



# Managing the tropical landscape: a comparison of the effects of logging and forest conversion to agriculture on ants, birds, and lepidoptera

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Received 28 July 2003; received in revised form 27 August 2003; accepted 9 December 2003

## Abstract

Most tropical forest will not be conserved, but instead will be used in some way, most often for logging, agriculture, or both. Management of tropical forest landscapes for diversity depends upon an understanding of how many and which species can persist in different types of managed ecosystems. I compared the effects of logging and conversion of forest to agriculture or pasture on ant, bird, and lepidoptera species richness by combining data from 34 studies from tropical forests in Africa, Asia, and the Americas. Forest conversion to agriculture or pasture decreased the species richness of ants and of animals overall, whereas logging did not decrease species richness overall or of ants, birds or lepidoptera. After sites were abandoned, the diversity of logged sites did not change over time. In contrast, the diversity of old fields increased with time. Ants, birds, and lepidoptera responded similarly to forest clearance or disturbance, whether it be for logging or conversion to agriculture or pasture. In terms of faunal diversity, selective logging appears to have much less impact on faunal diversity than does forest conversion, both initially and after sites are abandoned.

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*Keywords:* Forest conversion; Effects of logging; Tropical landscape

## 1. Introduction

Despite the frequent call for more research on the effects of tropical forest disturbance on fauna (e.g. [Didham et al., 1996](#); [Watt et al., 2000](#)), our understanding of which types of disturbance most adversely and persistently affect tropical fauna remains poor. The same could be said for our understanding of the relative susceptibility of different faunal groups to disturbance ([Lawton et al., 1998](#)). This is not due to a paucity of studies, but instead to a lack of compar-

ative studies. With very few exceptions (e.g. [Blair, 1999](#); [Burghouts et al., 1992](#); [Gascon et al., 1999](#); [Lawton et al., 1998](#); [Watt et al., 1997](#)), most of the many studies of the effects of logging, agriculture, hurricanes, and other disturbances on animals focus on a single taxonomic group and a single disturbance type.

As it is prohibitive, in terms of both time and money, to conduct replicated large-scale comparative experiments ([Lawton et al., 1998](#)), such studies will probably always be rare. Large-scale studies of anthropogenic disturbance have had little success in discerning differences among disturbance types or taxa even when they have been conducted ([Gascon et al., 1999](#);

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Lawton et al., 1998). When significant differences in the effects of different types of disturbance are found, it is impossible to know whether the patterns seen at a single location will hold at other sites. For example, Lawton et al. found that in Cameroon different types of forest clearance had different effects on different taxa. The diversity of birds and ants was reduced more by clear-cut logging than by forest conversion for small-scale agriculture. Unfortunately, without other large comparative studies it is impossible to know if the patterns documented by Lawton et al. (1998) are generalizable. Qualitative reviews of the published literature have suggested that taxa may differ consistently in their response to logging and forest conversion to agriculture or pasture (Bawa and Seidler, 1998; Ochoa and Soriano, 2001). Similarly, a number of studies have suggested that forest conversion may alter animal diversity less than does forest conversion to agriculture or pasture (e.g. Vasconcelos et al., 2000). Both hypotheses need to be tested explicitly.

In lieu of more large-scale studies like those in Cameroon (Lawton et al., 1998) or purely qualitative reviews of published studies, meta-analyses of multiple data sets have the potential to shed insight on large-scale questions (see Bender et al., 1998; Hartley and Hunter, 1998). Using data from 34 published studies in 29 field sites, I compared the effects of forest conversion to agriculture and logging of a variety of intensities on the species diversity of lepidoptera, birds and ants. I compared the change in diversity of those same groups over time as logged sites and old fields were abandoned. I also compared the relative effects of different logging intensities on ant, bird and lepidoptera richness.

## 2. Methods

I chose to focus on ants, birds and lepidoptera because these three taxa are often advocated as indicator taxa and because they are the taxa for which the most data are available. A priori, these taxa might also represent a gradient in specialization and disturbance susceptibility, with lepidoptera being the most host-specific, birds intermediate and ants the most generalized (e.g. Lawton et al., 1998).

I searched for published studies that examined the relationship between forest conversion or logging and

the species richness of particular taxa in tropical rain forest regions. I located papers on *Web of Science* (1994–2001) and *Cambridge Scientific Abstracts* (1982–2001) using the keywords, *logging, selective logging, disturbance, secondary forest, succession and pasture*. I then used the references found in those papers to locate other studies. I distinguish between converted sites and different kinds of logged sites, but not between different types of converted sites. While it might be interesting to compare different types of converted sites (e.g. pastures versus agricultural fields), the data presently available do not permit such analyses.

Some of the studies I included in the analyses presented multiple measures of species diversity, some presented only species richness and others only species density. When studies presented multiple measures of diversity, I always used species richness values, defined as the number of species observed after some standardized *number of individuals* has been collected. In cases in which species richness values were not presented in the original studies, I used species density data. I define species density as the number of species collected after a standardized *area* has been sampled. Species density is potentially more biased than is species richness (Colwell and Coddington, 1994; Gotelli and Colwell, 2001). There is no reason to expect such a bias to affect the diversity of logged forests and forests converted to agriculture (the two principal treatments I am comparing), in different directions, since a similar proportion of logged and converted data points come from studies that used species richness and species density respectively (11/15 and 19/29). Nonetheless, the measure of diversity used for each data point, species diversity or density, was included as a variable in the analyses, to assess whether the measure of diversity used explained some of the variation in the response variable, standardized species richness.

Unless all of the species from a site have been collected (a rarity in the tropics), both species density and species richness are estimates of the true diversity at a site. To make valid comparisons among multiple sites it is therefore necessary to take into account the fact that different numbers of individuals (and areas) have been sampled at different sites. One method would be to sample the same number of individuals from every sample at every site (or the same amount of

area for species density), an impossibility given the information provided in the studies I am including here. Instead, I chose to standardize the results from multiple sites by converting the species diversity of the study taxa in each sample in each site to a standardized species richness value. Standardized species richness in disturbed or regenerating forests was measured separately within each study site for each treatment and taxon. Standardized richness for a given treatment within a site is the diversity or richness of the focal taxon in that treatment divided by the respective measure of the focal taxon in a comparable mature forest *in the same region*. Thus, standardized richness can be greater than one hundred percent when a disturbed or secondary forest plot is more diverse than the corresponding mature forest.

The data points included in the analyses were not necessarily independent. For example, data from a given study might contribute data points for both logged sites and converted sites of several ages. Because the data were sometimes non-independent, I chose to use randomization-based ANOVAs and randomization based regressions (Edgington, 1980; Manly, 1997). I used a randomization based ANOVA to compare the initial effects of logging and forest conversion on faunal species richness, where the response variable ( $Y$ ) was standardized richness and the independent variable ( $X$ ) was clearance type (logging or conversion). For each ANOVA,  $Y$ -values were randomized with respect to the categorical variable, clearance type. The observed group variance was then compared to the distribution of group variance values from the simulations. A thousand randomizations were used for each ANOVA and each other randomization-based analysis.

I performed a regression with taxon, type of forest clearance (conversion or logging),  $\log_{10}$  (years since abandonment + 1), years since abandonment, sample size, and measure of diversity (species density or species richness) as independent variables and standardized species richness as the response variable ( $Y$ ). I then randomized  $Y$  variables relative to all independent variables. Once data were randomized, I compared the observed  $F$ -ratios to the distribution of  $F$ -ratios from the randomized data. An  $F$ -ratio was considered significantly large if it was among the highest five percent of randomized values (Edgington, 1980; Manly, 1997). The simplest model, with only an

intercept term, was fit first and then additional variables were added stepwise. Once the overall model was fit, I regressed the residuals for logged sites against logging intensity (percentage of trees harvested). Since many studies of the effects of logging do not document logging intensity, it was often necessary to estimate logging intensity from nearby sites.

I compared the slope of regression lines between logged sites and converted sites using a separate set of simulations run using Visual Basic. Each individual coordinate pair (e.g.  $\log(\text{age} + 1) = 0.1$ , standardized richness = 110) was fixed, but the labels corresponding to those points (e.g. “logged” or “converted”) were randomized. The difference between the observed slopes for logged and converted sites was then compared to the difference between the simulated slopes (Cushman et al., 1993; Manly, 1998).

### 3. Results

The 34 studies I included were from Africa, Asia, and the Americas, although most studies were from West Africa and South America (Appendix A). Only two studies compared different disturbance treatments and only two studies compared multiple taxa. The rest of the studies examined the effect of a single disturbance type on a single taxon and then the recovery of the richness of that taxon over time for a forest chronosequence. Logging intensity varied from a few trees per hectare (e.g. Whitman et al., 1998) to clear-cut logging. All clear-cut data came from a single study (Lawton et al., 1998), where clear-cuts were relatively small ( $\sim 1$  ha). All results were qualitatively similar whether those clear-cuts sites were included or not. Because of the small number of clear-cut sites included in the analyses, the comparisons here are essentially comparisons of forest conversion to agriculture and pasture, and selective logging.

Converted forests actively in use for agriculture or as pasture had a lower overall standardized species diversity than did recently logged sites. Converted forests also had a lower standardized species diversity relative to logged forests for ants considered separately, but not for birds (Table 1). Overall and for ants and birds separately, forest conversion reduced standardized species diversity relative to mature forest comparisons ( $P_{\text{overall}} = 0.001$ ,  $P_{\text{ants}} = 0.04$ ,  $P_{\text{birds}} =$

Table 1  
Initial effects of forest conversion to agriculture or pasture and logging on animal standardized richness

	Converted	Logged	P-value
	Mean (var)	Mean (var)	
All taxa	89.2 (495)	45.3 (344)	0.02
Ants	101.25 (156)	57.3 (456)	0.04
Birds	68.7 (2422)	26.5 (283.9)	0.28
Lepidoptera	94.8 (116)	65 ( $n = 1$ )	NA

Comparison includes data from recently logged sites (<1 year previously) and converted sites actively in use as agricultural fields or pastures. Values indicate the mean standardized richness for logged and converted sites for all taxa combined, and ants, birds and lepidoptera separately. P-values are for comparison of mean standardized diversity in converted and logged sites. NA indicates that the statistical test was not applicable because  $n$  for lepidoptera in active converted sites was one.

0.009). Lepidoptera were not considered separately, because sample size was too small. Logging did not significantly reduce standardized species diversity relative to mature forest comparisons overall, for lepidoptera or for birds ( $P_{\text{overall}} = 0.19$ ,  $P_{\text{lepidoptera}} = 0.29$ ,  $P_{\text{birds}} = 0.33$ ). No significant effect of logging on the standardized diversity of ants was detected ( $P = 0.1$ ).

In the overall regression, the effect of forest clearance type (logging or conversion to agriculture or pasture) was highly significant as were the effects of log (years since abandonment + 1) and the measure of diversity used ( $P = 0.001$ ,  $0.001$  and  $0.04$ , respectively). Standardized diversity increased with log (years since abandonment + 1). Standardized richness was also higher in logged sites than in converted sites and higher when species density was used as a measure of diversity than when species richness was used. Forty-six percent of the variation in standardized species diversity was explained by the regression model that included only log (years since abandonment + 1), measure of diversity, and clearance type as variables ( $P_{\text{overall}} = 0.001$ ). Neither taxon (ant, bird or lepidoptera) nor sample size was a significant predictor of standardized species richness in the overall regression model ( $P = 0.4$ ,  $0.5$ ). Years since abandonment did not explain a significant amount of variation once log (years since abandonment + 1) was already in the model ( $P = 0.34$ ), so years since abandonment was dropped from the final model.

Logged sites and converted sites differed significantly in the slope of the regression of standardized richness against log transformed years since abandonment ( $P < 0.01$ ; Fig. 1). After logged sites were abandoned, there was no statistical change in standardized species diversity with time since abandonment. After old fields and pastures were abandoned, standardized species diversity increased with log (years since abandonment + 1) (Fig. 1). Standardized species diversity was not correlated with logging intensity (percent of tree basal area removed;  $P = 0.25$ ,  $R = 0.04$ ).

#### 4. Discussion

My results demonstrate that selective logging has a less direct impact on faunal species richness than does conversion to agriculture or pasture. Overall, I found that forest conversion to agriculture reduced the richness of ants, birds, or lepidoptera, more so than did logging. Forests recovering from conversion to agriculture or pasture remain less diverse than mature forests and logged forests for at least a decade. Though several authors have suggested that forest conversion may have greater effects on fauna than does logging (e.g. Vasconcelos et al., 2000), this is the first study, to my knowledge, that empirically supports such a claim.

Higher intensity and larger-scale logging increases disturbance to habitat and food resources and may allow more disturbance-specialists to establish (Fimbel et al., 2001); essentially rendering logged sites more like converted sites. Consequently, more intensive logging practices may have a greater impact than lower impact logging. There is evidence that mammals are more susceptible to higher impact logging than to low-intensity logging. Mammal diversity and species composition are both more affected by high impact logging than low intensity logging (Chapman et al., 2000; Ochoa and Soriano, 2001). Similarly, Taylor and Haseler (1995) found that Tasmanian bird diversity was higher in less intensively logged sites. I found no significant correlation between logging intensity and ant, bird or lepidoptera diversity. However, the metric of logging intensity I used, number of trees removed, provides only a very rough estimate of true logging intensity. Two sites with the same number of trees removed may differ greatly in the actual

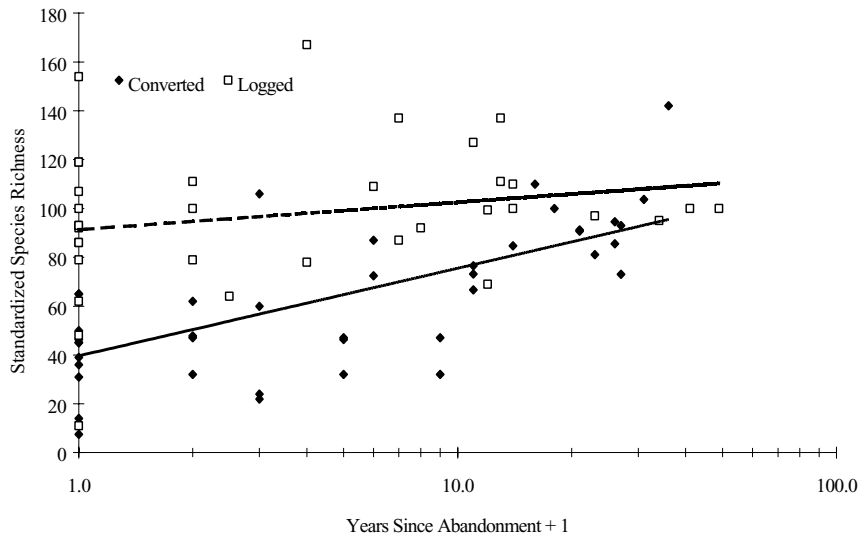


Fig. 1. Standardized species richness vs.  $\log_{10}$  (years since abandonment + 1) by clearance type. Slopes of the two lines differ significantly ( $P < 0.01$ ). Slope and intercept of the line fit to the data from converted sites are significantly different from the random expectation, whereas those for the logged sites were not. Best-fitting line for the converted sites was,  $y = 40.2 + 34.6x$  ( $R = 0.67$ ). Best-fitting line for the logged forest data was  $Y = 91.37 + 9.93X$  ( $R = 0.20$ ).

impact. In addition, the measurement of percent basal area removed varied greatly among studies.

In both logged and converted areas the richness and composition of species is affected by the habitat quality or template (Fimbel et al., 2001), the species pool of the surrounding area (Daily et al., 2001) and the dispersal ability of the taxon in question. Less vagile taxa and taxa with more specific habitat requirements have been hypothesized to be more susceptible to disturbance than other groups (Lawton et al., 1998). I found that ants, birds, and lepidoptera respond similarly in terms of species richness to both initial forest clearance and the abandonment of converted and logged sites. However, the three taxa are all relatively vagile. Ants, birds, and lepidoptera can all fly into newly abandoned sites. Consequently, the responses of the taxa studied here may represent a best-case scenario. Less vagile or more host specific taxa, such as canopy organisms and parasites respectively might respond very differently, but have been poorly studied. There is some evidence that small relatively poorly dispersing mammals and habitat sensitive bats (Chapman et al., 2000; Ochoa and Soriano, 2001; Soriano and Ochoa, 2001) are more negatively affected by logging than are other taxa, but

there were not enough mammal data available to consider mammals in the comparisons included here.

Even when species richness is not substantially reduced by logging or conversion, species composition and relative abundance may still be affected. Unfortunately, many studies of disturbance do not include comparisons of animal species composition among forest types, or stands. Those studies that do present species composition data use a variety of indices, making an overall statistical comparison difficult. Nonetheless, in converted sites, it has been shown that species composition is usually more affected by initial forest clearance than is species richness, and may in some cases never completely recover (Dunn, in press). Where it has been studied, logging also appears to affect species composition (Johns, 1992; Mason, 1996; Aleixo, 1999; Kalif et al., 2001; Vasconcelos et al., 2000; Willot, 1999; Willot et al., 2000) but not consistently (Lewis, 2001; Owunji and Plumptre, 1998; Whitman et al., 1998). Thus, the fact that species diversity is often not dramatically decreased by logging hides the fact that in most cases some mature forest species are being replaced by disturbance or edge specialists (Willot et al., 1998), that are often more widespread and less

likely to be at risk of local or global extinction (Fjeldsá, 1999).

Some of the variation among studies in terms of the effects of logging and forest conversion is due to the measure of diversity employed. The measure of species diversity that was used in a study explained 6.8% of the variation in standardized species richness. Studies that used species richness as a measure of diversity had higher standardized species richness in logged and converted forests than did studies that used species density. The observed pattern is likely a consequence of the fact that fewer individuals are often sampled in secondary and logged forests. Species density is easily biased by differences in the number of individuals sampled among treatments (Gotelli and Colwell, 2001). The fewer individuals are sampled, the lower species density will be, regardless of the true diversity. In all but a few exceptions (e.g. Moutinho, 1998), studies that used species density as a measure of diversity sampled fewer individuals in logged and converted forests than in mature forests (Andrade and Rubiotorgler, 1994; Bowman et al., 1990; Johns, 1991; Willot, 1999). In the future, studies would benefit from presenting both species richness and species density, so that the results obtained from the two measures of diversity can be compared directly within studies (Gotelli and Colwell, 2001).

After the complete model, including forest clearance type and forest age, was fit to the data, sixty four percent of the variation in standardized species richness was still left unexplained. Many spatial variables could be influential, including variation among sites in size of clearings, the distance to source populations, and spatial scale, all of which have been shown to affect measures of species richness (Gotelli and

Colwell, 2001; Hamer and Hill, 2000; MacNally, 1997; Ricketts et al., 2001). We remain naïve with regard to interactions between these variables and the effects of different types of disturbance. Some variation among studies may be due to differences among forest types. Most studies of the effects of disturbance on tropical forest fauna have focused on wet forest (see Appendix A), but different forest types may respond very differently to disturbance.

Overall, both small-scale, swidden-type agriculture and logging appear to be potentially reconcilable with conservation of species diversity—a relatively hopeful message for tropical forest management (Lugo, 1999). However, where converted lands are not allowed to regenerate, species richness will stay low or even decline further. Similarly, while many species can live in logged forests, logging is often part of a more complicated series of social and political actions. Logging is often associated with increased hunting pressures, arrival of colonists, fire (Nepstad et al., 2001; Nepstad et al., 1999; Struhsaker, 1997) and a variety of other factors that can act synergistically to magnify the direct impact of logging, with the potential for much greater effects on diversity.

### Acknowledgements

I thank Zoe Cardon, Eldridge Adams, Robert K. Colwell, Robin Chazdon, Pajaro Morales, Mark Schwartz, two anonymous reviewers, and Monica Sanchez for substantive comments on this manuscript. This work was funded in part by a Penner grant and a National Science Foundation Predoctoral Fellowship.

## Appendix A

Studies included in analyses are the studies with the same number after “country” were done at the same or nearby sites

	Country	Forest type	Taxon	Ages of sites (years)	Clearance type	Div.	Reference
1	Brazil (1)	HT	Birds	MF, Cl.	Log.	SD	Aleixo, 1999
2	Colombia (2)	HT	Birds	MF, 17-7, 1-5	Cult.	SD	Andrade and Rubiortogler, 1994
3	Ghana (3)	MSD	Leaf litter ants	MF, 8-40	Cult.	SR	Belshaw and Bolton, 1993
4	Costa Rica (4)	HT	Birds	MF, 20, 25-35	Cult.	SR	Blake and Loiselle, 2001
5	Papua New Guinea (5)	HT	Lepidoptera	MF, 26, 8, 4, 2, 1	Cult.	SD	Bowman et al., 1990
	Papua New Guinea (5)	HT	Birds	MF, 26, 8, 4, 2, 1	Cult.	SD	Bowman et al., 1990
6	Colombia (6)	CF	Leaf litter ants	MF, 25, 10	Past.	SD	Bustos and Ulloa-Chacón, 1996-1997
7	Colombia (7)	CF	Leaf litter ants	MF, 20, 10, Cl.	Past.	SD	Estrada and Fernandez, 1999
8	Mexico (8)	HT	Birds	MF, Cl.	Past., Cult.	SR	Estrada and Coates-Estrada, 1997
9	Bolivia (9)	SD	Birds	MF, Cl.	Log.	SD	Fredricksen et al., 1999
10	Indonesia (10)	HT	Lepidoptera	MF, 5	Log.	SD	Hill et al., 1995
11	Brazil (11)	HT	Birds	MF, 11, 1, Cl.	Log., Cult.	SD	Johns, 1991
12	Malaysia (12)	HT	Birds	MF, 12, 6	Log.	SD	Johns, 1996
13	Brazil (13)	HT	Leaf litter ants	MF, Cl.	Log.	SD	Kalif et al., 2001
14	Malaysia (12)	HT	Birds	MF, Cl.	Log.	SR	Lambert, 1992
15	Cameroon (14)	SD	Birds	MF, 40, 1	Log.	SD	Lawton et al., 1998
	Cameroon (14)	SD	Leaf litter ants	MF, 40, 1	Log.	SD	Lawton et al., 1998
16	Belize (15)	HT	Lepidoptera	MF, 1	Log.	SR	Lewis, 2001
17	Mexico (16)	HT	Leaf litter ants	MF, Cl.	Cult.	SD	MacKay et al., 1991
18	Indonesia (17)	HT	Birds	MF, 1-5 yr	Log.	SD	Mardsen, 1998
19	Venezuela (18)	HT	Birds	MF, 6, 1	Log.	SD	Mason, 1996
20	Brazil (19)	HT	Leaf litter ants	MF, 30, 4	Past.	SD	Moutinho, 1998
21	Uganda (20)	SD	Birds	MF, 45, 32, 11	Log.	SR	Owiunji and Plumptre, 1998
22	Panama (21)	HT	Birds	MF, Cl.	Past.	SR	Petit et al., 1999
23	Costa Rica (4)	HT	Leaf litter ants	MF, 20	Cac.	SR	Roth et al., 1994
24	India (22)	HT	Birds	MF, 100, 25, 10, 5, 1	Cult.	SD	Shankar Raman et al., 1998
25	Peru (23)	HT	Birds	MF, Cl.	Cult.	SR	Terborgh and Weske, 1969
26	French Guiana (24)	HT	Birds	MF, 10, 1	Log.	SD	Thiollay, 1992, 1997

**Appendix A.** (Continued)

	Country	Forest type	Taxon	Ages of sites (years)	Clearance type	Div.	Reference
27	Brazil (25)	HT	Leaf litter ants	MF, 13, 10, 1	Past.	SR	Vasconcelos, 1999
28	Brazil (26)	HT	Leaf litter ants	MF, 10, 4	Log.	SD	Vasconcelos et al., 2000
29	Peru (27)	HT	Leaf litter ants	MF, Cl.	Past.	SD	Verhaagh, 1991
30	Cameroon (14)	SD	Leaf litter ants	MF, Cl.	Log.	SR	Watt et al., 1997; Watt et al., 2000
	Cameroon (14)	SD	Lepidoptera	MF, 1, Cl.	Log.	SR	Watt et al., 1997
31	Belize (15)	HT	Birds	MF, 1	Log.	SD	Whitman et al., 1998
32	Borneo (28)	HT	Lepidoptera	MF, 5	Log.	SR	Willot, 1999
33	Borneo (28)	HT	Lepidoptera	MF, 5	Log.	SR	Willot et al., 2000
34	Malaysia (29)	HT	Birds	MF, 23	Log.	SD	Wong, 1985

Forest types are as follows: HT: humid tropical, MSD: moist semi-deciduous, SD: semi-deciduous, CF: cloud forest. Ages of sites represent years since abandonment. Clearance type indicates the original reason that mature forest was cleared from sites, where Cult: cultivation, Past.: pasture, Log: logging and Cac.: cacao. Div. indicates how diversity was measured in each study; SD: species density or species count, SR: species richness.

## References

- Aleixo, A., 1999. Effects of selective logging on a bird community in the Brazilian Atlantic rain forest. *Condor* 101, 537–548.
- Andrade, G.I., Rubiotorgler, H., 1994. Sustainable use of the tropical rain-forest: evidence from the avifauna in a shifting-cultivation habitat mosaic in the Colombian Amazon. *Conserv. Biol.* 8, 545–554.
- Bawa, K.S., Seidler, R., 1998. Natural forest management and conservation of biodiversity in tropical Forests. *Conserv. Biol.* 12, 46–55.
- Belshaw, R., Bolton, B., 1993. The effect of forest disturbance on the leaf litter ant fauna in Ghana. *Biodiv. Conserv.* 2, 656–666.
- Bender, D.J., Contreras, T.A., Fahrig, L., 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* 72, 517–533.
- Blair, R.B., 1999. Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity. *Ecol. Appl.* 9, 164–170.
- Blake, J.G., Loiselle, B.A., 2001. Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. *Auk* 118, 304–326.
- Bowman, D.M.J.S., Woinarski, J.C.Z., Sands, D.P.A., McShane, V.J., 1990. Slash-and-burn agriculture in the wet coastal lowlands of Papua New Guinea: response of birds, butterflies and reptiles. *J. Biogeogr.* 17, 227–239.
- Burghouts, T., Ernstring, G., Korthals, G., De Vries, T., 1992. Litterfall, leaf litter decomposition and litter invertebrates in primary and selectively logged Dipterocarp forest in Sabah, Malaysia. *Philos. Trans. R. Soc. London B* 335, 407–416.
- Bustos, J.H., Ulloa-Chacón, P., 1996–1997. Mirmecofauna y perturbación en un bosque de niebla neotropical (Reserva Natural Hato Viejo, Valle del Cauca, Colombia). *Revista de Biología Tropical* 44/45/1997, 259–266.
- Chapman, C.A., Balcomb, S.R., Gillespie, T.R., Skorupa, J.P., Struhsaker, T.T., 2000. Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conserv. Biol.* 14, 207–217.
- Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. London B* 34, 101–118.
- Cushman, J.H., Lawton, J.H., Manly, B.F.J., 1993. Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia* 95, 30–37.
- Daily, G.C., Ehrlich, P.R., Sanchez-Azofeifa, G.A., 2001. Country-side biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecol. Appl.* 11, 1–13.
- Didham, R.K., Ghazoul, J., Stork, N.E., Davis, A.J., 1996. Insects in fragmented forest: a functional approach. *Trends Ecol. Evol.* 11, 255–259.
- Dunn, R.R., in press. Recovery of faunal communities during tropical forest regeneration. *Conserv. Biol.*
- Edgington, E.S., 1980. *Randomization tests*. Marcel Dekker, New York.
- Estrada, A., Coates-Estrada, R., 1997. Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. *Biodiv. Conserv.* 6, 19–43.
- Estrada, C., Fernandez, F., 1999. Diversity of ants (Hymenoptera: Formicidae) in a successional gradient of a cloud forest (Narino, Colombia). *Revista de Biología Tropical* 47, 189–201.
- Fjeldsá, J., 1999. The impact of human forest disturbance on the endemic avifauna of the Udzungwa Mountains, Tanzania. *Bird Conserv. Int.* 9, 47–62.
- Fimbel, R.A., Grajal, A., Robinson, J.G., 2001. Logging-wildlife issues in the tropics: an overview. In: Fimbel, A., Grajal, Robinson, J.G. (Eds.), *The Cutting Edge: Conserving Wildlife in Logged Tropical Forests*. Columbia University Press, New York.
- Fredricksen, N.J., Fredricksen, T.S., Flores, B., Rumiz, D., 1999. Wildlife use of different-sized logging gaps in a tropical dry forest. *Trop. Ecol.* 40, 167–175.
- Gascon, C., Lovejoy, T.E., Bierregaard, R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M., Borges, S., 1999. Matrix habitat and species richness in tropical forest remnants. *Biol. Conserv.* 91, 223–229.
- Gotelli, N.J., Colwell, R.J., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and estimation of species richness. *Ecol. Lett.* 4, 379–391.
- Hamer, K.C., Hill, J.K., 2000. Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conserv. Biol.* 14, 1435–1440.
- Hartley, M.J., Hunter Jr., M.L., 1998. A meta-analysis of forest cover, edge effects, and artificial nest predation rates. *Conserv. Biol.* 12, 465–469.
- Hill, J.K., Hamer, K.C., Lace, L.A., Banham, W.M.T., 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *J. Appl. Ecol.* 32, 754–760.
- Johns, A.D., 1991. Responses of Amazonian rain forest birds to habitat modification. *J. Trop. Ecol.* 7, 417–437.
- Johns, A.D., 1992. Vertebrate responses to selective logging: implications for the design of logging systems. *Philos. Trans. R. Soc. London B* 335, 437–442.
- Johns, A.G., 1996. Bird population persistence in Sabahan logging concessions. *Biol. Conserv.* 75, 3–10.
- Kalif, K.A.B., Azevedo-Ramos, C., Moutinho, P., Malcher, S.A.O., 2001. The effect of logging on the ground-foraging ant community in Eastern Amazonia. *Stud. Neotrop. Fauna Environ.* 36, 215–219.
- Lambert, F.R., 1992. The consequences of selective logging for Bornean lowland forest birds. *Philos. Trans. R. Soc. London B* 335, 443–457.
- Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S., Watt, A.D., 1998. Biodiversity indicators, indicator taxa and effects of habitat modification in tropical forest nature. *Biodiv. Invent. Nat.* 391, 72–76.
- Lewis, O.T., 2001. Effect of experimental selective logging on tropical butterflies. *Conserv. Biol.* 15, 389–400.
- Lugo, A.E., 1999. Will concern for biodiversity spell doom to tropical forest management. *Sci. Total Environ.* 240, 123–131.
- MacKay, W.P., Rebeles, M.A., Arredondo, B.H.C., Rodríguez, R.A.D., González, D.A., Vinson, S.B., 1991. Impact of the

- slashing and burning of a tropical rain forest on the native ant fauna (Hymenoptera: Formicidae). *Sociobiology* 18:257–268.
- MacNally, R., 1997. Monitoring forest bird communities for impact assessment: the influence of sampling intensity and spatial scale. *Biol. Conserv.* 82, 355–367.
- Manly, B.F.J., 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman and Hall, London, New York.
- Manly, B.F.J., 1998. Testing for latitudinal and other body-size gradients. *Ecol. Lett.* 1, 104–111.
- Mardsen, S.J., 1998. Changes in bird abundance following selective logging on Seram, Indonesia. *Conserv. Biol.* 12, 605–611.
- Mason, D., 1996. Responses of Venezuelan understory birds to selective logging, enrichment strips, and vine cutting. *Biotropica* 28, 296–309.
- Moutinho, P., 1998. Impactos da formacao de pastagens sobre a fauna de formigas: consequencias para a recuperacao forestal na Amazonia oriental. In: Gascon, C., Moutinho, P. (Eds.), *Floresta Amazonica: Dinamica, Regeneracao e Manejo*, INPA, Brazil.
- Nepstad, D., Carvalho, G., Barros, A.C., Alencar, A., Capobianco, J.P., Bishop, J., Moutinho, P., Lefebvre, P., Silva, U.L., Prins, E., 2001. Road paving, fire regime feedbacks, and the future of Amazon forests. *For. Ecol. Manage.* 154, 395–407.
- Nepstad, D.C., Verissimo, A., Alencar, A., Nobres, C., Lima, E., Lefebvre, P., Schlesinger, P., Potter, C., Moutinho, P., Mendoza, E., Cochrane, M., Brooks, V., 1999. Large-scale impoverishment of Amazonian forests by logging and fire. *Nature* 398, 505–508.
- Ochoa, J., Soriano, P.J., 2001. The effects of logging on nonvolant small mammal communities in neotropical forests. In: Fimbel, R.A., Grajal, A., Robinson, J.G. (Eds.), *The Cutting Edge: Conserving Wildlife in Logged Tropical Forests*. Columbia University Press, New York.
- Owiunji, I., Plumptre, A.J., 1998. Bird communities in logged and unlogged compartments in Budongo Forest, Uganda. *For. Ecol. Manage.* 108, 115–126.
- Petit, L.J., Petit, D.R., Christian, D.G., Powell, H.D.W., 1999. Bird communities of natural and modified habitats in Panama. *Ecography* 22, 292–304.
- Ricketts, T.H., Daily, G.C., Ehrlich, P.R., Fay, J.P., 2001. Country-side biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conserv. Biol.* 15, 378–388.
- Roth, D.S., Perfecto, I., Rathcke, B., 1994. The effects of management systems on ground-foraging ant diversity in Costa Rica. *Ecol. Appl.* 4, 423–436.
- Shankar Raman, T.R., Rawat, G.S., Johnsingh, A.J.T., 1998. Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. *J. Appl. Ecol.* 35, 214–231.
- Soriano, P.J., Ochoa, J., 2001. The Consequences of Timber Exploitation for Bat Communities In: *Tropical America*. In: Fimbel, R.A., Grajal, A., Robinson, J.G. (Eds.), *The Cutting Edge: Conserving Wildlife in Logged Tropical Forests*. Columbia University Press, New York.
- Struhsaker, T.T., 1997. *Ecology of An African Rain Forest: Logging in Kibale and the Conflict Between Conservation and Exploitation*. University of Florida Press, Gainesville.
- Taylor, R.J., Haseler, M.E., 1995. Effects of partial logging systems on bird assemblages in Tasmania. *For. Ecol. Manage.* 72, 131–149.
- Terborgh, J., Weske, J.S., 1969. Colonization of secondary habitats by Peruvian birds. *Ecology* 50, 765–782.
- Thiollay, J.M., 1992. Influence of selective logging on bird species diversity in a Guianan rain forest. *Conserv. Biol.* 6, 47–63.
- Thiollay, J.M., 1997. Disturbance, selective logging and bird diversity: A Neotropical forest study. *Biodiv. Conserv.* 6, 1155–1173.
- Vasconcelos, H.L., 1999. Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia. *Biodiv. Conserv.* 8, 409–420.
- Vasconcelos, H.L., Vilhena, J.M.S., Caliri, G.J.A., 2000. Responses of ants to selective logging of a central Amazonian forest. *J. Appl. Ecol.* 37, 508–514.
- Verhaagh, M., 1991. Clearing a tropical rain forest—effects on the ant fauna. In: Erdelen, W., Ishwaran, N., Muller, P. (Eds.), *Tropical Ecosystems*. Saarbrücken, Germany.
- Watt, A.D., Stork, N.E., Eggleton, P., Srivastava, D., Bolton, B., Larsen, T.B., Martin, J.D., Bignell, D.E., 1997. Impact of forest loss and regeneration on insect abundance and diversity. In: Watt, A.D., Stork, N.E., Hunter, M.D. (Eds.), *Forests and Insects*. Chapman & Hall, London.
- Watt, A.D., Stork, N.E., Bolton, B., 2000. The Diversity and abundance of ants in relation to forest disturbance and plantation establishment in southern Cameroon. *J. Appl. Ecol.* 39, 18–30.
- Watt, A.D., Stork, N.E., McBeath, C., Lawson, G.L., 1997. Impact of forest management on insect abundance and damage in a lowland tropical forest in southern Cameroon. *J. Appl. Ecol.* 34, 985–998.
- Whitman, A.A., Hagan, J.M., Brokaw, N.V.L., 1998. Effects of selection logging on birds in northern Belize. *Biotropica* 30, 449–457.
- Willot, S.J., 1999. The effects of selective logging on the distribution of moths in a Bornean rainforest. *Philos. Trans. R. Soc. Lond.* 354, 1783–1790.
- Willot, S.J., Lim, D.C., Compton, S.G., Sutton, S.L., 2000. Effects of selective logging on the butterflies of a Bornean rainforest. *Conserv. Biol.* 14, 1055–1065.
- Wong, M., 1985. Understory birds as indicators of regeneration in a patch of selectively logged West Malaysian rainforest. In: Diamond, A.W., Lovejoy, T.E. (Eds.), *Conservation of Tropical Forest Birds*. International Council for Bird Preservation, Cambridge, England.