

Thresholds of Logging Intensity to Maintain Tropical Forest Biodiversity

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Summary

Primary tropical forests are lost at an alarming rate, and much of the remaining forest is being degraded by selective logging [1–5]. Yet, the impacts of logging on biodiversity remain poorly understood, in part due to the seemingly conflicting findings of case studies: about as many studies have reported increases in biodiversity after selective logging as have reported decreases [2, 6–11]. Consequently, meta-analytical studies that treat selective logging as a uniform land use tend to conclude that logging has negligible effects on biodiversity [2, 6, 12]. However, selectively logged forests might not all be the same [2, 13–15]. Through a pantropical meta-analysis and using an information-theoretic approach, we compared and tested alternative hypotheses for key predictors of the richness of tropical forest fauna in logged forest. We found that the species richness of invertebrates, amphibians, and mammals decreases as logging intensity increases and that this effect varies with taxonomic group and continental location. In particular, mammals and amphibians would suffer a halving of species richness at logging intensities of 38 m³ ha⁻¹ and 63 m³ ha⁻¹, respectively. Birds exhibit an opposing trend as their total species richness increases with logging intensity. An analysis of forest bird species, however, suggests that this pattern is largely due to an influx of habitat generalists into heavily logged areas while forest specialist species decline. Our study provides a quantitative analysis of the nuanced responses of species along a gradient of logging intensity, which could help inform evidence-based sustainable logging practices from the perspective of biodiversity conservation.

Results and Discussion

Our meta-analysis data set, resulting from a literature review, comprises 98 response ratios from 48 tropical studies (Figure 1). Each response ratio (hereafter, relative species richness) corresponds to the species richness at a logged site divided by the species richness at a control site. Only studies that fully described the selection of an appropriate control site

were included in the literature review (see the [Experimental Procedures](#)). The predictors for relative species richness we considered include (1) logging intensity, (2) time since last selective logging event, (3) area of logged forest parcel, (4) total area of forest fragment, (5) proportion of forest fragment logged, (6) prelogging stem density, (7) distance to nearest primary forest, (8) geographic location, (9) altitude, and (10) taxonomic group (Table S1 available online). Our funnel plot appears to be symmetrical, suggesting that our sample of studies does not suffer from a publication bias (Figure S1).

Model Selection and Parameter Estimates

From the set of 34 candidate models proposed to explain the difference in species richness between a logged forest and an equivalent primary forest site, the most parsimonious one was model M13 (richness ~ taxon * logging intensity). This model had the lowest AICc (Akaike Information Criterion corrected for a small sample size) value and explained 30% of deviance in the data relative to the null model, M0 (Table 1). Model M13 indicates that logging intensity, within the range considered in this study (0.7 m³ ha⁻¹ to 200 m³ ha⁻¹), is a good predictor of the impact of selective logging on species richness. Additionally, the nature of this relationship differs among the four taxonomic groups we considered (mammals, amphibians, invertebrates, and birds).

The second most parsimonious model was model M29 (richness ~ taxon * logging intensity * continent), which also had a relatively low AICc value ($\Delta AICc = 0.28$) and explained 52% of deviance in the data (Table 1). This more complex model further implies that the relationship between species richness, logging intensity, and taxonomic group also varies according to the continental location of the study site (Afrotropical, Indomalayan, or Neotropical).

The final, best model, obtained from the model averaging of the two most parsimonious models, can be expressed as

$$S_{ij} = \alpha_{ij} + \beta_{ij}L + \varepsilon_{ij}, \quad (\text{Equation 1})$$

where $i \in (1, 2, 3, 4)$, $j \in (1, 2, 3)$, and $\varepsilon_{ij} \approx N(0, \sigma^2)$ and where the relative species richness, S , of taxonomic group, i , on continent, j , depends on logging intensity, L , taxon- and continent-specific intercept, α , and slope, β (Table S3).

Our final model suggests that logging intensity, taxonomic group, and continental location are more important for predicting logging impacts than are the other explanatory variables on which we have sufficient information, such as area of forest fragment, isolation from primary forests, time since disturbance, or proportion of the forest that has been logged [16–18]. This is also shown by the high cumulative Akaike weight of the two best models (0.98).

Our results from model averaging show that there are more species of mammals, amphibians, and invertebrates in lightly logged forests than in primary forests (Figures 2 and S2 and Table S3). However, as logging intensity increases, the relative species richness of these three taxonomic groups decreases linearly, dropping below their primary forest richness at logging thresholds of 10 m³ ha⁻¹ for mammals (95% confidence interval [CI]: 4–18 m³ ha⁻¹), 23 m³ ha⁻¹ for amphibians (95% CI: 0–49 m³ ha⁻¹), and 41 m³ ha⁻¹ for invertebrates

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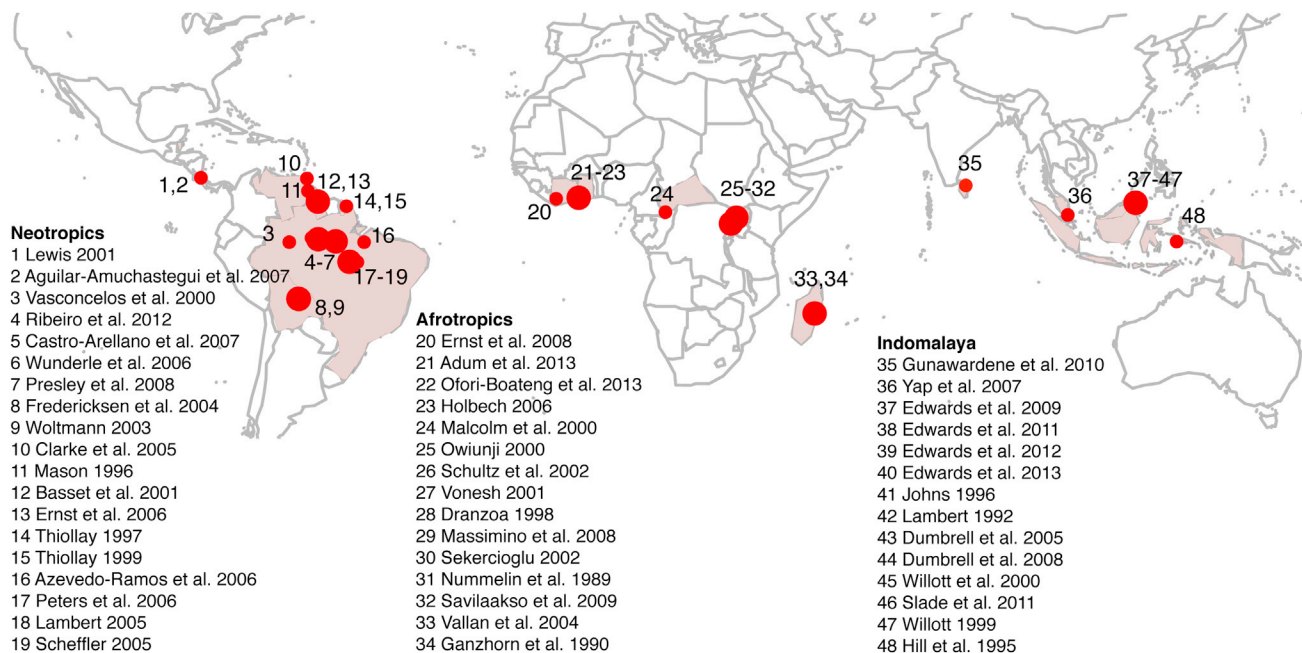


Figure 1. Studies Included in the Meta-analysis on the Impacts of Selective Logging on Species Richness

All studies had to fulfill the inclusion criteria specified in the literature review (Supplemental Experimental Procedures). See also Figure S1.

(95% CI: 0–78 $\text{m}^3 \text{ha}^{-1}$). Crucially, mammals and amphibians would drop below 50% of their species richness in primary forests at the logging intensities of 38 $\text{m}^3 \text{ha}^{-1}$ and 63 $\text{m}^3 \text{ha}^{-1}$, respectively, if the linear trend of decreasing richness continues (95% prediction interval: 18–140 $\text{m}^3 \text{ha}^{-1}$ for mammals and 3–200 $\text{m}^3 \text{ha}^{-1}$ for amphibians).

Mammals

We found that mammals and amphibians are the most sensitive groups to selective logging in terms of the rate of decline in species richness (Figure 2 and Table S3). Every increase of 20 $\text{m}^3 \text{ha}^{-1}$ in logging intensity results in an approximately 35% decrease in mammal species richness. In contrast, recent reviews conclude that mammals are the least sensitive taxonomic group to logging [2, 12]. Whereas most previous studies focused on analyzing the average response of species to selective logging as a uniform land use (mean effect size), we explicitly quantified the responses of species along a gradient of logging intensity.

The high sensitivity of mammals to selective logging may be due to the increased hunting and poaching pressure, often associated with the increased incursion into forests through logging roads [19]. Although we excluded studies that confirmed hunting in either the logged or control study sites (see the Experimental Procedures), it is nevertheless possible that hunting might be underreported in some logged forests [20, 21].

Primates are not included in our data set, as the vast majority of studies on the impact of logging on primates measures primate abundance, rather than richness, which is typically very low [22].

Amphibians

The steep decline of amphibian species richness in logged areas may be due to their high sensitivity to hotter and drier microclimates, which are created by selective logging

[23, 24]. This effect of climate might be compounded by the lower vagility of amphibians [25]. Additionally, direct mortality of amphibians during a logging operation might be higher than that for other, more vagile, taxa. In broader and global studies of forest conversion, including secondary forests and agroforestry, amphibian richness has been found to decrease with decreasing canopy cover and leaf litter depth [21, 26].

Invertebrates

Invertebrates showed a relatively gradual decrease in species richness with logging intensity. The invertebrate data set included mainly studies on butterflies, dung beetles, ants, and a few other terrestrial taxa. Butterfly richness in disturbed and secondary forests has been previously found to depend on the spatial scale of the study [27], and dung beetle richness in secondary forests depends in part on the forest fragment size [28]. However, focusing exclusively on selectively logged forests, we found that logging intensity is the most important determinant of invertebrate species richness. In temperate forests, a similar relationship of species richness declining with decreasing forest retention levels has been shown for certain invertebrate groups [29, 30].

Birds

Birds exhibit a contrasting trend, whereby their species richness gradually increases with logging intensity (Figure 2 and Table S3). An equivalent pattern of increasing bird species richness with increasing logging intensity has been found in Ghana, where, however, only low logging intensities were considered [14]. Similarly, in temperate forests, increasing intensity of forest thinning has also been found to be correlated with higher bird species richness [31].

Our analysis of the forest specialist bird species shows that when total species richness of birds increases above the control site richness, the richness of forest specialist birds, S_{FS} , decreases (Figure 3). The relative richness of habitat

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Table 1. Candidate Models Explaining the Relative Species Richness in Logged Tropical Forests, Ranked According to Increasing Value of ΔAIC_c

Model	Equation	$\log(L)^a$	K^b	ΔAIC_c^c	w_i^d	DE (%) ^e
13	richness ~ taxon * intensity	-405.75	9	0	0.52	30
29	richness ~ taxon * continent * intensity	-388.46	21	0.28	0.46	52
11	richness ~ taxon * continent	-406.45	11	6.5	0.02	29
15	richness ~ taxon * distance to unlogged	-411.98	9	12.46	0	20
3	richness ~ logged area	-420.33	3	15.28	0	5
0	richness ~ 1	-422.49	2	17.44	0	0
33	richness ~ taxon * continent * intensity + taxon * time + altitude + distance to unlogged + logged area + forest area + stems	-391.79	24	17.57	0	48
30	richness ~ taxon * continent * time	-397.51	21	18.37	0	42
5	richness ~ intensity	-421.97	3	18.54	0	1
2	richness ~ continent	-420.94	4	18.67	0	3
8	richness ~ distance to unlogged	-422.14	3	18.89	0	1
7	richness ~ altitude	-422.18	3	18.97	0	1
9	richness ~ proportion logged	-422.2	3	19.02	0	1
4	richness ~ time	-422.27	3	19.15	0	0
6	richness ~ intensity	-422.31	3	19.23	0	0
20	richness ~ intensity + time	-421.8	4	20.39	0	1
22	richness ~ time + proportion logged	-421.82	4	20.42	0	1
25	richness ~ intensity + stems	-421.82	4	20.44	0	1
23	richness ~ intensity + proportion logged	-421.9	4	20.6	0	1
21	richness ~ time + distance to unlogged	-421.96	4	20.71	0	1
1	richness ~ taxon	-421.54	5	22.12	0	2
27	richness ~ intensity + time + stems	-421.67	5	22.36	0	2
12	richness ~ taxon + intensity	-420.88	6	23.08	0	3
10	richness ~ taxon + continent	-419.76	7	23.18	0	6
14	richness ~ taxon + distance to unlogged	-421.15	6	23.62	0	3
24	richness ~ taxon * altitude	-417.72	9	23.94	0	10
18	richness ~ taxon + proportion logged	-421.32	6	23.95	0	2
16	richness ~ taxon + time	-421.35	6	24.02	0	2
26	richness ~ taxon + proportion logged + continent	-419.07	8	24.2	0	7
28	richness ~ taxon + intensity + stems	-420.83	7	25.31	0	4
31	richness ~ taxon + time + stems	-421.73	7	25.81	0	4
17	richness ~ taxon * time	-419.17	9	26.85	0	7
19	richness ~ taxon * proportion logged	-420.21	9	28.92	0	5
32	richness ~ taxon + continent + time + intensity + altitude + distance to unlogged + logged area + forest area + stems	-416.44	14	34.61	0	12

Response variable is the relative total species richness for all taxa. Variable codes re described in the [Experimental Procedures](#). See also [Table S1](#).

^aMaximum log likelihood.

^bNumber of parameters.

^c $\Delta AIC_c = AIC_c - AIC_{c_{min}}$.

^dAkaike weights.

^eDeviance explained by the model $DE_i = ((D_{null} - D_i) / D_{null})100$.

generalists, S_{FG} , increases linearly with the total relative species richness of all birds ([Figure 3](#)). This means that whenever logging leads to higher total bird species richness, the number of forest specialist species markedly decreases, which is outweighed by the strong increase in the richness of habitat generalists.

This suggests that the seemingly low susceptibility of birds to selective logging, when all species are considered, is due to an influx of habitat generalists ([Figure 2](#) and [3](#)). A similar pattern has been suggested by numerous studies in both temperate and tropical forests under various forms of degradation [[15](#), [21](#), [32](#)] but had previously not been quantified in logged tropical forests.

To some extent, the positive response of total bird species richness to logging intensity could be also explained by an observational bias. Birds are more easily detected in disturbed habitats, including logged forests [[33](#)]. Additionally, some bird species, being more mobile, might be overall less susceptible to logging, as they might be using different patches of (logged) forests for different resource needs. Certain frugivorous and nectarivorous species may successfully forage in forests

logged at intermediate intensities, where food is more abundant, while still nesting in primary forests [[34](#)].

On the other hand, the decreasing richness of forest specialists at higher logging intensities might be further exacerbated by unreported hunting of large bird species, such as hornbills, macaws, or pigeons [[35](#), [36](#)]. Further, it is possible that historical hunting pressure had removed most hunted birds in some control and logged forests, which would mask some effects of logging [[35](#), [37](#), [38](#)].

Continental Difference

Neotropical fauna appears to be more sensitive to logging intensity than Afrotropical and Indomalayan fauna, apart from mammals, which decline even more steeply in richness in Africa than in the Neotropics ([Figure S2](#) and [Table S3](#)). There is a lack of studies of species richness in selectively logged forests on mammals and amphibians from the Indomalayan region. The differential responses of fauna to logging on the three continents might be connected with different total, per hectare of biomass, as well as with different logging practices.

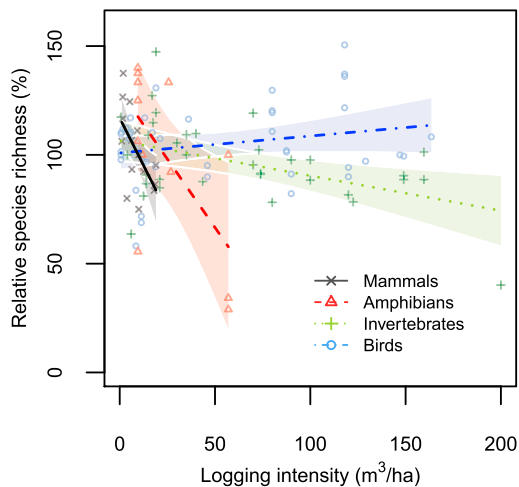


Figure 2. The Influence of Logging Intensity and Taxonomic Group on Relative Species Richness in Selectively Logged Forests

Parameter estimates for logging intensity and taxonomic group obtained from model averaging of the two most parsimonious models. Relative species richness refers to the absolute species richness at a logged forest site divided by the absolute species richness at an equivalent primary forest control site. Shaded areas represent 95% confidence intervals. Each point is one response ratio. See also [Figure S2](#) and [Table S3](#).

Limitations

Our conclusions cannot be extrapolated beyond the logging intensities considered in our analysis (approximately 0.2 to 20 trees ha^{-1}). Nonetheless, through our comprehensive review of logging studies, our analysis reflects a realistic range of logging intensity occurring in the tropics. We recognize that a weighted meta-analysis could have improved the confidence with which we can estimate our model parameters and logging intensity thresholds. However, inconsistent error reporting across individual logging studies precluded us from doing so. During the literature review, we faced a tradeoff between the number of data points that we include (over 200 studies could have potentially been included) and their quality. To maintain high standards of the meta-analysis, we have included only data that fulfilled our quality criteria, as described in the [Experimental Procedures](#). We also recognize that some logging studies might suffer from pseudoreplication in their sampling design [7]. Nonetheless, this potential problem would not affect a meta-analysis of species richness, which we are primarily interested in (as opposed to similarity in species composition) [7]. While we realize that there are multiple metrics of biodiversity (e.g., beta diversity or functional diversity), we focused on local species richness (alpha diversity) because it is the most widely reported metric in the context of selective logging. Species richness has to be interpreted with caution, as shown also by our supplemental findings on forest specialist and generalist bird species.

Management Implications

The quest for finding meaningful thresholds of harvest intensity that might be crucial to biodiversity is not unique to tropical forest conservation. In temperate and boreal regions, retention forestry has become widely practiced over the last three decades. Whereas selective logging focuses mainly on how much timber is harvested, retention forestry prescribes how many trees remain after harvest without the intention of

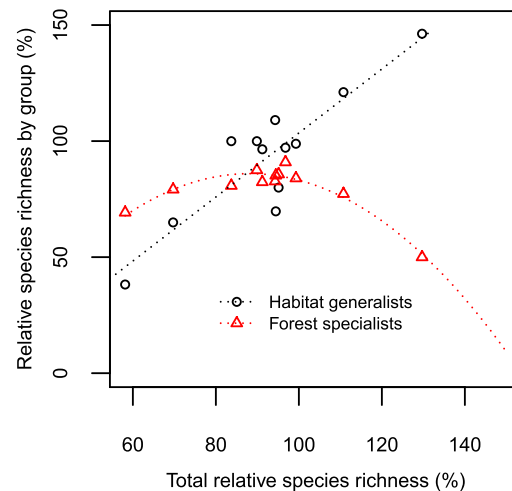


Figure 3. Detailed Analysis of Bird Species Richness in Logged Forests

Red triangles indicate the relative species richness of forest specialist bird species in selectively logged forests and the relationship with total relative species richness ($p < 0.001$; adjusted $R^2 = 0.91$). Black circles indicate the relative species richness of bird habitat generalists and a positive linear relationship with total species richness ($p < 0.001$, adjusted $R^2 = 0.78$). Forest specialist classification is described in the [Experimental Procedures](#). See also [Table S2](#).

extracting them in the future. Despite different goals, parallels can be drawn. Several studies have for example examined how different levels (and spatial configuration) of retention logging affect biodiversity [29, 39, 40]. However, a consensus on optimal retention level thresholds for biodiversity conservation is yet to be found [30, 41].

Our results show that the volume of timber extracted is the most important predictor of species richness in logged forests. However, logging intensity should not be the sole basis of forest management strategies. First, a wealth of studies shows that reduced-impact logging is a desirable practice in tropical forestry for maintaining plant diversity, soil quality, and carbon accumulation [42, 43]. Second, there is mounting evidence that forests should be managed as complex adaptive systems [44]. Therefore, adaptation of logging intensities should be accompanied by, for example, the maintenance of ecosystem legacies, such as hollow trees that are not valuable to timber production but are crucial to biodiversity [21, 45]. Additionally, which individuals will be spared from harvest should not be dictated purely by the evolving marketability of tropical timber species.

Conclusions

Selectively logged forests are becoming an increasingly dominant component of many tropical landscapes [2]. And yet, the conservation value of selectively logged tropical forests is less understood, and most likely more overestimated, than those of more dramatic land cover changes, such as deforestation driven by agriculture or tree-plantation developments. Our analysis reveals that mammals and amphibians are particularly sensitive to logging intensity and would suffer halving of species richness at logging intensities of just 38 $\text{m}^3 \text{ha}^{-1}$ and 63 $\text{m}^3 \text{ha}^{-1}$, respectively. On the other hand, most taxonomic groups would be resilient to selective logging at intensities of less than 10 $\text{m}^3 \text{ha}^{-1}$. Our study provides a quantitative analysis of the nuanced responses of species along a gradient

of logging intensity that could help inform evidence-based sustainable logging practices from the perspective of biodiversity conservation.

Experimental Procedures

We carried out a literature review to compile a database of studies on the impact of selective logging on tropical forest fauna, including birds, mammals, amphibians, and invertebrates. To search for publications, extract data, and evaluate data quality, we used guidelines for systematic reviews that are designed to provide an exhaustive and unbiased summary of information available in the literature (Supplemental Experimental Procedures) [46]. Using the compiled database, we performed a meta-analysis of species richness response to selective logging.

Meta-analysis

We constructed a funnel plot to test for any publication bias [47, 48]. We plotted relative species richness on the x axis against a measure of study precision on the y axis (total sample size of each study). An asymmetrical funnel plot would indicate a likely publication bias [48, 49].

We analyzed relative species richness, S , in selectively logged forest as the main response variable. We calculated S for each study by dividing the absolute species richness of the logged forest site, S_{log} , by the absolute species richness of the control site of an equivalent size or of an equivalent sampling effort, S_{prim} , namely, $S = S_{log} / S_{prim}$. For ease of interpretation, we express S as a percentage value.

For birds, we analyzed two additional response variables. S_{FS} corresponded to the relative species richness of forest specialist species at a logged site. We calculated S_{FH} as the absolute number of forest specialist species at the logged site divided by the absolute number of forest specialist species at the control site of an equivalent size. In the same manner, we calculated the relative richness of habitat generalists, S_{FG} .

We extracted data on habitat use by birds from checklists, which were available for 12 out of 28 data points for birds [50–53]. All bird species in the checklists were assigned to be forest specialist or habitat generalist, according to their habitat use (Table S2). Species are classified as forest specialists if their primary habitat is forest and they can utilize not more than two additional habitat types besides forest (e.g., forest only; forest and riparian; or forest, riparian, and wetland), based on a database of ecology of the world's birds [54]; all other forest species are classified as habitat generalists.

We used the information-theoretic approach to identify the most parsimonious combination of predictors that could explain changes in species richness, S , in response to selective logging [55–57]. Each of the candidate models corresponds to a particular, biologically realistic hypothesis (Table 1).

An additional advantage of choosing the information-theoretic approach is that we were able to evaluate all the competing hypotheses, analyzed as a set of a priori candidate models (Table 1), without increasing the probability of type I error, which is one of the problems of multiple hypothesis testing [55, 58, 59]. We fitted these models to our data set and identified the most parsimonious model based on the Kullback-Leibler information, estimated by the AICc [60]. The most parsimonious model has the lowest value of AICc [55, 60].

Our data set has a nested structure, whereby a data point is nested within a study, which is nested within a forest, and a forest is nested within a country and continent. We used a mixed-effect modeling approach to account for this nested structure in our data by specifying “study,” “forest,” and “country” as nested random effects in our model (Table S1) [61]. Continent, having only three possible levels, was considered as a fixed effect. We only included the random effects in the final model if they explained additional variance compared to the fixed effects-only model [61].

Based on the model averaging of the most parsimonious models, we derived the logging intensity at which a taxonomic group would suffer a 50% decrease in species richness with respect to its species richness in a control site (primary forest) [55].

We carried out all analyses in the statistical software R, version 3.0.1 [62].

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, two figures, and three tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.06.065>.

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