

Do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles

Filipe França^{1,2*†}, Julio Louzada^{1,2}, Vanesca Korasaki^{1,3}, Hannah Griffiths^{1,2,4}, Juliana M. Silveira¹ and Jos Barlow^{1,2,5}

¹Departamento de Biologia, Universidade Federal de Lavras, Lavras, MG 37200-000, Brazil; ²Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster LA1 4YQ, UK; ³Universidade do Estado de Minas Gerais, Av. Prof. Mario Palmério, 1001, Frutal, MG 38200-000, Brazil; ⁴School of Environmental Sciences, University of Liverpool, Liverpool L69 3GP, UK; and ⁵Museu Paraense Emilio Goeldi, Av. Magalhães Barata, 376, Belém, PA 66040-170, Brazil

Summary

1. Human alteration of the global environment is leading to a pervasive loss of biodiversity. Most studies evaluating human impacts on biodiversity occur after the disturbance has taken place using spatially distinct sites to determine the undisturbed reference condition. This approach is known as a space-for-time (SFT) substitution. However, SFT substitution could be underestimating biodiversity loss if spatial controls fail to provide adequate inferences about pre-disturbance conditions.

2. We compare the SFT substitution with a before–after control–impact (BACI) approach by assessing dung beetles before and after a logging exploration in the Brazilian Amazon. We sampled 34 logging management units, of which 29 were selectively logged with different intensities after our first collection. We used dung beetle species richness, species composition and biomass as our biodiversity response metrics and the gradient of selective logging intensity as our explanatory metric.

3. Only the BACI approach consistently demonstrated the negative impacts of logging intensification on all dung beetle community metrics. Moreover, the BACI approach explained significantly more of the variance in all the relationships and it doubled the estimates of species loss along the gradient of logging intensity when compared to SFT.

4. *Synthesis and applications.* Our results suggest that space-for-time (SFT) substitution may greatly underestimate the consequences on local species diversity and community turnover. These results have important implications for researchers investigating human impacts on biodiversity. Incentivizing before–after control–impact (BACI) approaches will require longer-term funding to gather the data and stronger links between researchers and landowners. However, BACI approaches are accompanied by many logistical constraints, making the continued use of SFT studies inevitable in many cases. We highlight that non-significant results and weak effects should be viewed with caution.

Key-words: before–after control–impact, Brazilian Amazon, Chronosequences, land-use change, rain forest, reduced-impact logging, resampling, selective logging, space-for-time substitution, species diversity

Introduction

It is well known that human alteration of the global environment is leading to a pervasive loss of biodiversity (Cardinale *et al.* 2012; Newbold *et al.* 2015). Habitat loss

and degradation remain the main causes of biodiversity loss and species extinctions across the world (Krauss *et al.* 2010; Mantyka-pringle, Martin & Rhodes 2012). This is particularly so in the tropics, which contain most of the world's biodiversity and have some of the highest rates of land-use change (Lambin, Geist & Lepers 2003; Romdal, Araújo & Rahbek 2013).

Understanding the rate and spatial distribution of biodiversity loss requires accurate assessments of the

[†]Present address: Departamento de Biologia, Setor de Ecologia, Universidade Federal de Lavras, Lavras, MG 37200-000, Brazil

*Correspondence author. E-mail: filipeufla@gmail.com.

impacts of land-use change and land management (Gibson *et al.* 2011; Romdal, Araújo & Rahbek 2013). Much ecological research has been directed at this, and there are a growing number of attempts to summarize this in meta-analyses (Gibson *et al.* 2011; Newbold *et al.* 2012, 2015; Bicknell *et al.* 2014b; Burivalova, Şekercioğlu & Koh 2014; Pfeifer *et al.* 2014). For example, a global meta-analysis clearly shows how land-use changes and associated pressures reduce the local terrestrial biodiversity (Newbold *et al.* 2015), while a pan-tropical meta-analysis provides some hope by highlighting the relatively great biodiversity value from selectively logged forests (Gibson *et al.* 2011). Despite the obvious appeal of these global syntheses, any such meta-analyses will only ever be as reliable as the design of the many studies that supply the data. It is therefore timely and important to examine whether the most frequently used study designs are likely to reveal the true impacts of human activities, and provide information that can be used for developing effective conservation strategies.

One important problem researchers face when evaluating human impacts on biodiversity is that the main disturbance events have already taken place. As a result, studies are forced to use spatial reference sites in nearby regions where the human impact of interest has not yet occurred (e.g. Edwards *et al.* 2011, 2012a,b; Thomaz *et al.* 2012; Berenguer *et al.* 2014). This approach is known as a space-for-time (SFT) substitution and dominates the literature on land-use change. For example, we reviewed the available literature evaluating selective logging impacts on tropical invertebrates and found that 49 out of 53 publications evaluating these effects were based on space-for-time approaches (see Appendix S1 in Supporting Information). However, such approaches assume that spatial controls accurately represent pre-disturbance conditions where the disturbance has taken place, which may be undermined by spatial heterogeneity in biodiversity and the non-random location of disturbance events (Pickett 1989; Johnson & Miyanishi 2008). In an ideal world, when researchers are able to sample prior to the disturbance event, they therefore use a before–after control–impact (BACI) design (Smith 2002). BACI designs have been conducted in several experimental landscape manipulations (Forkner *et al.* 2006; Kibler, Tullós & Kondolf 2011; Chai, Healey & Tanner 2012) and studies (e.g. see Appendix S1). While most researchers recognize the potential benefits of a BACI design (Kibler, Tullós & Kondolf 2011; Bicknell, Struebig & Davies 2015), it is not clear to what extent a reliance on SFT studies could be affecting inferences about human impacts on biodiversity in terrestrial environments.

We address this by using a planned commercial logging operation in the Brazilian Amazon to assess whether space-for-time assessments could result in an underestimation of biodiversity loss in tropical forests. We focus on selective logging as it is one of the most important economic activities in tropical forests (Guariguata *et al.* 2010; Wilson *et al.* 2010) and has been suggested as less environmentally dam-

aging compared to other anthropogenic disturbances like fire, agriculture and fragmentation (e.g. Barlow *et al.* 2006; Gibson *et al.* 2011; Edwards *et al.* 2012a,b). We use the dung beetle as a model system, since it is considered as a cost-effective and responsive taxonomic group for evaluating the biological impacts of forestry practices (Scheffler 2005; Gardner *et al.* 2008; Edwards *et al.* 2011, 2012b; Slade, Mann & Lewis 2011; Bicknell *et al.* 2014a).

In particular, we examine to what extent space-for-time and before–after control–impact approaches yield different conclusions regarding the relationship between selective logging intensity and changes in local dung beetle species richness, species composition and biomass. We focus on richness and composition as they have been frequently used in previous studies on a range of tropical taxa (Barlow *et al.* 2007; Gibson *et al.* 2011; Edwards *et al.* 2012b; Imai *et al.* 2012; Bicknell *et al.* 2014b; Burivalova, Şekercioğlu & Koh 2014; Solar *et al.* 2015). We include biomass as this has been extensively used to assess the impacts of tropical forest disturbance on dung beetles (Scheffler 2005; Slade, Mann & Lewis 2011; Nichols *et al.* 2013a). Finally, we compare SFT with BACI by focusing on the difference in effect size (slope of regression) and proportion of explained variance (R^2).

Materials and methods

SITE DESCRIPTION

Sampling was carried out in the *Jari Florestal* landholding, located at the State of Pará in the north-eastern Brazilian Amazon (0°27'S 51°40'W). The primary forests in the region are subject to low levels of disturbance from subsistence hunting and extraction of non-timber forest products (Barlow *et al.* 2010; Parry, Barlow & Peres 2009). The climate is characterized as hot-humid (Köppen's classification), with annual average temperature and precipitation of 26 °C and 2115 mm respectively (Coutinho & Pires 1996).

Reduced-impact commercial logging started in 2003, with plans to log approximately 544 000 ha of native forest over a 30-year cutting cycle. This management is certified by the Forest Stewardship Council (FSC) and is one of the largest certified logging concessions in the Amazon with average annual production of 30 000 m³ of timber (FSC 2014). Logging activities are planned following FAO guidelines (Dykstra & Heinrich 1996), which included a pre-harvest mapping and measuring of all commercially viable trees with d.b.h. ≥45 cm. The harvesting and extraction of timber along skid trails generally take place during the dry season (August to November), and directional felling is used to minimize incidental damage to other trees. During the pre-harvest inventory the logging concession is subdivided into 10-ha (250 × 400 m) planning units. Commercially viable trees are mapped across all of these planning units, and this forms the basis for planning the logging operation in the following year.

SPATIAL DESIGN

We used the company's pre-harvest inventory and operational logging plan to select 34 sample units situated along a gradient of

planned logging intensity. These included five control sites that would not be logged during the course of the study, and 29 logging units which were destined to be logged between July and September 2012 (Fig. S1). As logging impacts are related to logging intensity (Picard, Gourlet-Fleury & Forni 2012; Burivalova, Şekercioğlu & Koh 2014), we aimed to assess logging impact as a continuous (rather than categorical) effect. We therefore selected logging units along the gradient of planned logging intensities, which resulted in a gradient from 0 to 7.9 trees ha⁻¹ (or 0–50.31 m³ ha⁻¹) of timber that was eventually extracted. The five unlogged control units included in this range were the same area as the logged units, and held dung beetle communities representative of undisturbed primary forests in our study region (see Appendix S2). They were located approximately 6.5 km from the closest logging operations to ensure sampling independence and to avoid any spillover effects from the logging operation (Block *et al.* 2001). As such, they are representative of the distance between logged and undisturbed reference sites in many logging studies using space-for-time approaches (Appendix S1).

We used the number of removed trees in each 10-ha sampled unit as our measure of logging intensity for all analyses, as a priori we assumed that the number of treefall events and skidding trails would be the most important predictor of ecological impacts. Moreover, like others we found high colinearity ($N = 34$, $r = 0.91$, $P < 0.001$) among number of trees and volume of removed timber by selective logging (c.f. Picard, Gourlet-Fleury & Forni 2012).

TEMPORAL DESIGN

We carried out two dung beetle collections in all 34 sample units. The first collection gathered pre-logging data and occurred between June and July 2012, approximately 45 days before the logging operation began. The second collection took place in 2013, and gathered post-logging data approximately 10 months after logging activities ended. It also occurred in June and July, to minimize possible effects from seasonal variation. At all sites, dung beetles were sampled in exactly the same locations, and following the same methods, in both sample periods. Sampling locations were relocated based on marking tape, or by GPS when disturbance from logging activities meant this could not be found.

SAMPLING OF DUNG BEETLES

In both collection periods, dung beetles were sampled in each unit using six pitfall traps spaced 100 m apart in a 2 × 3 rectangular grid, so that traps were at least 75 m from the edge of the logging unit (Fig. S2). This spacing of traps helped ensure an even spatial coverage of each logging unit. Pitfall traps were plastic containers (19 cm diameter and 11 cm deep) buried with their opening at ground level, containing approximately 250 mL of a saline solution. A plastic lid was placed above the top as a rain cover. A small plastic cup containing approximately 35 g of pig dung mixed with human dung (4:1 pig-to-human ratio; Marsh *et al.* 2013) was attached by a wire above each pitfall. Data from the six pitfall traps in each unit were pooled to get an aggregate value and improve representation.

We restricted our sample window to 24 h in each collection period, as short sample periods are known to be efficient at attracting a representative sample of the local beetle community (Braga *et al.* 2013; Nichols *et al.* 2013b). Moreover, longer sam-

ple periods would have increased the probability of attracting dung beetles from outside of the sample units (Silva & Hernández 2015), and therefore from units with different logging intensities. Finally, evidence from data collected in the same region suggests a 24-h sampling period as a good predictor of community metrics from longer sampling durations (see Appendix S2).

All dung beetles that fell in pitfall traps were dried and transported to the laboratory where they were identified to species, or morphospecies where this was not possible. We calculated the average biomass of each species from the dry weight of 15 individuals (when possible) using a Shimadzu AY220 balance with precision to 0.0001 g. Voucher specimens were added to the Reference Collection of Neotropical Scarabaeinae in the Insect Ecology and Conservation Laboratory, Universidade Federal de Lavras, Brazil.

DATA ANALYSES

We ran all analyses and statistical models in the R Software version 3.2.0 (R Core Team 2015). We used generalized linear models (GLMs) to obtain the slope, R^2 and P -value of the relationship between logging intensity and the dung beetle species richness, composition and biomass (Fig. 1). All GLMs were submitted to residual inspection to evaluate the adequacy of error distribution (Crawley 2002). We outline the two different sets of GLMs below.

Before–After Control–Impact (BACI)

The pre-logging dung beetle community metrics were used as a temporal control/baseline to examine post-logging effects under the BACI approach. Thus, we used Δ species richness, Δ species composition and Δ biomass as response variables. Δ was based on the difference between total species richness and biomass from post-logging minus pre-logging collection within each sampled unit. The Δ species composition was measured as the pairwise beta-diversity (Socolar *et al.* 2016) based on the Bray–Curtis similarity index (1 – dissimilarity) among pre- and post-logging collections within each sample unit.

Space-for-Time (SFT)

We only considered the post-logging values of species richness, species composition, and biomass. Species composition was estimated as the average Bray–Curtis similarity between each of the 29 logged units and the five control units. For control units, species composition was considered as the average similarity between each control plot and the other four control units. Species composition was calculated through the *vegdist* function (vegan package; Oksanen *et al.* 2015). Lastly, we tested whether our control sites represent typical undisturbed forest communities by comparing them with eleven primary forest sites sampled in the same year across the landscape (see Appendix S2).

To compare the relationship between logging intensity (the number of removed trees) and biological metrics between sample designs (BACI or SFT) we used a resampling procedure based on 1000 bootstrap samples with replacement in the *boot.ci* function from *boot* package (Canty & Ripley 2012; Davison and Hinkley, 1997). This function was also used to estimate frequency distributions, median precision and 95% confidence intervals of regression slopes and R^2 s from the SFT and BACI linear models (Fig. 2).

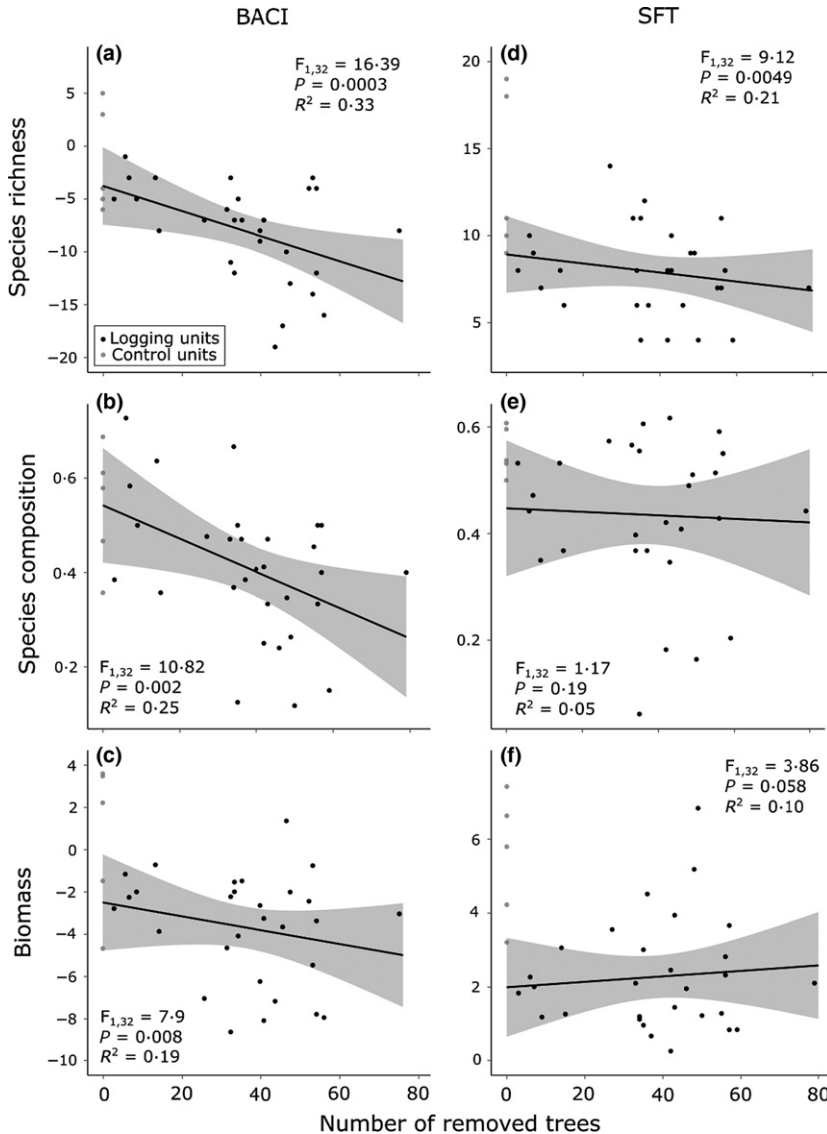


Fig. 1. Differences between a before–after control–impact (BACI) approach and space-for-time (SFT) substitution for (a) Δ species richness; (b) Δ species composition; (c) Δ biomass; (d) post-logging species richness; (e) post-logging species composition; and (f) post-logging biomass of dung beetles ($N = 34$) versus increased number of removed trees ($n.10 \text{ ha}^{-10}$) in the Amazon forest, Brazil. Black dots represent the 29 logging units with different selective logging intensities and the five grey dots represent the five unlogged control units. The lines result from fitting the data to the generalized linear models with respective family distribution.

As adjacent sites may be more similar and naturally hold more closely related biological communities (Soininen, McDonald & Hillebrand 2007; Kühn & Dormann 2012), we checked for spatial autocorrelation by performing Pearson-based Mantel tests (Legendre & Legendre 1998) with 1000 permutations in the mantel function (vegan package; Oksanen *et al.* 2015). We repeated the Mantel tests using both the pre- and post-logging dung beetle data, allowing us to examine whether spatial autocorrelation existed on both sets of analysis. We also repeated these including and removing the five control plots, to examine whether our controls were important in changing patterns. Finally, we plotted the residuals from the GLMs themselves on spatial maps of the sample sites, providing an intuitive visual assessment of the presence of spatial effects in the analysis (Baddeley *et al.* 2005; Kühn & Dormann 2012) (see Appendix S2 for details of Mantel tests and residual plots).

Results

Across our 34 sample units, we recorded 4846 dung beetles (pre-logging: 3720; post-logging: 1126) from 53 species (pre-logging: 49; post-logging: 40). Irrespective of where

or when we sampled, undisturbed forests (i.e. the control sites pre-logging, the control sites post-logging, and the logging units pre-logging) held statistically similar numbers of dung beetle species (Appendix S2).

The Mantel tests of distances among sampled units with corresponding dung beetle species richness and biomass showed a weak but significant degree of spatial autocorrelation in the pre-logging data (species richness $r = 0.18$, $P = 0.005$; biomass $r = 0.12$, $P = 0.035$). Importantly, this spatial autocorrelation disappeared in the post-logging collection (species richness $r = -0.41$, $P = 0.999$; biomass $r = -0.42$, $P = 0.999$), even when control units were excluded from the analysis, and there was no discernible visual association between model residuals and geographical location (see Appendix S2).

BACI AND SFT COMPARISONS

The BACI approach was the only approach to show significant negative effects of logging intensification at $P < 0.05$ for all three dung beetle community metrics

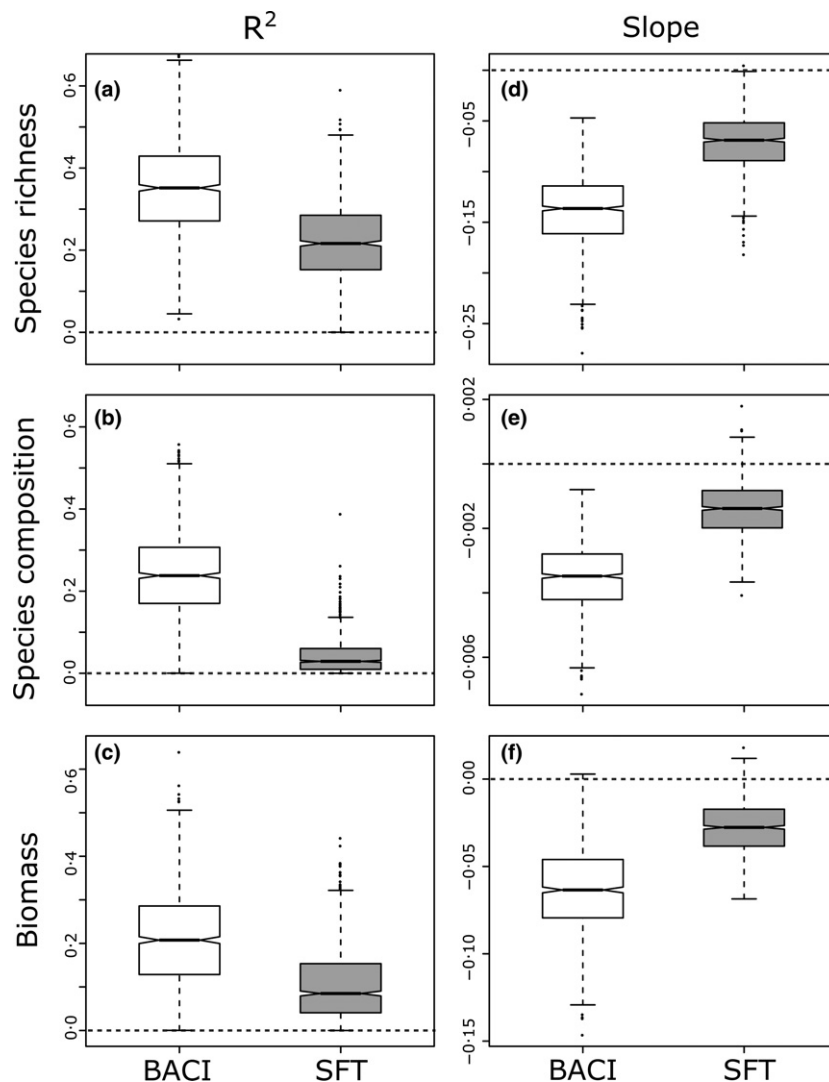


Fig. 2. Accuracy comparison regarding the proportion of explanation (R^2) and effect size (slope of fitted regression) from generalized linear models through the before–after control–impact (BACI) and space-for-time (SFT) approaches. Proportion of explanation and effect size comparisons were made for dung beetle species richness (a, d), species composition (b, e) and biomass (c, f) facing the increased number of removed trees ($n.10 \text{ ha}^{-10}$) by selective logging in the Amazon forest, Brazil. Bootstrapped confidence intervals (represented by vertical dashed lines) were created by resampling procedure based on 1000 bootstrap samples with replacement. On the boxplots, the notch area marks the 95% of confidence intervals for the medians (black horizontal lines). The grey and dashed horizontal line marks the zero line, and outliers are shown in black dots.

(Fig. 1). SFT returned significant negative effects for species richness, but with much weaker effects than the BACI approach, which showed more than double the rate of species loss along the gradient of logging intensity (Fig. 1). The greater statistical power of the BACI approach for detecting changes in the local species richness, species composition and biomass was clearly demonstrated using bootstrapping: BACI had significantly higher R^2 values than SFT (Fig. 2a–c), and the bootstrapped regression slopes for species richness, composition and biomass were significantly lower for BACI than SFT (Fig. 2e–f).

Discussion

Although both before–after control–impact and space-for-time approaches identified some disturbance effects on dung beetle communities, our comparison provide important evidence that BACI approaches highlight more severe consequences of human disturbance on local (α) diversity (species richness) and β -diversity (compositional similar-

ity; Socolar *et al.* 2016). Crucially, BACI approaches revealed more than double the number of species lost from the most disturbed plots, as well as significantly higher estimates of changes in dung beetle species composition and biomass. The significantly weaker effects revealed by the SFT approach are of great concern: SFT designs are the most commonly used method for assessing the biological consequences of selective logging on tropical invertebrates (Appendix S1), and underpin most assessments of biodiversity and ecosystem functioning losses caused by anthropogenic forest disturbances (e.g. Edwards *et al.* 2011, 2012b; a; Thomaz *et al.* 2012; Berenquer *et al.* 2014; Solar *et al.* 2015).

Although our comparison is restricted to a single taxa and a single disturbance event, the magnitude in the scale of effects revealed by BACI and SFT approaches for dung beetle α and β diversity suggests that the potential issues of SFT could apply to other anthropogenic disturbances (such as wildfire, hunting or land-use intensification) and other taxa. Furthermore, the robustness of our conclusions was supported by the Mantel test results and spatial

residual plots (Appendix S2) showing that these patterns were driven by logging intensity and not by any spatial autocorrelation in the data. However, our post-logging collection was conducted about 1 year after logging operations, when logged sites are in their most disturbed state (West, Vidal & Putz 2014). It would be important to evaluate how BACI and SFT studies compare when examining longer-term recovery post-disturbance. Likewise, although providing evidence that the BACI approach better detects changes in species diversity and composition at local scales (Kappes, Sundermann & Haase 2010; Chai, Healey & Tanner 2012), further work is needed to examine how SFT studies, which often contribute to global or pan-tropical meta-analyses (e.g. Gibson *et al.* 2011; Newbold *et al.* 2015), alter effect sizes based on gamma diversity.

Despite the advantages of BACI studies, there are good reasons why they have not been used with more frequency (Kibler, Tullos & Kondolf 2011). When disturbance events have not yet occurred, it is mostly impossible to accurately predict where and when they will happen. This makes it particularly hard to apply BACI designs to wildfires, illegal logging or land-use change. Moreover, even where activities are planned 2–3 years in advance, as in the case of licensed and certified selective logging, it is necessary to have effective communication between researchers, decision-makers and practitioners (companies, planners, and resource managers) in order for BACI studies to take place. The fact that most assessments of the biological impact of selective logging rely on SFT approaches (Appendix S1) shows the difficulty of developing these relationships within the time frame of research projects. Our results therefore support calls to close this ‘knowledge–doing’ gap that exists throughout conservation science (Boreux, Born & Lawes 2009; Habel *et al.* 2013), and show how effective communication and partnerships between researchers and the private sector could be used to support effective conservation practice (Wu & Hobbs 2002). These partnerships need to start long before research is undertaken, both to improve the experimental design and integrate or overcome concerns from researchers and stakeholders.

We also highlight an important logistical constraint of BACI, in that it needs at least two field surveys compared to just one in the SFT approach (Smith 2002). Achieving the pre- and post-disturbance samples in BACI inevitably increases both the time and costs required to collect data, and this additional time may be an equally important limiting factor: most research projects, including postgraduate studies, are a maximum of 3–5 years in duration, which limits the data collection phase of projects to just 1–2 years. It is clearly difficult for students and researchers to undertake BACI studies in relatively short-term research projects or doctoral theses, which rarely allow time enough for two or more field seasons. This can be resolved by longer-term research partnerships that transcend individual studies.

Finally, if the biological baseline as a whole has been shifted by widespread disturbance, then BACI approaches themselves risk underestimating biodiversity loss. We were fortunate that *Jari* landholding has relatively undisturbed primary forests prior to logging operations (Barlow *et al.* 2010; Parry, Barlow & Peres 2009). This allowed us to sample both pre- and post-logging, and verify the intactness of our pre-logging controls by comparing them with other sites in undisturbed primary forests (Appendix S2). However, where forests have been affected by widespread anthropogenic activities (e.g. fires or hunting), the biota present in the before survey will have been filtered by previous disturbances and will not contain the most disturbance-sensitive species. In these cases, BACI comparisons risk underestimating biodiversity loss, and need to be interpreted accordingly (Baum & Myers 2004; Gardner *et al.* 2009; Kibler, Tullos & Kondolf 2011).

CONCLUSIONS

Our study has broad implications for applied ecology and conservation science, as we show that the most frequently used experimental design may lead us to underestimate the consequences of land-use change and forest disturbances on local species diversity and their turnover. While BACI approaches are accompanied by many logistical constraints (e.g. they require a longer time and more sample effort), we believe they should be strongly encouraged in order to re-evaluate human impacts on biodiversity. Finally, although our main aim was to compare methodological approaches, our results also have some important implications for reduced-impact logging which is being planned in timber concessions across 400 Mha of tropical forest (Blaser *et al.* 2011), as they demonstrate high rates of community turnover as well as sharp losses in species diversity and dung beetle biomass, particularly at high logging intensities (c.f. Burivalova, Şekercioğlu & Koh 2014). This emphasizes the need for careful planning and further research before forest management can be termed sustainable for biodiversity conservation.

Acknowledgements

The authors are grateful to Jari Forestal for logistical support. We thank our field assistants Edivar Dias Correa and Jucelino Alves dos Santos, as well as Lisiane Zanella, Ricardo Solar, Teotônio de Carvalho and Fábio Frazão for essential statistical advice and help with figures. We are grateful to Fernando Z. Vaz-de-Mello for help in the identification of specimen material. The manuscript benefited from comments by Luiz Fernando Magnago, Carla Ribas and Alistair Campbell, also from the editors and two anonymous reviewers. This research was supported by grants from the MCTI/CNPq/FAPs (Nº.34/2012) CNPq-PELD site 23 (403811/2012-0). F.F. was awarded by a CAPES studentship (BEX 5528/13-5; DTI-B-B 383744/2015-6). J.B. was supported by CNPq (400640/2012-0). J.M.S was funded by a postdoctoral FAPEMIG fellowship.

Data accessibility

All relevant data used in this manuscript are publicly available at Dryad Digital Repository: doi:10.5061/dryad.1536g (França *et al.* 2016).

References

- Baddeley, A., Turner, R., Møller, J. & Hazelton, M. (2005) Residual analysis for spatial point processes. *Journal of the Royal Statistical Society Series B-Statistical Methodology*, **67**, 617–651.
- Barlow, J., Peres, C.A., Henriques, L.M.P., Stouffer, P.C. & Wunderle, J.M. (2006) The responses of understorey birds to forest fragmentation, logging and wildfires: an Amazonian synthesis. *Biological Conservation*, **128**, 182–192.
- Barlow, J., Gardner, T.A., Araujo, I.S., Avila-Pires, T.C., Bonaldo, A.B., Costa, J.E. *et al.* (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18555–18560.
- Barlow, J., Louzada, J., Parry, L., Hernández, M.I.M., Hawes, J., Peres, C.A., Vaz-de-Mello, F.Z. & Gardner, T.A. (2010) Improving the design and management of forest strips in human-dominated tropical landscapes: a field test on Amazonian dung beetles. *Journal of Applied Ecology*, **47**, 779–788.
- Baum, J.K. & Myers, R.A. (2004) Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters*, **7**, 135–145.
- Berenguer, E., Ferreira, J., Gardner, T.A., Aragão, L.E.O.C., De Camargo, P.B., Cerri, C.E. *et al.* (2014) A large-scale field assessment of carbon stocks in human-modified tropical forests. *Global Change Biology*, **2005**, 1–14.
- Bicknell, J.E., Struebig, M.J. & Davies, Z.G. (2015) Reconciling timber extraction with biodiversity conservation in tropical forests using reduced-impact logging (ed C Baraloto). *Journal of Applied Ecology*, **52**, 379–388.
- Bicknell, J.E., Phelps, S.P., Davies, R.G., Mann, D.J., Struebig, M.J. & Davies, Z.G. (2014a) Dung beetles as indicators for rapid impact assessments: evaluating best practice forestry in the neotropics. *Ecological Indicators*, **43**, 154–161.
- Bicknell, J.E., Struebig, M.J., Edwards, D.P. & Davies, Z.G. (2014b) Improved timber harvest techniques maintain biodiversity in tropical forests. *Current Biology*, **24**, R1119–R1120.
- Blaser, J., Sarre, A., Poore, D. & Johnson, S. (2011) *Status of Tropical Forest Management 2011*. International Tropical Timber Organization, Yokohama, Japan.
- Block, W.M., Franklin, A.B., Ward Jr, J.P., Ganey, J.L. & White, G.C. (2001) Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. *Restoration Ecology*, **9**, 293–303.
- Boreux, V., Born, J. & Lawes, M.J. (2009) Sharing ecological knowledge: opportunities and barriers to uptake. *Biotropica*, **41**, 532–534.
- Braga, R.F., Korasaki, V., Andresen, E. & Louzada, J. (2013) Dung beetle community and functions along a habitat-disturbance gradient in the Amazon: a rapid assessment of ecological functions associated to biodiversity. *PLoS ONE*, **8**, e57786.
- Burivalova, Z., Şekerciöglü, Ç.H. & Koh, L.P. (2014) Thresholds of logging intensity to maintain tropical forest biodiversity. *Current Biology*, **24**, 1893–1898.
- Canty, A. & Ripley, B. (2012) boot: bootstrap R (S-Plus) functions. R package version 1.3-4., www.r-project.org
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature*, **489**, 59–67.
- Chai, S., Healey, J.R. & Tanner, E.V.J. (2012) Evaluation of forest recovery over time and space using permanent plots monitored over 30 years in a Jamaican montane rain forest. *PLoS ONE*, **7**, e48859.
- Coutinho, S.D.C. & Pires, M.J.P. (1996) *Jari: Um Banco Genético Para O Futuro*. Imago Edit, Rio de Janeiro.
- Crawley, M.J. (2002) *Statistical Computing: An Introduction to Data Analysis Using S-Plus*. John Wiley & Sons Ltd, London.
- Davison, A.C. & Hinkley, D.V. (1997) *Bootstrap methods and their application*, 1st edn. Cambridge University Press, Cambridge.
- Dykstra, D. & Heinrich, R. (1996) *FAO Model Code of Forest Harvesting Practice*. Food and Agriculture Organization of the United Nations, Rome.
- Edwards, D.P., Larsen, T.H., Docherty, T.D.S., Ansell, F.A., Hsu, W.W., Derhe, M.A., Hamer, K.C. & Wilcove, D.S. (2011) Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 82–90.
- Edwards, D.P., Backhouse, A.R., Wheeler, C., Khen, C.V. & Hamer, K.C. (2012a) Impacts of logging and rehabilitation on invertebrate communities in tropical rainforests of northern Borneo. *Journal of Insect Conservation*, **16**, 591–599.
- Edwards, D.P., Woodcock, P., Edwards, F.A., Larsen, T.H., Hsu, W.W., Benedick, S. & Wilcove, D.S. (2012b) Reduced-impact logging and biodiversity conservation: a case study from Borneo. *Ecological Applications*, **22**, 561–571.
- Forest Stewardship Council. (2014) FSC, <https://us.fsc.org/>
- Forkner, R.E., Marquis, R.J., Lill, J.T. & Le Corff, J. (2006) Impacts of alternative timber harvest practices on leaf-chewing herbivores of oak. *Conservation Biology*, **20**, 429–440.
- França, F., Louzada, J., Korasaki, V., Griffiths, H., Silveira, J. & Barlow, J. (2016) Data from: do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles. *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.1536g>.
- Gardner, T.A., Barlow, J., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E. *et al.* (2008) The cost-effectiveness of biodiversity surveys in tropical forests. *Ecology Letters*, **11**, 139–150.
- Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A. & Sodhi, N.S. (2009) Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, **12**, 561–582.
- Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J. *et al.* (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, **478**, 378–381.
- Guariguata, M.R., García-Fernández, C., Sheil, D., Nasi, R., Herrero-Jáuregui, C., Cronkleton, P. & Ingram, V. (2010) Compatibility of timber and non-timber forest product management in natural tropical forests: perspectives, challenges, and opportunities. *Forest Ecology and Management*, **259**, 237–245.
- Habel, J.C., Gossner, M.M., Meyer, S.T., Eggermont, H., Lens, L., Dengler, J. & Weisser, W.W. (2013) Mind the gaps when using science to address conservation concerns. *Biodiversity and Conservation*, **22**, 2413–2427.
- Imai, N., Seino, T., Aiba, S., Takyu, M., Titin, J. & Kitayama, K. (2012) Effects of selective logging on tree species diversity and composition of Bornean tropical rain forests at different spatial scales. *Plant Ecology*, **213**, 1413–1424.
- Johnson, E.A. & Miyanishi, K. (2008) Testing the assumptions of chronosequences in succession. *Ecology Letters*, **11**, 419–431.
- Kappes, H., Sundermann, A. & Haase, P. (2010) High spatial variability biases the space-for-time approach in environmental monitoring. *Ecological Indicators*, **10**, 1202–1205.
- Kibler, K.M., Tullis, D.D. & Kondolf, G.M. (2011) Learning from dam removal monitoring: challenges to selecting experimental design and establishing significance of outcomes. *River Research and Applications*, **27**, 967–975.
- Krauss, J., Bommarco, R., Guardioli, M., Heikkinen, R.K., Helm, A., Kuussaari, M. *et al.* (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters*, **13**, 597–605.
- Kühn, I. & Dormann, C.F. (2012) Less than eight (and a half) misconceptions of spatial analysis. *Journal of Biogeography*, **39**, 995–998.
- Lambin, E.F., Geist, H.J. & Lepers, E. (2003) Dynamics of land-use and land-cover change in tropical regions. *Annual Review of Environment and Resources*, **28**, 205–241.
- Legendre, P. & Legendre, L.F.J. (1998) *Numerical Ecology*, 2nd edn. Elsevier Science BV, Amsterdam.
- Mantyka-pringle, C.S., Martin, T.G. & Rhodes, J.R. (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, **18**, 1239–1252.
- Marsh, C.J., Louzada, J., Beiroz, W. & Ewers, R.M. (2013) Optimising bait for pitfall trapping of Amazonian dung beetles (Coleoptera: Scarabaeinae). *PLoS ONE*, **8**, e73147.
- Newbold, T., Hudson, L., Purves, D.W., Scharlemann, J.P.W., Mace, G.M. & Purvis, A. (2012) PREDICTS: Projecting Responses of Ecological Diversity in Changing Terrestrial Systems. *Frontiers of Biogeography*, **4**, 155–156.
- Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A. *et al.* (2015) Global effects of land use on local terrestrial biodiversity. *Nature*, **520**, 45–50.
- Nichols, E., Uriarte, M., Bunker, D.E., Favila, M.E., Slade, E.M., Vulinec, K. *et al.* (2013a) Trait-dependent response of dung beetle populations to tropical forest conversion at local and regional scales. *Ecology*, **94**, 180–189.
- Nichols, E., Uriarte, M., Peres, C.A., Louzada, J., Braga, R.F., Schiffer, G., Endo, W. & Spector, S.H. (2013b) Human-induced trophic cascades

- along the fecal detritus pathway (ed M Krkosek). *PLoS ONE*, **8**, e75819.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B. *et al.* (2015) *vegan: Community Ecology Package. R package version 2.3-0*. <http://CRAN.R-project.org/package=vegan>.
- Parry, L., Barlow, J. & Peres, C.A. (2009) Hunting for sustainability in tropical secondary forests. *Conservation Biology*, **23**, 1270–1280.
- Pfeifer, M., Lefebvre, V., Gardner, T.A., Arroyo-Rodriguez, V., Baeten, L., Banks-Leite, C. *et al.* (2014) BIOFRAG – a new database for analyzing BIOdiversity responses to forest FRAGmentation. *Ecology and Evolution*, **4**, 1524–1537.
- Picard, N., Gourlet-Fleury, S. & Forni, É. (2012) Estimating damage from selective logging and implications for tropical forest management. *Canadian Journal of Forest Research*, **42**, 605–613.
- Pickett, S.T.A. (1989) Space-for-time substitution as an alternative to long-term studies. *Long-Term Studies in Ecology* (ed G.E. Likens), pp. 110–135. Springer New York, New York, NY.
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Romdal, T.S., Araújo, M.B. & Rahbek, C. (2013) Life on a tropical planet: niche conservatism and the global diversity gradient. *Global Ecology and Biogeography*, **22**, 344–350.
- Scheffler, P.Y. (2005) Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. *Journal of Tropical Ecology*, **21**, 9–19.
- Silva, P.G. & Hernández, M.I.M. (2015) Spatial Patterns of Movement of Dung Beetle Species in a Tropical Forest Suggest a New Trap Spacing for Dung Beetle Biodiversity Studies. *PLOS ONE*, **10**, e0126112.
- Slade, E.M., Mann, D.J. & Lewis, O.T. (2011) Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes. *Biological Conservation*, **144**, 166–174.
- Smith, E.P. (2002) BACI design. *Encyclopedia of Environmetrics*, **1**, 141–148.
- Socolar, J.B., Gilroy, J.J., Kunin, W.E. & Edwards, D.P. (2016) How should beta-diversity inform biodiversity conservation? *Trends in Ecology & Evolution*, **31**, 67–80.
- Soininen, J., McDonald, R. & Hillebrand, H. (2007) The distance decay of similarity in ecological communities. *Ecography*, **30**, 3–12.
- Solar, R.R.D.C., Barlow, J., Ferreira, J., Berenguer, E., Lees, A.C., Thomson, J.R. *et al.* (2015) How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecology Letters*, **18**, 1108–1118.
- Thomaz, S.M., Agostinho, A.A., Gomes, L.C., Silveira, M.J., Rejmánek, M., Aslan, C.E. & Chow, E. (2012) Using space-for-time substitution and time sequence approaches in invasion ecology. *Freshwater Biology*, **57**, 2401–2410.
- West, T.A.P., Vidal, E. & Putz, F.E. (2014) Forest biomass recovery after conventional and reduced-impact logging in Amazonian Brazil. *Forest Ecology and Management*, **314**, 59–63.
- Wilson, K.A., Meijaard, E., Drummond, S., Grantham, H.S., Boitani, L., Catullo, G. *et al.* (2010) Conserving biodiversity in production landscapes. *Ecological Applications*, **20**, 1721–1732.
- Wu, J. & Hobbs, R. (2002) Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. *Landscape Ecology*, **17**, 355–365.

Received 15 September 2015; accepted 16 March 2016

Handling Editor: Ralph Mac Nally

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Study site location.

Fig. S2. Experimental design within each sampled unit.

Appendix S1. Literature review.

Appendix S2. Supplementary experimental procedures.