Although these groups of species are few in number, they may still contribute significantly to the overall biomass and in turn to the functioning of this community (Tilman *et al.* 2006). Though we test patterns of ant diversity among sites that differ in their histories of habitat fragmentation and selective logging intensity, other human activity is inherently more difficult to measure (*e.g.*, small-scale firewood removal), so the degree to which these activities differ between sites and in turn may influence biodiversity remains unclear (Schleuning *et al.* 2011).

The contribution of historic and recent logging activity to biodiversity may not be easy to disentangle, as selective logging can lead to positive legacy effects (Azevedo-Ramos *et al.* 2006), whereas recent logging activity is likely to detrimentally reorganize ecological communities (Ewers *et al.* 2015). Although our data appear to show a slight and nonsignificant positive relationship between taxonomic richness and historic logging intensity (Fig. 1) and an interactive effect of historic logging intensity and habitat fragment size on community composition (Fig. 2), we believe that the effects of recent and current logging activity may overshadow potential legacy effects in this system. Yet, determining the effect of habitat degradation on communities is inherently difficult without pre-disturbance data. For systems such as Kakamega forest which have undergone much historic disturbance, we can only indirectly infer that current patterns of diversity have been shaped by land use change. This may be a widespread issue, with many areas of the world having long histories of disturbance (Morris 2010, Laurance *et al.* 2014). Studies such as ours may thus contribute to our understanding of disturbance regimes by comparing communities under different current and historic levels of disturbance.

Studies often detail changes in community composition but not in richness or abundance in response to selective logging (*e.g.*, Vasconcelos *et al.* 2000), highlighting the novelty of our findings. Further, our results may have implications for ecosystem functioning since ants are important and functionally diverse components of the tropical rain forest food webs (Hoffmann & Andersen 2003, Andersen & Majer 2004). We did not empirically measure the contribution of ant groups to ecosystem functioning, so we cannot directly infer that our findings have knock-on impacts on ecosystem functioning. However, it seems likely that if recent logging activity is shaping abiotic conditions and ecological community structure—at least of ants—then some aspect of ecosystem functioning may be compromised either now or in future with the continued degradation of these habitats (Naeem *et al.* 1994, but see Edwards *et al.* 2013).

In conclusion, our study supports much past empirical work by documenting differences in biodiversity among sites of varying selective logging intensities (Peters *et al.* 2008, 2011, Schleuning *et al.* 2011, Edwards *et al.* 2013, Barlow *et al.* 2016). We revealed a differential relationship between recent selective logging intensity and forest versus open habitat specialists, with the abundance and richness of forest ants declining with increasing recent logging intensity, Yet, this is likely not the whole picture. For conservation practices to more efficiently maximize biodiversity protection in East Africa, we must consider not only the impacts of selective logging and habitat fragmentation on biodiversity, but also the impact of other anthropogenic land-uses, as agricultural areas continue to expand and replace natural habitats (Laurance *et al.* 2014, Kuppler *et al.* 2015, Newbold *et al.* 2015). Additionally, to better understand how well these ecosystems are functioning under mounting anthropogenic pressure, we should turn our attention to the functional component of biodiversity which has the potential to reveal patterns of biodiversity that cannot be gleaned from taxonomic diversity alone (McGill *et al.* 2006, Hillebrand *et al.* 2018). However, where this information is not available, studies like ours that assess patterns of taxonomic diversity under global change should continue to be of value for conservation management.

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DATA AVAILABILITY

The ant biodiversity data collected and used in this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8hq75j7 (Ross *et al.* 2018) and habitat affinity data are available in Table S2—Online Supplementary Material. Voucher specimens of all species listed in this study are deposited in the Hymenoptera collection of the Zoological Research Museum Koenig, Bonn, Germany.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *List of 12 study sites and biodiversity values in Kakamega forest.*

Table S2. Species list with habitat affinity data (see main text). Data are based on a large sampling effort from across the kakamega region: forest specialists were found primarily (almost exclusively) within Kakamega forest; open habitat specialists were found primarily in the surrounding agricultural land; and habitat generalists did not appear to have a clear preferenc for either habitat based on occurrence data.

FIGURE S1. Map of the study site.

FIGURE S2. GLM model residuals for minimum adequate models.

LITERATURE CITED

Andersen, A. N., and J. D. Majer. 2004. Ants show the way Down Under: Invertebrates as bioindicators in land management. Front. Ecol. Environ. 2: 291–298.

Asner, G. P., D. E. Knapp, E. N. Broadbent, P. J. C. Oliveira, M. Keller, and J. N. Silva. 2005. Selective logging in the Brazilian Amazon. Science 310: 480–482.

Azevedo-Ramos, C., O. de Carvalho, and B. D. do Amaral. 2006. Short-term effects of reduced-impact logging on eastern Amazon fauna. Forest Ecol. Manag. 232: 26–35.

Barlow, J., G. D. Lennox, J. Ferreira, E. Berenguer, A. C. Lees, R. Mac Nally, J. R. Thomson, S. F. Ferraz, J. Louzada, V. H. Oliveira, L. Parry, R. R. Solar, I. C. Vieira, L. E. Aragão, R. A. Begotti, R. F. Braga, T. M. Cardoso, R. C. de Oliveira, Souza. C. M. Jr, Jr, N. G. Moura, S. S. Nunes, J. V. Siqueira, R. Pardini, J. M. Silveira, F. Z. Vaz-de-Mello, R. C. Veiga, A. Venturieri, and T. A. Gardner. 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature 535: 144–147.

Bestelmeyer, B. T., D. Agosti, L. E. Alonso, C. R. F. Brandao, W. L. Brown, J. H. C. Delabie, and R. Silvestre. 2000. Field techniques for the study of ground-dwelling ants. *In* D. Agosti, J. D. Majer, L. Alonso, and T. R. Schultz (Eds.). Ants: Standard methods for measuring and monitoring biodiversity, pp. 122–144. Smithsonian Institution Press, Washington, DC.

Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: Analyzing patterns and processes of population synchrony. Trends Ecol. Evol. 14: 427–432.

Blackett, H. L. 1994. Forest Inventory Report No. 3: Kakamega. Forest Department/Kenya Indigenous Forest Conservation Programme (KIFCON), Nairobi, Kenya.

Bleher, B., D. Uster, and T. Bergsdorf. 2006. Assessment of threat status and management effectiveness in Kakamega Forest, Kenya. Biodiv. Conserv. 15: 1159–1177.

Bolton, B. 1994. Identification guide to the ant genera of the world. Harvard University Press, Cambridge.

Bradshaw, F. J. 1992. Quantifying edge effect and patch size for multiple-use silviculture—a discussion paper. Forest Ecol. Manag. 48: 249–264.

Broadbent, E. N., G. P. Asner, M. Keller, D. E. Knapp, P. J. C. Oliveira, and J. N. Silva. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biol. Conserv. 141: 1745–1757.

Brooks, T. M., S. L. Pimm, and J. O. Oyugi. 1999. Time lag between deforestation and bird extinction in tropical forest fragments. Conserv. Biol. 13: 1140–1150.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociol. Methods Res. 33: 261–304.

Chapman, C. A., S. R. Balcomb, T. R. Gillespie, J. P. Skorupa, and T. T. Struhsaker. 2000. Long-term effects of logging on African primate communities: A 28-year comparison from Kibale National Park, Uganda. Conserv. Biol. 14: 207–217.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Austral Ecol. 18: 117–143.

Colwell, R. K. 2009. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2. User's Guide and application published at: http://purl.oclc.org/estimates

Colwell, R. K., and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *In* D. L. Hawksworth (Ed.). Biodiversity: Measurement and estimation, pp. 101–116. Chapman & Hall in Association with The Royal Society, London.

Dunn, R. R. 2004. Managing the tropical landscape: A comparison of the effects of logging and forest conversion to agriculture on ants, birds, and lepidoptera. Forest Ecol. Manag. 191: 215–224.

Edwards, F. A., D. P. Edwards, K. C. Hamer, and R. G. Davies. 2013. Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland. The Ibis 155: 313–326.

Edwards, F. A., J. Finan, L. K. Graham, T. H. Larsen, D. S. Wilcove, W. W. Hsu, V. K. Chey, and K. C. Hamer. 2017. The impact of logging roads on dung beetle assemblages in a tropical rainforest reserve. Biol. Conserv. 205: 85–92.

Edwards, D. P., P. Woodcock, F. A. Edwards, T. H. Larsen, W. W. Hsu, S. Benedick, and D. S. Wilcove. 2012. Reduced-impact logging and biodiversity conservation: A case study from Borneo. Ecol. Appl. 22: 561–571.

Espira, A. 2001. Variations in the ground ant communities of Kakamega Forest, Western Kenya: Potential indicators of forest disturbance. University of Oxford, Oxford.

Ewers, R. M., M. J. W. Boyle, R. A. Gleave, N. S. Plowman, S. Benedick, H. Bernard, T. R. Bishop, E. Y. Bakhtiar, V. K. Chey, A. Y. C. Chung, R. G. Davies, D. P. Edwards, P. Eggleton, T. M. Fayle, S. R. Hardwick, R. Homathevi, R. L. Kitching, M. S. Khoo, S. H. Luke, J. J. March, R. Nilus, M. Pfeifer, S. V. Rao, A. C. Sharp, J. L. Snaddon, N. E. Stork, M. J. Struebig, O. R. Wearn, K. M. Yusah, and E. C. Turner. 2015. Logging cuts the functional importance of invertebrates in tropical rainforest. Nat. Commun. 6: 6836.

Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69: 57–68.

Farwig, N., N. Sajita, and K. Böhning-Gaese. 2008. Conservation value of forest plantations for bird communities in western Kenya. Forest Ecol. Manag. 255: 3885–3892.

Fischer, G., F. Hita Garcia, and M. K. Peters. 2012. Taxonomy of the ant genus *Pheidole* Westwood (Hymenoptera: Formicidae) in the Afrotropical zoogeographic region: Definition of species groups and systematic revision of the *Pheidole pulchella* group. Zootaxa 3232: 1–43.

Fisher, B. L. 1999. Improving inventory efficiency: A case study of leaf litter ant diversity in Madagascar. Ecol. Appl. 9: 714–731.

Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: A review. Biodivers. Conserv. 7: 1221–1244.

Gibson, L., T. M. Lee, L. P. Koh, B. W. Brook, T. A. Gardner, J. Barlow, C. A. Peres, C. J. Bradshaw, W. F. Laurance, T. E. Lovejoy, and N. S. Sodhi. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478: 378–381.

Gotelli, N. J., A. M. Ellison, R. R. Dunn, and N. J. Sanders. 2011. Counting ants (Hymenoptera: Formicidae): Biodiversity sampling and statistical analysis for myrmecologists. Myrmecol. News 15: 13–19.

Gunawardene, N. R., J. D. Majer, and J. P. Edirisinghe. 2010. Investigating residual effects of selective logging on ant species assemblages in Sinharaja Forest Reserve, Sri Lanka. Forest Ecol. Manag. 259: 555–562.

Hamer, K. C., R. J. Newton, F. A. Edwards, S. Benedick, S. H. Bottrell, and D. P. Edwards. 2015. Impacts of selective logging on insectivorous birds in Borneo: The importance of trophic position, body size and foraging height. Biol. Conserv. 188: 82–88.

Heydon, M. J., and P. Bulloh. 1997. Mousedeer densities in a tropical rainforest: The impact of selective logging. J. Appl. Ecol. 34: 484–496.

Hillebrand, H., B. Blasius, E. T. Borer, J. M. Chase, J. Downing, B. K. Eriksson, C. T. Filstrup, W. S. Harpole, D. Hodapp, S. Larsen, and A. M. Lewandowska. 2018. Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. J. Appl. Ecol. 55: 169–184. https://doi.org/10.1111/1365-2664.12959

Hita Garcia, F., G. Fischer, M. K. Peters, R. R. Snelling, and J. W. Wägele. 2009. A preliminary checklist of the ants (Hymenoptera: Formicidae) of Kakamega Forest (Kenya). J. East African Nat. Hist. 98: 147–165.

Hita Garcia, F., E. Wiesel, and G. Fischer. 2013. The Ants of Kenya (Hymenoptera: Formicidae)—Faunal overview, first species checklist, bibliography, accounts for all genera, and discussion on taxonomy and zoogeography. J. East African Nat. Hist. 101: 127–222.

Hoffmann, B. D., and A. N. Andersen. 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. Austral Ecol. 28: 444–464.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, and B. Schmid. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol. Monogr. 75: 3–35.

Koerner, S. E., J. R. Poulsen, E. Blanchard, J. Okouyi, and C. J. Clark. 2017. Vertebrate community composition and diversity declines along a defaunation gradient radiating from rural villages in Gabon. J. Appl. Ecol. 54: 805–814.

Kuppler, J., J. Fricke, C. Hemp, I. Steffan-Dewenter, and M. K. Peters. 2015. Conversion of savannah habitats to small-scale agriculture affects grasshopper communities at Mt. Kilimanjaro, Tanzania. J. Insect Conserv. 19: 509–518.

Lattke, J. E. 2000. Specimen processing - building and curating an ant collection. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz (Eds.). Ants: Standard methods for measuring and monitoring biodiversity, pp. 155–170. Smithsonian Press, Washington, DC.

Laurance, W. F., J. Sayer, and K. G. Cassman. 2014. Agricultural expansion and its impacts on tropical nature. Trends Ecol. Evol. 29: 107–116.

Laurance, W. F., and D. C. Useche. 2009. Environmental synergisms and extinctions of tropical species. Conserv. Biol. 23: 1427–1437.

Longino, J. T. 2000. What to do with the data. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz (Eds.). Ants: Standard methods for measuring and monitoring biodiversity, pp. 186–203. Smithsonian Institution Press, Washington, DC.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21: 178–185.

McIntyre, S., and S. Lavorel. 1994. Predicting richness of native, rare, and exotic plants in response to habitat and disturbance variables across a variegated landscape. Conserv. Biol. 8: 521–531.

Miklós, I., and J. Podani. 2004. Randomization of presence-absence matrices: Comments and new algorithms. Ecology 85: 86–92.

Miranda, P. N., F. B. Baccaro, E. F. Morato, M. A. Oliveira, and J. H. C. Delabie. 2017. Limited effects of low-intensity forest management on ant assemblages in southwestern Amazonian forests. Biodivers. Conserv. 26: 2435–2451.

Mitchell, N., B. Bleher, and H. Dalitz. 2004. BIOTA East Report No. 1 – The exploitation and disturbance history of Kakamega Forest, Western Kenya. Bielefelder Ökologische Beiträge 20: 1–75.

Mitchell, N., and G. Schaab. 2008. Developing a disturbance index for five East African forests using GIS to analyse historical forest use as an important driver of current land use/cover. Afr. J. Ecol. 46: 572–584.

Morante-Filho, J. C., V. Arroyo-Rodríguez, and D. Faria. 2016. Patterns and predictors of β-diversity in the fragmented Brazilian Atlantic forest: A multiscale analysis of forest specialist and generalist birds. J. Anim. Ecol. 85: 240–250.

Morris, R. J. 2010. Anthropogenic impacts on tropical forest biodiversity: A network structure and ecosystem functioning perspective. Philos. T. Roy. Soc. B. 365: 3709–3718.

Mutangah, J. G. 1996. An investigation of vegetation status and process in relation to human disturbance in Kakamega Forest, western Kenya. Ph.D thesis, University of Wales, UK.

Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368: 734–737.

Newbold, T., L. N. Hudson, S. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Börger, D. J. Bennett, A. Choimes, B. Collen, J. Day, A. De Palma, S. Díaz, S. Echeverria-Londoño, M. J. Edgar, A. Feldman, M. Garon, M. L. Harrison, T. Alhusseini, D. J. Ingram, Y. Itescu, J. Kattge, V. Kemp, L. Kirkpatrick, M. Kleyer, D. L. Correia, C. D. Martin, S. Meiri, M. Novosolov, Y. Pan, H. R. Phillips, D. W. Purves, A. Robinson, J. Simpson, S. L. Tuck, E. Weiher, H. J. White, R. M. Ewers, G. M. Mace, J. P. Scharlemann, and A. Purvis. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520: 45–50.

Nichols, E., T. Larsen, S. Spector, A. L. Davis, F. Escobar, M. Favila, K. Vulinec, and The Scarabaeinae Research Network. 2007. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. Biol. Conserv. 137: 1–19.

Oksanen, J, F. G., Blanchet., M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. M. Stevens, E. Szoecs, and H. Wagner 2017. vegan: Community Ecology Package. R package version 2.4-2. https://CRAN.R-project.org/package=vegan

Peters, M. K., G. Fischer, F. Hita Garcia, T. Lung, and J. W. Wägele. 2013. Spatial variation in army ant swarm raiding and its potential effect on biodiversity. Biotropica 45: 54–62.

Peters, M. K., G. Fischer, G. Schaab, and M. Kraemer. 2009. Species compensation maintains abundance and raid rates of African swarm-raiding army ants in rainforest fragments. Biol. Conserv. 142: 668–675.

Peters, M. K., S. Likare, and M. Kraemer. 2008. Effects of habitat fragmentation and degradation on flocks of African ant-following birds. Ecol. Appl. 18: 847–858.

Peters, M. K., T. Lung, G. Schaab, and J. W. Wägele. 2011. Deforestation and the population decline of the army ant *Dorylus wilverthi* in western Kenya over the last century. J. Appl. Ecol. 48: 697–705.

Philpott, S. M., and I. Armbrecht. 2006. Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. Ecol. Entomol. 31: 369–377.

Piggott, J. J., C. R. Townsend, and C. D. Matthaei. 2015. Reconceptualizing synergism and antagonism among multiple stressors. Ecol. Evol. 5: 1538–1547.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Ross, S. R. P.-J., F. Hita Garcia, G. Fischer, and M. K. Peters. 2018. Data from: Selective logging intensity in an East African rain forest predicts reductions in ant diversity. Dryad Digital Repository. https://doi.org/10.5061/dryad.8hq75j7.

Ross, S. R. P.-J., C. Hassall, W. J. E. Hoppitt, F. A. Edwards, D. P. Edwards, and K. C. Hamer. 2017. Incorporating intraspecific trait variation into functional diversity: Impacts of selective logging on birds in Borneo. Methods Ecol. Evol. 8: 1499–1505. https://doi.org/10.1111/2041-210X.12769

Schleuning, M., N. Farwig, M. K. Peters, T. Bergsdorf, B. Bleher, R. Brandl, H. Dalitz, G. Fischer, W. Freund, M. W. Gikungu, M. Hagen, F. Hita Garcia, G. H. Kagezi, M. Kaib, M. Kraemer, T. Lung, C. M. Naumann, G. Schaab, M. Templin, D. Uster, J. W. Wägele, and K. Böhning-Gaese. 2011. Forest fragmentation and selective logging have inconsistent effects on multiple animal-mediated ecosystem processes in a tropical forest. PLoS ONE 6: e27785.

Stone, L., and A. Roberts. 1990. The checkerboard score and species distributions. Oecologia 85: 74–79.

Thiollay, J. M. 1999. Responses of an avian community to rain forest degradation. Biodivers. Conserv. 8: 513–534.

Tilman, D., P. B. Reich, and J. M. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441: 629–632.

TYLIANAKIS, J. M., E. LALIBERTÉ, A. NIELSEN, AND J. BASCOMPTE. 2010. Conservation of species interaction networks. Biol. Conserv. 143: 2270–2279.

VANDERWOUDE, C., L. A. LOBRY de BRUYN, AND A. P. HOUSE. 2000. Long-term ant community responses to selective harvesting of timber from Spotted Gum (*Corymbia variegata*)-dominated forests in south-east Queensland. Ecol. Manage. Restor. 1: 204–214.

VASCONCELOS, H. L., J. M. S. VILHENA, AND G. J. A. CALIRI. 2000. Responses of ants to selective logging of a central Amazonian forest. J. Appl. Ecol. 37: 508–514.

VENABLES, W. N., AND B. D. RIPLEY. 2002. Modern applied statistics with S. 4th edn. Springer, New York, NY.

WALTHER, B. A., AND S. MORAND. 1998. Comparative performance of species richness estimation methods. Parasitology 116: 395–405.

WOODCOCK, P., D. P. EDWARDS, T. M. FAYLE, R. J. NEWTON, C. V. KHEN, S. H. BOTTRELL, AND K. C. HAMER. 2011. The conservation value of South East Asia's highly degraded forests: Evidence from leaf-litter ants. Philos. T. Roy. Soc. B. 366: 3256–3264.