



Trophic Flexibility and the Persistence of Understory Birds in Intensively Logged Rainforest

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Abstract: *Effects of logging on species composition in tropical rainforests are well known but may fail to reveal key changes in species interactions. We used nitrogen stable-isotope analysis of 73 species of understory birds to quantify trophic responses to repeated intensive logging of rainforest in northern Borneo and to test 4 hypotheses: logging has significant effects on trophic positions and trophic-niche widths of species, and the persistence of species in degraded forest is related to their trophic positions and trophic-niche widths in primary forest. Species fed from higher up the food chain and had narrower trophic-niche widths in degraded forest. Species with narrow trophic-niche widths in primary forest were less likely to persist after logging, a result that indicates a higher vulnerability of dietary specialists to local extinction following habitat disturbance. Persistence of species in degraded forest was not related to a species' trophic position. These results indicate changes in trophic organization that were not apparent from changes in species composition and highlight the importance of focusing on trophic flexibility over the prevailing emphasis on membership of static feeding guilds. Our results thus support the notion that alterations to trophic organization and interactions within tropical forests may be a pervasive and functionally important hidden effect of forest degradation.*

Keywords: community resilience, diet, ecosystem functioning, extinction risk, food webs, functional guilds, selective logging

Flexibilidad Trófica y la Persistencia de Aves de Sotobosque en un Bosque Lluvioso Talado Intensivamente

Resumen: *Los efectos de la tala sobre la composición de especies en bosques lluviosos tropicales son bien conocidos pero pueden fallar en la revelación de cambios clave en las interacciones de especies. Utilizamos análisis de isótopos estables de nitrógeno de 73 especies de aves de sotobosque para cuantificar las respuestas tróficas a la tala intensiva del bosque lluvioso en el norte de Borneo y para probar 4 hipótesis: la tala tiene efectos significativos sobre posiciones tróficas y la amplitud de nicho de las especies, y la persistencia de especies en el bosque degradado está relacionado con sus posiciones tróficas y amplitud de nicho trófico en el bosque primario. Las especies se alimentaron más arriba en la cadena trófica y tuvieron nichos más angostos en el bosque degradado. Las especies con nichos angostos en bosques primarios tuvieron menor probabilidad de persistir después de la tala, resultado que indica que especies con dietas especializadas tienen mayor vulnerabilidad a la extinción local después de una perturbación de hábitat. La persistencia de especies en bosque degradado no se relacionó con la posición trófica. Este resultado indica cambios en la organización trófica que no fueron aparentes con los cambios en la composición de especies y resaltan la importancia de concentrarse en la flexibilidad trófica en vez del énfasis prevaeciente en la membresía de gremios alimenticios estáticos. Por lo tanto, nuestros resultados soportan la noción de que las alteraciones de la organización trófica y las interacciones en los bosques tropicales pueden ser un efecto oculto, dominante e importante funcionalmente, de la degradación de bosques.*

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Palabras Clave: dieta, funcionamiento del ecosistema, gremios funcionales, redes alimenticias, resiliencia de la comunidad, riesgo de extinción, tala selectiva

Introduction

Habitat destruction and degradation are major drivers of species extinctions (Barnosky et al. 2011), and attention is increasingly focusing on how different traits of species affect their ability to persist in degraded habitats (Koh et al. 2004; Ockinger et al. 2010). Trophic ecology is central to this question and has potentially far-reaching consequences for ecosystem processes, functioning, and long-term stability (Estes et al. 2011; Stouffer et al. 2012). However, quantifying species' trophic interactions is difficult and time-consuming, especially in the most complex and species-rich ecosystems such as tropical forests (Lewis 2009). For instance, a recently described plant-herbivore food web for lowland rain forest in Papua New Guinea included >6800 feeding links and approximately 1500 species of herbivores from 11 distinct feeding guilds (Novotny et al. 2010). Detailed data for higher trophic levels are lacking and, for practical reasons, largely confined to restricted sets of species such as cavity-nesting bees and wasps and their parasitoids (Tylianakis et al. 2007). Yet data are vital for understanding how habitat degradation affects both individual species and the interactions among them (McCann 2007; Tylianakis et al. 2010).

Over half the world's remaining rainforests have been logged, making the fate of biodiversity within such degraded forests of critical importance to conservation. Many researchers have examined changes in species richness and composition following logging (e.g., Sekercioglu 2002; Peters et al. 2006; Edwards et al. 2011) but fewer have focused on how logging affects species with different trophic requirements. For birds, which are one of the best-studied taxa in tropical regions, there is some evidence that frugivores and insectivores are more prone to local extinctions from logged forests, but some insectivores increase in abundance after logging, and the responses of other feeding guilds are also unclear (see meta-analysis by Gray et al. [2007]) (Cleary et al. 2007; Edwards et al. 2009). One possible reason for this uncertainty is that many birds in tropical forests have mixed diets that incorporate food items from different trophic levels, and this fact makes such guilds imprecise and difficult to define. A related problem is that species within a guild may differ greatly in trophic position, depending, for example, on whether the main prey of insectivores are herbivorous or predatory insects. In addition, although species typically possess flexibility in their foraging traits and behaviors (Beaudoin et al. 1999; Carnicer et al. 2009; Pasqualet al. 2010), and recent models explore how flexibility in resource use may affect both species- and community-level responses to anthropogenic disturbance (Kaiser-Bunbury et al. 2010; Stan-

iczenko et al. 2010), comparisons of species' responses within different feeding guilds do not account for such trophic flexibility.

Stable-isotope analysis can overcome these problems because it provides a rapid means of precisely quantifying an organism's average trophic position (Bearhop et al. 2004; Layman et al. 2007). Tissue ratios of ^{15}N to ^{14}N (expressed as $\delta^{15}\text{N}$) are enriched by $\sim 2\text{--}3\text{‰}$ with each trophic transfer up the food chain (Vanderklift & Ponsard 2003) and thus indicate an organism's mean trophic level during the period of tissue synthesis (Blüthgen et al. 2003; Caut et al. 2009). A population-level measure of trophic-niche width can then be derived through the use of variation in trophic position among individuals (Bearhop et al. 2004).

We use stable nitrogen isotopes to examine the effects of intensive selective logging on both the mean trophic positions (MTPs) and the trophic-niche widths of a community of understory birds in tropical forest. We tested 4 hypotheses: logging has significant effects on trophic position and trophic-niche widths of species, and the persistence of species in degraded forest is related to species' trophic positions and their trophic-niche widths in primary forest. Logging may result in a net decrease in the trophic positions of species as a result of simplification of food webs and shortening of food chains. Conversely, however, if logging decreases the abundance or availability of food resources at low trophic levels, this could result in a net increase in species' trophic positions. We collected quantitative data on both the direction and magnitude of changes in trophic positions and niche widths for a community of understory birds encompassing a range of different feeding guilds.

Methods

Study Site

The island of Borneo is a global biodiversity hotspot, where much of the remaining forest is now highly degraded following multiple rounds of selective logging that removed nearly all medium- to large-diameter trees (Edwards et al. 2011). Our study area was the Yayasan Sabah logging concession in Sabah, Borneo ($4^{\circ} 58' \text{N}$, $117^{\circ} 48' \text{E}$). The concession encompasses production forest within the Ulu Segama-Malua Forest Reserve (US-MFR) (238,000 ha) and unlogged primary forest within the Danum Valley Conservation Area and Palum Tambun Watershed Reserve (45,200 ha), and forms one contiguous forest (Supporting Information). Primary forests in the region are dominated numerically by large trees of

the family Dipterocarpaceae, which are valuable timber species. Degraded forests within the US-MFR have been logged twice (first rotation, 1987–1991; second rotation, 2001–2007). The total timber yield was approximately 145 m³/ha, one of the highest rates of timber removal globally (Fisher et al. 2011).

Avifaunal and Vegetative Sampling

We conducted fieldwork from July to August 2007 and May to August 2008 along transects comprising 15 mist nets (12 × 2.7 m) erected end-to-end in a straight line within primary forest ($n = 8$ transects) and degraded forest ($n = 8$). In primary forest, transects were ≥ 500 m apart (Supporting Information). In degraded forest, we grouped transects into 4 sites, each with 2 transects separated by 500–800 m and spaced such that the primary forest was central between 2 sites to the southeast and 2 to the northwest. Distances between degraded forest transects (28.3 km [SE 3.7]) were similar to those between degraded and primary forest transects (23.6 km [SE 0.5]) (Supporting Information). Results of studies in tropical forests indicate that mist-net census points separated by >200 m are statistically independent (Hill & Hamer 2004). In our study, no individuals were captured in both forest types and only 3 individuals were recaptured between transects within a forest type. In addition, there was no spatial autocorrelation in our data on trophic positions (see Data Analyses later). We sampled all transects during the dry period (Walsh et al. 2011), and sampling years were similar in terms of environmental conditions (no mast fruiting and no droughts or floods). Hence, we are confident our data were representative of the effects of logging on trophic organization.

We opened mist nets from 06:00 to 12:00 for 3 consecutive days (4860 mist-net hours) (see Edwards et al. [2009] for further details) and every bird captured was marked with an individually numbered metal ring to prevent resampling of individuals. We took nail clippings, which integrate diet over a period of several weeks (Bearhop et al. 2003), from the central front claw and rear claw of both feet for stable-isotope analysis (see later) and stored them in a labeled vial. Nail clipping occasionally caused slight bleeding, and in these cases, we applied pressure to the cut end of the nail and the bird was released only when bleeding had stopped (typically within 1–2 min). We also collected pairs of leaves from 2 understory plants every 15 m along each transect (20 plants per transect) to determine baseline isotope compositions against which trophic position could be assessed (Woodcock et al. 2012).

Stable-Isotope Analyses

We analyzed claws whole and ground leaf samples into a fine powder with a mixer mill (MM301, RETSCH, Haan).

We placed samples into tin capsules with the amount of material adjusted to produce a peak of between 3 and 8 nA (birds = 0.3–0.8 mg; plants = 2–3 mg). We analyzed samples on a continuous flow, isotope ratio monitoring mass spectrometer system consisting of a Eurovector 3028HT elemental analyser with Costech zero-blank autosampler coupled to a GV Isoprime mass spectrometer (see Supporting Information for further details).

The trophic position of each understory bird sampled was calculated as $\lambda + (\delta^{15}\text{N}_{\text{bird}} - \delta^{15}\text{N}_{\text{baseline organism}})/E$, where λ is the trophic level of the organisms used to estimate $\delta^{15}\text{N}_{\text{baseline organism}}$ ($\lambda = 1$ for plants used in this study) and E is the enrichment in $\delta^{15}\text{N}$ per trophic level (Post et al. 2000). As the value of $\delta^{15}\text{N}_{\text{baseline organism}}$ we used the mean $\delta^{15}\text{N}$ for the 20 leaves collected from the same transect as each bird sample (Woodcock et al. [2012] for further details). We used $E = 2.5$ as the most appropriate enrichment factor for our study system, consistent with 2 extensive reviews (Vanderklift & Ponsard 2003; Caut et al. 2009). Trophic-niche widths were calculated for each species as the coefficient of variation in trophic position: $(\text{SD}/\text{MTP}) \times 100$, where MTP is the mean trophic position (among individuals) of a species and SD is the standard deviation of the mean.

Data Analyses

We removed species with only one record in either habitat from our data set (primary forest, 14 species; degraded forest, 14 species; one shared species), and thus had means of 9.8 (SE 1.4) trophic measures per species in primary forest and 11.4 (SE 1.7) in degraded forest.

We used linear mixed-effects models (LMEs) (Pinheiro & Bates 2000) in the `lme` function in the `nlme` package of R (version 2.13.0) to determine whether the trophic positions of individuals differed between primary and degraded forest. The lack of a phylogeny for our study species precluded the use of phylogenetic contrasts to control for phylogenetic nonindependence. As an alternative, following Koh et al. (2004), we included family as a random effect in our analyses ($n_{\text{family}} = 14$). Species identities of individuals were nested within family to account for repeated measures per species (models had the form $\text{trophic position} \sim \text{forest, random} = \sim 1 | \text{family/species}$). Changes in the trophic positions of individual species recorded in both types of forest (≥ 10 samples in each habitat) were then examined separately with general linear models (GLMs) in R (version 2.13.0). We also used LMEs to compare the trophic position of shared species with those species that were exclusive to each type of forest and to compare the trophic positions of species grouped within feeding guilds between primary and degraded forest (both models of form $\text{trophic position} \sim \text{forest, random} = \sim 1 | \text{family/species}$).

To check for spatial autocorrelation in these data, we used Mantel tests with 9999 iterations in R (version

2.13.0) to examine residuals from a GLM of the average trophic positions of species within each type of forest. There was no spatial autocorrelation of the model residuals, either for the average trophic positions of all species sampled on each transect (Mantel test $p > 0.9$) or for the average trophic positions of individual species recorded in both types of forest (≥ 10 samples in each forest type, 10 models, all $p > 0.1$). Hence the spatial arrangement of our sampling sites did not confound our comparison between primary and degraded forest.

We used LMEs to compare the trophic-niche widths of shared species between primary and degraded forest (trophic-niche width~forest, random = ~1|family/species, to account for paired data). We also compared shared species with those that were exclusive to each type of forest (trophic-niche width~forest, random = ~1|family). Finally, we used LMEs to compare the MTP with trophic-niche width of species in each type of forest, again including family as a random effect. In all cases, we present statistics only for fixed effects (i.e., those affecting population means) (Pinheiro & Bates 2000).

Results

Trophic Position

We obtained trophic positions for 1156 individuals of 73 species in total, 508 individuals of 52 species in primary forest, and 648 individuals of 57 species in degraded forest (Supporting Information). The trophic position of birds was almost half a trophic level higher in degraded forest (mean [SE] = 3.56 [0.02]) than in primary forest (3.06 [0.02]; LME: $F_{1,1082} = 318.6, p < 0.0001$). This result indicates birds, their prey, or both are more predatory in logged, degraded forest. This difference was not due to species turnover: there was no significant difference between the trophic positions of species found in both types of forest and either those of species found only in primary forest ($F_{1,37} = 0.2, p = 0.7$) or those of species found only in degraded forest ($F_{1,39} = 1.8, p = 0.3$). Trophic position did not, therefore, determine which species were more likely to persist after logging. Instead, individual analyses of those 10 species with ≥ 10 samples in each forest type revealed that such shared species elevated their trophic positions. Nine species occupied a significantly higher trophic position in degraded forest, whereas the remaining species showed no significant difference (Fig. 1).

For the 36 species that were present in both habitats, there was a significant negative relation between a species' MTP in primary forest and its change in trophic position following forest degradation (Fig. 2a) (LME: $F_{1,24} = 10.3, p = 0.004$). There was also a similar negative relation between a species' MTP and its proportional change

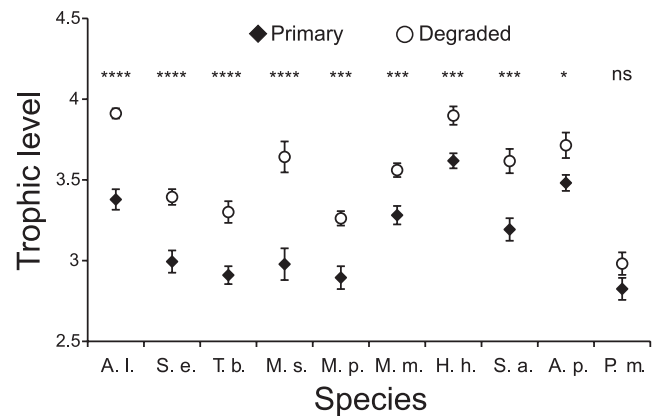


Figure 1. The mean trophic level of species in primary forest and degraded forest. Species with ≥ 10 records in each forest type are ordered from the largest to smallest statistical difference in trophic level between forest types (general linear models: ns ≥ 0.05 , * $p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$; error bars, 1 SE; A.l., *Arachnothera longirostra*, $n = 140$; S.e., *Stachyris erythroptera*, $n = 55$; T.b., *Trichastoma bicolor*, $n = 40$; M.s., *Malacocincla septaria*, $n = 22$; M.p., *Macronous ptilosus*, $n = 43$; M.m., *Malacocincla malaccensis*, $n = 56$; H.h., *Hypogramma hypogrammicum*, $n = 48$; S.a., *Sasia abnormis*, $n = 38$; A.p., *Alophoixus phaeocephalus*, $n = 45$; P.m., *Prionochilus maculatus*, $n = 46$).

in trophic position (Supporting Information). Hence although all but one species occupied higher trophic positions in degraded forest, the largest differences were among those species that occupied relatively low trophic positions in primary forest.

Within each forest type, there was a difference of greater than a trophic level in MTP among species in the same feeding guild (Supporting Information). For instance, MTPs of species defined as being solely insectivores ranged from 2.6 (consumption of insects and fruit) to 3.9 (consumption of mainly predatory insects). Between forest types, the trophic position of individuals in 5 of the 6 feeding guilds increased after forest degradation, with frugivores revealing no difference (Table 1). Similar results were found with the 36 species that inhabited both forest types (Supporting Information). The differences in trophic positions would thus have been obscured if species were grouped into static feeding guilds.

Trophic-Niche Width

The trophic-niche widths of species recorded in both habitats were significantly lower in degraded forest (mean [SE] = 8.22 [0.8]) than in primary forest (10.02 [0.8]; $F_{1,35} = 5.1, p = 0.029$). This result indicates less variation in trophic position among individuals after logging.

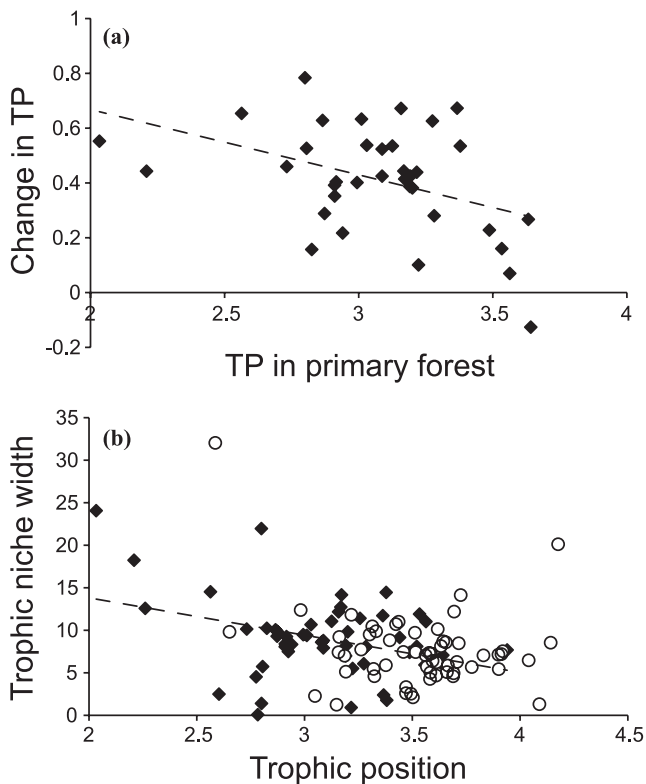


Figure 2. Relations between (a) a species' mean trophic position (TP) in primary forest and the change in trophic position following forest degradation ($\Delta\text{mean TP} = \text{mean TP}_{\text{degraded}} - \text{mean TP}_{\text{primary}}$) and between (b) trophic-niche width and mean trophic position in primary forest (diamonds) and degraded forest (circles) (dashed line, significant relation for primary forest).

For such shared species, trophic-niche widths within primary forest were also significantly higher than those of the 16 species recorded only in primary forest (6.93 [0.6]; $F_{1,37} = 5.45$, $p = 0.025$); thus, species with narrower trophic-niche widths did not persist following logging. In addition, there was a significant negative relation between MTP and trophic-niche width in primary forest

(Fig. 2b) ($F_{1,37} = 7.9$, $p = 0.008$), whereas there was no such relation in degraded forest ($F_{1,39} = 4.1$, $p = 0.1$).

Discussion

Changes in Trophic Organization

This is the first study to test the effects of logging on the trophic positions and trophic-niche widths of species within a tropical rainforest. MTPs of species in primary forest were consistent with previous information on birds' diets (Supporting Information) but also revealed extensive and previously unknown differences in trophic positions within what were previously considered largely homogenous feeding guilds (see Supporting Information for further discussion). Our data indicate a significant elevation in the trophic positions of understory birds in response to intensive logging of tropical rainforest.

Results of recent studies suggest that nitrogen-enrichment factors may vary physiologically (Dennis et al. 2010; Hahn et al. 2012) and, in particular, that apparently elevated trophic positions can result from changes in nitrogen metabolism associated with lowered body condition (Vanderklift & Ponsard 2003; Lee Cruz et al. 2012). However, there was no difference between forest types in the body masses of our study species (means in primary and degraded forest, for 29 species with ≥ 2 measurements in each habitat, were 23.4 g [SE 2.3] and 23.1 g [2.1], respectively; $F_{1,27} = 0.87$, $p = 0.4$). Apparent changes in trophic position can also arise from variation in baseline isotopic ratios (Woodcock et al. 2012), but we accounted for this variation by using baseline $\delta^{15}\text{N}$ values for individual transects where birds were sampled. Hence, we are confident that our data reveal systematic changes in the trophic positions of our study species. More limited evidence of elevations in trophic position in degraded forest has also been recorded elsewhere among small mammals (Nakagawa et al. 2007).

Elevation of trophic positions in degraded forest may have resulted from birds altering their diets (feeding less on fruit and nectar in degraded forest and in the case of insectivores feeding more on predatory arthropods) or

Table 1. Mean (SD) trophic position of feeding guilds in primary and degraded forest.^a

Feeding guild ^b	Primary forest mean (SD)	Degraded forest mean (SD)	df	F	p
F	2.03 (0.5)	2.59 (0.8)	1,30	1.9	0.18
F,I	3.06 (0.5)	3.49 (0.3)	1,242	37.2	<0.0001
I	3.06 (0.4)	3.48 (0.3)	1,494	207.1	<0.0001
I,C	3.16 (0.4)	3.93 (0.5)	1,20	10.1	0.0047
N,I	3.38 (0.5)	3.88 (0.3)	1,142	72.1	<0.0001
O	3.29 (0.5)	3.52 (0.5)	1,149	16.8	0.0001

^aStatistics are outputs from linear mixed-effects models.

^bAbbreviations: F, frugivore; I, insectivore (including snails, spiders, and other arthropods); C, carnivore (small fish and amphibians); N, nectarivore; O, omnivore (3 or more of the above guilds).

from increases in the trophic positions of their prey or both (Post et al. 2000; Post & Takimoto 2007; McHugh et al. 2010). The notion that some prey species may have altered their trophic positions is supported by results that show elevated trophic positions of arboreal ants in young secondary rainforest regrowth on abandoned agricultural land (Blüthgen et al. 2003). Several researchers have reported a decline in key fruiting trees such as figs (*Ficus* spp.) following logging (reviewed by Meijaard et al. 2006). In addition, small-fruited pioneer trees (e.g., *Macaranga* spp.) become abundant in Dipterocarp forest only after a period of regeneration, and they produce fruit only sporadically, probably leading to a lower availability of fruit in recently logged forest compared with primary forest (Cleary et al. 2007). Hence our findings probably reflect both changes in the diets of our study species and changes in the trophic positions of some of their prey.

The compression of trophic-niche widths we found suggests there were fewer differences among individuals in the proportions of prey from different trophic levels in degraded forest. This suggestion supports the notion that species consumed more restricted diets, at least in terms of the diversity of trophic levels incorporated in food items. For instance, among the most frequently sampled species, the MTP of Little Spiderhunter ($n = 140$) increased from 3.4 in primary forest to 3.9 in degraded forest and was accompanied by a halving of the coefficient of variation in trophic position, from 14.5% to 7.2% (Fig. 2a & Supporting Information). The increase in trophic position and reduction in coefficient of variation probably indicate a shift to feeding mainly on predatory arthropods (spiders). Similar compression of trophic niches has been recorded in fragmented aquatic ecosystems, where it may also indicate declines in resource diversity at lower trophic levels (Rooney et al. 2006; Layman et al. 2007).

Species Persistence in Degraded Forest

Across all species, about 80% of those recorded in undisturbed forest were still present in heavily logged forest (Supporting Information) (Edwards et al. 2011). Those not recorded after logging included frugivores and insectivores, in keeping with previous studies (Cleary et al. 2007; Gray et al. 2007). This partly reflected the mode of foraging (e.g., terrestrial vs. sallying insectivores [Cleary et al. 2007; Edwards et al. 2009]) but not consistently so. For example, among terrestrial insectivores, Bornean Ground-babbler (*Ptilocichla leucogrammica*) was recorded only in primary forest, Black-headed Pitta (*Pitta ussberti*) was recorded only in degraded forest, and Blue-headed Pitta (*Pitta baudii*) was recorded in both (Supporting Information). The likelihood of species persistence did not differ systematically with trophic position and thus provided no support for the hypothesis that

the persistence of species in degraded forest is related to species' trophic positions in primary forest.

However, those species with narrower trophic-niche widths in primary forest were less likely to persist, in keeping with other studies indicating a higher vulnerability of dietary specialists to local extinction following habitat disturbance (Boyles & Storm 2007; Ockinger et al. 2010). Dietary flexibility may thus provide a key mechanism for explaining the retention of high biological value within logged rainforests. However, the significant compression of trophic-niche widths following logging that we found (Fig. 2b) suggests species assemblages and food webs in intensively logged forest are likely to be less resilient to any further changes, in particular changes associated with fire. Although repeated fires in primary forest allow considerable retention of species in this region (Slik & Van Balen 2006), the combined effects of intensive logging and a severe burn could have more serious negative consequences for communities.

Static Feeding Guilds and Trophic Flexibility

Many researchers have grouped birds in static feeding guilds to determine the effects of disturbance on community composition (Lambert 1992; Cleary et al. 2007; Gray et al. 2007; Edwards et al. 2009) and functional diversity (Flynn et al. 2009; Hidasi-Neto et al. 2012). Such groupings have implications for our understanding of changes to ecosystem functions and services. However, our study reveals that the ecological roles of species within such static groups are likely to differ widely. We found that species spanned more than a trophic level within individual feeding guilds (Supporting Information) and that trophic positions were elevated within most feeding guilds after rainforest disturbance (Supporting Information). Our results also highlight that birds can be incorrectly categorized into feeding guilds (e.g., supposedly obligate insectivores that also eat fruit). Hidden flexibility within feeding guilds, plus the imprecise grouping of species, could lead to erroneous conclusions about the functional effects of disturbance on ecosystem services, such as seed dispersal, predation, and pollination (Tilman et al. 1997; Hidasi-Neto et al. 2012), and about the role of feeding ecology in determining species persistence after disturbance (as highlighted by Kaiser-Bunbury et al. 2010; Staniczenko et al. 2010). Our study thus provides impetus for the use of flexible measures of trophic level over categorization in static feeding guilds.

We found widespread changes in trophic organization that were not apparent from changes in species composition. Our data highlight the importance of focusing on trophic flexibility over the prevailing emphasis on membership of static feeding guilds and our data thus support the notion that alterations to trophic organization and interactions within tropical forests may be a pervasive and functionally important hidden effect of forest

degradation (Tylianakis et al. 2007). Our data indicate that, from a practical perspective, ensuring the protection of degraded forests from any further disturbance is likely to be of critical importance for conserving biodiversity, particularly within Southeast Asia where most forests have been or are designated to be logged. Our results also highlight the importance of maintaining protected areas of intact forest to preserve not only individual species but also the complex networks of trophic interactions within which those species are embedded.

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Supporting Information

Map of sample locations (Appendix S1), methods for stable isotope analysis (Appendix S2), table of feeding guilds, trophic positions, and abundances of recorded species (Appendix S3), figure of the proportional change in trophic position following logging against trophic position in primary forest (Appendix S4), table of mean trophic positions of shared species grouped within feeding guilds (Appendix S5), and discussion of trophic positions within primary forest (Appendix S6) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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