LETTER

The cost-effectiveness of biodiversity surveys in tropical forests

Toby A. Gardner,[1]* Jos Barlow,[1,2,8] Ivanei S. Araujo,[2] Teresa Cristina Ávila-Pires,[2] Alexandre B. Bonaldo,[2] Joana E. Costa,[2] Maria Cristina Esposito,[2] Leandro V. Ferreira,[2] Joseph Hawes,[1] Malva I. M. Hernandez,[3] Marinus S. Hoogmoed,[2] Rafael N. Leite,[4] Nancy F. Lo-Man-Hung,[2] Jay R. Malcolm,[5] Marlucia B. Martins,[2] Luiz A. M. Mestre,[6] Ronildon Miranda-Santos,[2] William L. Overal,[2] Luke Parry,[1] Sandra L. Peters,[7] Marco Antônio Ribeiro-Junior,[2] Maria N. F. da Silva,[4] Catarina da Silva Motta[4] and Carlos A. Peres[1]

Abstract

The identification of high-performance indicator taxa that combine practical feasibility and ecological value requires an understanding of the costs and benefits of surveying different taxa. We present a generic and novel framework for identifying such taxa, and illustrate our approach using a large-scale assessment of 14 different higher taxa across three forest types in the Brazilian Amazon, estimating both the standardized survey cost and the ecological and biodiversity indicator value for each taxon. Survey costs varied by three orders of magnitude, and dung beetles and birds were identified as especially suitable for evaluating and monitoring the ecological consequences of habitat change in our study region. However, an exclusive focus on such taxa occurs at the expense of understanding patterns of diversity in other groups. To improve the cost-effectiveness of biodiversity research we encourage a combination of clearer research goals and the use of an objective evidence-based approach to selecting study taxa.

INTRODUCTION

There is a critical shortage of biodiversity data with which to meet some of the primary challenges facing conservation (Balmford *et al.* 2005), such as understanding effective reserve design and location, species persistence in converted or modified forest habitats and the long-term sustainability of forest management options. For example, protected areas are frequently located on the basis of environmental surrogates of biodiversity rather than on actual data on species distributions (Brooks *et al.* 2004), we have a poor understanding of the wildlife value of areas outside reserves (Lindenmayer & Franklin 2002), and it is currently unclear

whether there are proven examples of sustainably managed forests anywhere in the world (Sayer & Maginnis 2005). At larger spatial scales, biodiversity monitoring is urgently needed to evaluate progress towards the Convention on Biological Diversity's 2010 target to achieve a significant reduction in the current rate of biodiversity loss (Balmford *et al.* 2005), yet we are poorly equipped to assess progress towards this goal, and current attempts rely heavily on data from relatively unimportant areas in terms of global biodiversity conservation (Dudley *et al.* 2005).

A primary explanation for this biodiversity data shortage is the widespread under-funding of conservation science, especially in the species-rich tropics (Balmford & Whitten

[1]*Centre for Ecology, Evolution and Conservation, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK*

[2]*Museu Paraense Emílio Goeldi (MPEG), Av. Perimetral 1901, Bairro Terra Firme, Belém – Pará 66077-530, Brazil*

[3]*Departmento de Sistemática e Ecologia, Universidade Federal da Paraiba, Cidade Universitária-Campus, I CEP: 58059-900 João Pessoa/Paraiba, Brazil*

[4]*Insituto Nacional de Pesquisas da Amazonia, Av. André Araújo, 2936, Petrópolis, CEP 69083-000, Manaus – Amazonas, Brazil*

[5]*Faculty of Forestry, University of Toronto, ON M5S 3B3, Canada*

[6]*Laboratório de Ornitologia – CEM – Universidade Federal do Paraná, Av. Beira-mar, s/n., CEP 83.255-000, Pontal do Sul – Paraná, Brazil*

[7]*Department of Biology, University of Western Ontario, London, ON N6A 4B8, Canada*

[8]*Lancaster Environment Centre, Lancaster University, LA1 4QY, United Kingdom*

Correspondence: E-mail: tobyagardner@gmail.com

2003), and the financial cost of multi-taxa field studies typically exceeds the limited budget of most conservation projects (Margules & Austin 1991; Lawton *et al.* 1998). One approach towards limiting the cost of biodiversity research is to focus individual projects on sampling a limited set of indicator species or taxonomic groups that, in the context of a specific objective, can act as a surrogate for wider patterns of biodiversity (Caro & O'Doherty 1999) and ecological integrity (Angermeier & Karr 1994). While many selection criteria have been proposed for such indicator taxa (Rempel *et al.* 2004), encompassing a myriad of different applications (Niemi & McDonald 2004), the selection process invariably represents a trade-off between choosing taxa that reflect some useful measure of ecological integrity, and those that can be feasibly sampled. Taxa that satisfy both demands have a high strategic value for practical applications concerned with evaluating and monitoring biodiversity. We describe such taxa as 'high-performance indicator taxa', to distinguish them from other taxa that are described solely by theoretical measures of 'indicator value' (e.g. Dufrene & Legendre 1997), and lack any consideration of cost-effectiveness, as well as those that are the object of study for their own right.

Selecting high-performance indicator taxa for evaluating and monitoring biodiversity requires (i) the identification of a clear conservation objective or question, (ii) the use of ecologically meaningful selection criteria that can identify indicator taxa relevant to this objective, (iii) an analysis of the cost-effectiveness of sampling different taxa and (iv) the availability of multi-taxa field data that can provide an empirical basis for the selection process. However, indicators currently used in conservation and management are often subjectively chosen in the absence of clear objectives, 'and' instead on the basis of largely anecdotal evidence, 'expert' opinion, and ease of sampling (Kneeshaw *et al.* 2000). Few indicator studies have sampled a variety of focal taxonomic groups (Basset *et al.* 2004), and none have explicitly attempted to evaluate the monetary cost of sampling different taxa using a standardized approach that accounts for differences in survey effort.

We present a generic method for the strategic selection of high-performance indicator taxa through a comparison of the costs and benefits of sampling different higher taxonomic groups. We illustrate our approach with respect to the objective of monitoring and evaluating the ecological consequences of changes in the structural integrity of managed tropical forest landscapes.

Habitat change in forested ecosystems is typically measured in terms of change in the aerial extent of native forest and human land-uses. Despite the fact that we have a very poor understanding of the adequacy of such coarse-scale measures as indicators of actual changes in biodiversity (Dudley *et al.* 2005), for much of the world these data are all

that are available to inform policy makers of the progress (or lack thereof) towards sustainable use (e.g. Balmford *et al.* 2005). To improve this situation it is therefore necessary to translate the consequences of forest land-use change into changes in actual species and populations, without which our understanding of the conservation value of degraded lands will remain grossly inadequate.

In order for a given taxon to qualify as being of high-performance in addressing this objective it must maximize the amount of information returned (i.e. by being exceptionally sensitive to changes in structural habitat integrity) for any given investment. From a conservation perspective, there are three main reasons why it is useful to identify high-performance indicator taxa that are capable of discriminating between different land-uses. First, such indicator taxa are essential for evaluating whether forest regeneration in degraded land can provide a suitable refuge for the species currently threatened by deforestation and intensive agriculture (see Daily 2001). The lack of this empirical basis can lead to unsubstantiated claims (e.g. Wright & Muller-Landau 2006) that conservation biologists may have overestimated the tropical forest biodiversity crisis (see Gardner *et al.* 2007; Laurance 2007). Second, the identification of such taxa provides a cost-effective means of distinguishing sets of species that are characteristic of intact primary forest (i.e. those of greatest conservation concern) that can then be used to measure future changes in habitat integrity and progress towards sustainable use. Finally, this selection process also serves to indicate by proxy the higher taxa that are most likely to encompass individual species that can discriminate more subtle and finer scale (within habitat) changes in habitat structure (e.g. cutting schedules, stand management, variability in corridor design, etc.). It is extremely unlikely that higher taxa which fail to discriminate gross changes in habitat type will encompass species that can effectively discriminate between finer scale habitat changes.

To provide a case study we used data from a comprehensive multi-taxa biodiversity study conducted in Brazilian Amazonia that examined the ecological effects of plantation forestry and native forest regeneration (together with primary forest controls) for 14 taxonomic groups (see Barlow *et al.* 2007). First, we calculated the standardized cost for surveying each taxonomic group in each of the three forest types, based on samples of equal quality (i.e. equal coverage of the estimated total number of species). We then calculated two different measures of 'indicator value', which could be derived from sampling each taxon. To address our primary objective, we measured the value of each taxonomic group as ecological indicators capable of discriminating changes in habitat integrity (*sensu* McGeoch 1998). Taxa that are particularly sensitive to changes in habitat structural integrity will provide the most meaningful information on

the value of degraded areas for a measured component of biodiversity. In addition, changes in such taxa can be directly linked to changes in management interventions. To better understand the limitations of focusing on a restricted suite of indicator taxa we also measured the value of each taxon as broad surrogates or indicators of biodiversity in the literal sense (i.e. high cross-taxon congruency in spatial patterns of diversity or assemblage structure, see Caro & O'Doherty 1999). The selection of taxa whose response patterns provide an accurate indication of changes in other taxa can further improve the cost-effectiveness of biodiversity surveys.

Using a defensible and novel analytical framework we evaluate these data to compare the relative costs and benefits of surveying different taxa for monitoring a managed forest landscape in the Brazilian Amazon. In doing so we are successful in identifying both dung beetles and birds as having strong empirical support as high-performance indicator taxa suitable for forest monitoring and evaluation programmes in this region.

MATERIALS AND METHODS

Field data were collected within the Jari region in the State of Pará in north-eastern Brazilian Amazonia. Data on 13 different faunal taxa, as well as woody trees and lianas, were collected from across five study sites (maximizing spatial independence of individual sites by distributing them an area of > 500 000 ha, see Appendix S1, Fig. S1) in each of primary, secondary and *Eucalyptus* plantation forests – thus providing a broad gradient of structural integrity representative of dominant patterns of land-use change in tropical forests elsewhere. We explicitly measure indicator performance in relation to the ability of different taxa to discriminate changes in habitat integrity across these three forest types.

Taxa were chosen based on the availability of standardized sampling methodologies (see Appendix S1) and adequate taxonomic expertise. Faunal taxa included leaf-litter amphibians, lizards, large mammals, small non-volant mammals, bats, birds, epigeic arachnids (orders Amblypygi, Araneae, Opiliones, Scorpiones and Uropygi, sampled as one taxon), scavenger flies (carrion flies, blow flies and flesh flies; Diptera: Calliphoridae, Mesembrinellidae and Sarcophagidae, sampled as one taxon), dung beetles (Coleoptera: Scarabaeinae), fruit-feeding butterflies (Lepidoptera: Nymphalidae), fruit flies (Diptera: Drosophilinae), moths (Lepidoptera: Arctiidae, Saturniidae and Sphingidae, sampled as one taxon), and orchid bees (Hymenoptera: Apinae and Euglossini). Taxa were grouped by sampling method rather than differences in phylogeny to reflect the approach taken by earlier multi-taxa studies of indicator species, the unresolved taxonomy of some groups, and the practicalities of sampling biodiversity in tropical forests. Samples for each

taxon were repeated during different seasons whenever possible, and the sampling order for all groups was randomized among habitat types to further account for seasonal effects. Sampling was conducted using standardized sampling methods for each taxon (see Appendix S1). Where possible all species were identified to species level, but in cases where the taxonomy was too poorly developed, we assigned specimens to morphospecies, which were then verified by relevant experts.

Further details of the study area and sampling methods are given in Appendix S1 and Fig. S1. The total number of individuals captured (or records in the case of large mammals and birds) and species recorded for each taxon are given in Table 1.

Sampling costs

There are three main interrelated resource requirements for sampling biodiversity: monetary cost, time investment and the availability of adequate technical expertise. Time and money can be thought of in similar terms (i.e. they are partly convertible), whereas technical expertise represents a possible constraint (if it is not available, the work cannot be done). We quantified the monetary cost and necessary time allocation to survey a given taxon by combining both the field sampling and the subsequent preparation and identification of specimens, or recordings.

Although we recognize that the life-expectancy of survey equipment often varies across different taxa, the monetary cost (in US dollars) for the main analysis included the cost of all necessary field and laboratory equipment (including non-perishable laboratory equipment such as microscopes), together with salaries of local assistants, field and laboratory technical assistants and expert biologists necessary for both sampling and identification. We repeated the analyses to exclude all non-perishable capital laboratory equipment (to reflect a situation where research is being conducted by a well-funded institution) and the results were qualitatively similar, although there were changes in the specific ranking of standardized survey costs for some invertebrate groups (e.g. fruit flies and epigeic arachnids; see Fig. S2). To allow for direct comparisons between taxa, we standardized the salary requirements for surveying each taxon by using three types of worker, and salary levels that are representative of amounts payable in the region at the time of the study: (i) unskilled field assistants, $20 per day, (ii) skilled technicians (usually trained graduates), $50 per day and (iii) scientific experts (capable of both sampling and identifying their study taxa to high level of quality), $100 per day. Additional expenses not directly related to biodiversity surveying that were not included in our analyses include capital and hidden costs. Capital costs such as accommodation for field staff and the cost of transport between sites, vary significantly

Table 1 Study taxa (vertebrates, invertebrates, trees and lianas) sampled in Jari, north-east Brazilian Amazonia

Taxon*	Number of individuals	Observed species†	Sample representation‡			Per cent morphospecies	Species level key or guide	Experts – global§	Experts – Brazil¶
			Primary forest	Secondary forest	Eucalyptus				
Leaf-litter amphibians	1739	23	92.2	77.7	89.9	8.6	No	20	10
Lizards	1937	30	88.2	85.3	87.2	3.3	Yes	20–30	8
Large mammals	280	19	81.3	71.3	NA	0.0	Yes	> 250	> 150
Small mammals	219	32	65.1	54.2	50.2	9.4	No	20	10
Bats	4125	54	88.6	74.5	83.5	0.0	No	30	10
Birds	6865	255	87.4	76.5	90.9	0.0	Yes	> 50	15–20
Scavenger flies	5365	30	89.9	86.0	92.5	20.0	No	NA	5
Fruit-feeding butterflies	10 588	130	80.0	78.5	81.0	0.8	No	> 50	20
Dung beetles	9203	85	88.2	83.1	84.2	35.3	No	3	1
Epigeic arachnids**	3176	116	75.0	79.3	67.1	75.9	No	30	20
Fruit flies	5085	38	52.9	76.6	82.9	5.3	No	4	3
Orchid bees	2363	22	84.3	78.1	82.2	18.2	Yes	30	10
Moths	1848	335	53.2	46.7	50.6	50.7	No	15	3
Trees and lianas††	7600	219	79.1	86.2	100.0	NA	NA	NA	NA
Total	60 393	1388							

*Full taxon descriptions are given in the text.
†Number of species sampled in primary, secondary and plantation forest sites in our study landscape in the Jari region, State of Pará, Brazil.
‡Estimate of true species richness is the average of three abundance-based richness estimators (Chao 1, Jack 1 and ACE; see Colwell 2005).
§Estimate of the number of experts in the world who would be able to identify samples of their taxonomic group from Jari to the level of species or morphospecies without extensive consultation with reference material or other scientists.
¶Estimate of the number of experts in Brazil who would be able to identify samples of their taxonomic group from Jari to the level of species or morphospecies without extensive consultation with reference material or other scientists.
**Does not include the subclass Acari (ticks and mites).
††Only genus level information included for trees and lianus.

depending on the particular nature of a given study site, and greatly distort our ability to reveal direct differences in survey costs. Similarly, hidden costs also vary greatly according to site localities and logistics, and often are covered by the overheads of collaborating institutions. These costs include salaries for time spent on the project outside of actual surveying (i.e. project planning, logistic support, data analysis and report writing), the cost of identifying specimens by specialists outside our own institutions, cost of training for field technicians and taxonomic experts, the cost of building and maintaining the reference collections of biological specimens in host institutions that were used to identify voucher material, the long-term cost of curating voucher specimens, and the costs of publishing and disseminating project results. Nevertheless, we believe that the cost structure used for our analyses is realistic for most similar short-term conservation projects, and allows a standardized comparison of the costs of surveying our different study taxa.

We defined time investment as the total time necessary to survey each taxonomic group, which was split into field and laboratory time, as well as by the amount of work conducted by different worker categories. All totals were calculated in terms of person-hours, assuming an 8 h working day. Given that the total cost in monetary terms and time invested across different taxa were strongly correlated ($r = 0.91$, $P < 0.001$; see Figs S3 and S4), we used only the monetary cost for all subsequent analyses. Taxonomic expertise was defined as the availability of experts that are necessary to survey each taxon. To quantify this, we compiled estimates of the number of scientists, both globally and within Brazil, able to identify our samples to the level of species or morphospecies. Estimates were made through consultation with a leading expert for each taxonomic group (including many of the authors; see Appendix S1 for those researchers responsible for each taxon). Each expert was asked to identify the number of people who would be able to separate a collection of specimens from the Jari region to the level of species or morphospecies without extensive consultation with reference materials or other scientists. This distinguishes real experts from perceptive and trained technicians and students who may be able to separate the majority of specimens, but would still need their work to be verified by an appropriate expert.

Data analysis

Standardization of survey costs

Although considerable effort was made to ensure that representative samples of all taxa were collected for each of the three forest types, differences in sample coverage (representation of total estimated richness, and relative position along species accumulation curves) among taxa were inevitable (Table 1). To account for these differences, and allow for the calculation of a standardized survey cost for each taxon, we employed the following procedure. First, individual-based rarefaction curves were constructed for each taxon, using the analytical formula available in ESTIMATES v.7.5 (Colwell 2005). Second, to account for differences in the total species richness of each taxon for a given forest type, we recalibrated the *y*-axis scale so that it represented the proportion of the estimated total number

of species for each level of sampling effort (i.e. number of individuals) – where the estimated 'true' species richness was calculated using the average of three nonparametric statistical estimators: ACE, Chao 1 and Jack 1 (Colwell 2005). Third, the total cost of surveying each taxon in each forest type was calculated and used to estimate the survey cost per individual or encounter. Fourth, to account for differences between taxa in the total number of individuals or encounters, the *x*-axis of each rarefaction curve was recalibrated to represent survey cost in US dollars rather than individuals. Finally, to calculate the standardized survey costs for all taxa, the cost of surveying each higher taxon was rarefied to equate to the point at which the sample representation was equivalent to that of the least effectively sampled taxon. This point provides a measure of survey cost at a standardized level of sample coverage (referred to in the text as 'standardized survey cost'; see
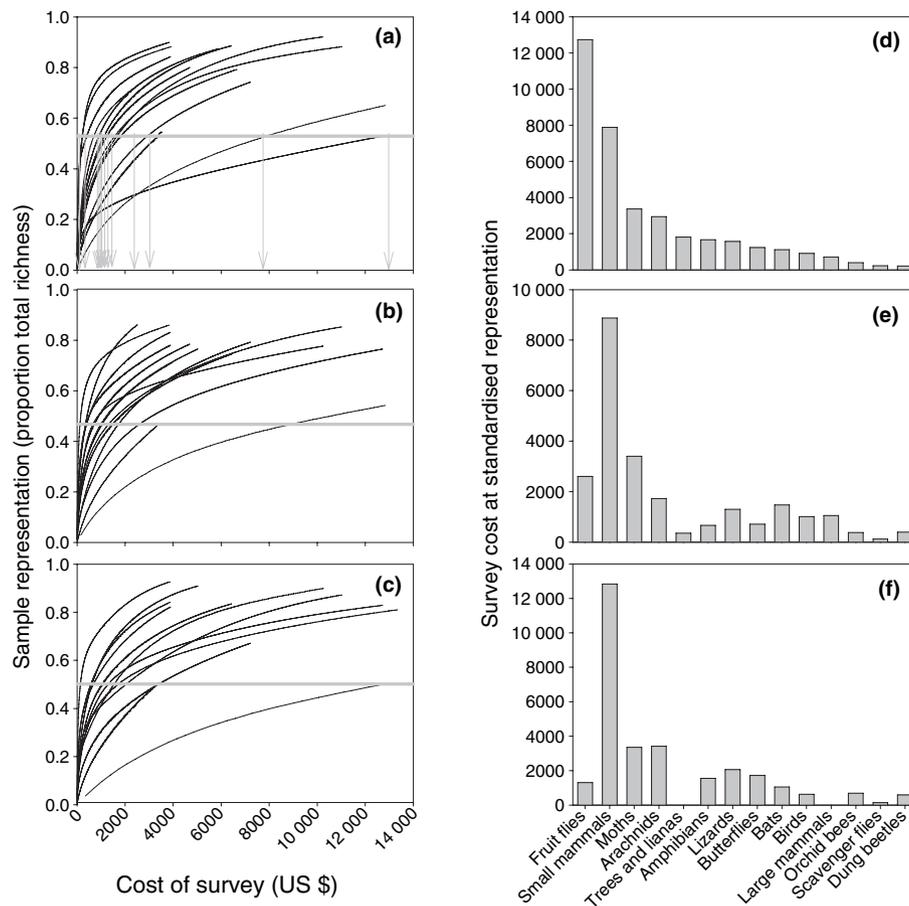
Figure 1 Effort-standardized survey costs for 14 higher taxa in the Brazilian Amazon. An analytical procedure based on rarefaction curves was used to calculate the standardized survey costs of a variety of focal taxa in primary, secondary and plantation forests in the Brazilian Amazon (a–c, respectively). See text for a complete description of each taxon. Values of standardized survey costs are extracted at the point of equal sample quality (defined by sample representation), and are presented separately for primary, secondary and plantation forests (d–f, respectively).

Fig. 1a–c). Points of rarefaction in each forest type were defined by fruit flies in primary forest (minimum of 53% of estimated total richness), moths in secondary forest (minimum of 47% of estimated total richness) and small mammals in *Eucalyptus* plantations (minimum of 50% of estimated total richness). Rarefaction curves could not be compiled for large mammals or trees and lianas in plantation forests because of the low number of encounters. For comparison we also calculated cross-taxon differences in survey quality (measured as sample representation using the per cent total estimated richness as above) for a standardized investment (based on the cost of the least expensive group – i.e. the inverse of the above procedure).

Benefit metrics

We used two alternative metrics to describe the indicator value of information derived from each taxon.

Ecological indicator value

Based on the Indicator Value (IndVal) metric (Dufrene & Legendre 1997) to measure the ability of each taxon to discriminate between the three forest types (i.e. their performance as ecological indicators). This method combines measures of both habitat specificity (through patterns of abundance) and habitat fidelity (through patterns of presence–absence), producing a percentage indicator value (IndVal) for each species. Dufrene & Legendre's (1997) random reallocation procedure of sites within site groups was used to test the significance of the IndVal measure for each species. To measure the indicator performance of each taxon we recorded the number of significant indicator species as a percentage of the total number of species captured in that forest type, and then calculated the average percentage of significant indicators for each taxon across all three forest types. Comparing these percentage values across all higher taxa provides an effective means of identifying which individual taxa were best able to discriminate coarse-scale changes in habitat structural integrity within our samples – thereby directly addressing our primary objective.

Biodiversity indicator value

Recent research has demonstrated that metrics of community similarity provide a more powerful test of cross-taxon congruency than species richness (Su *et al.* 2004). Barlow *et al.* (2007) present a detailed analysis of cross-taxon response metrics for the same data used in this study, and provide further strong support for the use of composite community similarity indices for measuring cross-taxon congruency in responses to habitat change. In particular, Barlow *et al.* (2007) demonstrate that community similarity indices provide a much more appropriate measure of response congruency than more traditional measures of species richness, which retain little biological information, and are highly sensitive to sampling effort.

To provide a measure of the 'biodiversity indicator value' of each taxon, we used the arithmetic mean of all pairwise correlation coefficients between species-abundance matrices of each taxon and those of all other taxa in turn (see also Barlow *et al.* 2007). The higher the value of this index (0–1), the greater the congruence in cross-taxon responses. Matrix correlations were executed using the Relate test (a nonparametric version of the Mantel test) available in PRIMER v.5 (Clarke & Warwick 2001), and were based on site-standardised species-abundance data.

Identifying high-performance indicator taxa

To evaluate the relationship between standardized survey cost and benefit among taxa in each forest type we used simple linear regression with log-transformed cost data. We did not attempt to standardize the two benefit metrics by sampling effort because (i) most taxa were sampled to a high level of representation (Table 1) and (ii) there was no relationship across taxa between sample representation and either ecological or biodiversity indicator value ($r = 0.37$, $P = 0.19$, and $r = 0.02$, $P = 0.95$, respectively). We were therefore confident that any observed differences in indicator value among taxonomic groups were not sampling artefacts.

RESULTS

Sampling

Considering all three forest types combined, we recorded 53 725 individuals comprising *c.* 1169 species from 13 vertebrate and invertebrate groups (Table 1). In addition, we sampled 7600 trees and woody lianas comprising 219 genera (Table 1). The proportion of species (or genera) that could not be identified varied considerably between taxonomic groups (Table 1). Only three groups could be completely identified on the basis of existing taxonomy (large mammals, bats and birds), and in two cases most species could only be assigned to numbered morphospecies (epigeic arachnids and moths). Sample representation (defined as the proportion of total number of estimated species, see Methods) was consistently high for most taxonomic groups in all three habitats, with more than 70% of the estimated total number of species sampled for 79%, 86% and 71% of all taxa in primary, secondary and plantation forests, respectively (Table 1).

Survey costs

The total in-country monetary cost of the project, including all field and laboratory equipment, and all salary costs of

project personnel involved in sampling and identification, was *c.* $145 550. While a non-trivial sum, in comparison with the cost of a single postdoctorate position in a north-American or European institution this represents remarkable value for money. Approximately 66% this was spent on salaries, and the remainder was split evenly between the cost of field and laboratory equipment. The total labour cost (salary) was proportionately lower for invertebrates (54%, as a proportion of total invertebrate cost) than for vertebrates (71%). Vertebrates also required greater relative investment in field equipment than invertebrates (25% vs. 12% of total respective costs) although invertebrates required much greater identification and laboratory costs (34% vs. 4%). The actual un-standardized marginal cost of sampling each taxon in our study is given in the online Supplementary Material (Figs S3 and S4). An additional overall capital cost of *c.* $100 000 was spent on accommodation and transport. These costs were excluded from cross-taxon comparisons as they were highly site-specific. The total project cost was reduced by *c.* $27 000 (a saving of 16% from the total budget) by exploiting the economies of scale from surveying different taxa that are amenable to the same sampling methodology with little additional modification, and surveying different taxa that can be simultaneously sampled by the same field workers. For example, combining lizards and leaf-litter amphibians provided a saving of 41% on the cost of surveying both taxa independently; terrestrial small mammals with herpetofauna (lizards and leaf-litter amphibians) provided a saving of 34%; arachnids and herpetofauna provided a saving of 19%; and dung beetles and blow flies provided a saving of 16%. To allow for standardized comparisons, however, all analyses used the cost of sampling each taxon independently from any other.

Time and taxonomic expertise

The total survey time allocated to all taxa was *c.* 18 200 person-hours (or 8.1 person-years, using 8 h day^{-1} and 280 days year^{-1}); 76% of this total was allocated to field sampling, with the remainder split almost evenly between specimen preparation and specimen identification. Vertebrates required proportionately more field time than laboratory time (87% and 13%, respectively) than invertebrates (68% and 32%, respectively). The availability of adequately trained taxonomists varied considerably among taxa (Table 1), while the total number of taxonomists currently working in Brazil was estimated to be 10 or fewer for each group except large mammals, birds, arachnids and fruit-feeding butterflies, and the total number of taxonomists globally was estimated to be fewer than 100 for all groups except large mammals. In addition, no complete species level key or field guide was available for nine of the 14 taxa sampled (Table 1).

Standardized survey costs

Standardized survey costs for different higher taxa varied by three orders of magnitude in each of the three forest types (Fig. 1), and the cost was roughly consistent for the same taxon in different forest types, with some notable exceptions. For example, fruit flies were disproportionately expensive to sample in primary forest (because of low sample representation and high laboratory costs; Table 1, Methods and Fig. S3) compared to elsewhere (Figs 1d–f and S3). While small mammals, leaf-litter amphibians and lizards were consistently expensive to sample to an equal standard, there was no consistent pattern between vertebrates and invertebrates, both of which included relatively cheap and expensive taxa (Fig. 1d–f). Comparing patterns of survey quality for a standardized investment revealed a
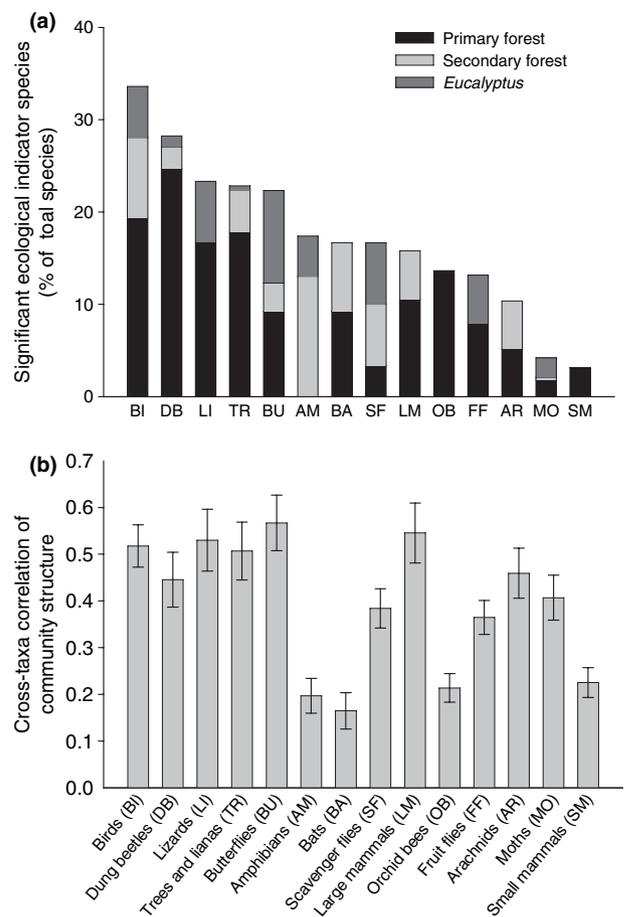
Figure 2 A comparison of the benefits of sampling different taxa across a gradient of structural habitat integrity (primary, secondary and plantation forests) in the Brazilian Amazon for a variety of focal taxonomic groups, with respect to (a) ecological indicator value and (b) biodiversity indicator value. See main text for a full description of each taxon and definition of value metrics.

similar pattern, and taxa that were relatively expensive for a given level of survey quality also return a relatively poor quality of survey for a given investment (correlations between standardized costs and standardized sample representation; primary forest: $r = -0.91$, $P < 0.001$, secondary forest: $r = -0.86$, $P < 0.001$, *Eucalyptus*: $r = -0.87$, $P < 0.001$).

Benefits of sampling different taxa

Cross-taxon patterns of benefit varied according to the choice of metric. In addressing our main objective (the identification of taxa with a high ecological indicator value), the ability of our samples of individual species from different higher taxonomic groups to effectively discriminate between different forest types varied markedly (Fig. 2a). Most taxa that included species that are characteristic of primary forest habitat (the most useful quality) also included species that are characteristic of other forest types (i.e. there is a wide variability among constituent species in per cent indicator values for each forest type, and they therefore can be characterized as having a high generic ecological indicator value as defined by the IndVal technique. Comparison of average-forest and primary forest indicator values; $r = 0.99$, $P < 0.001$), with a few notable exceptions (e.g. leaf-litter amphibians; Fig. 2a). However, the cross-taxon pattern of ecological indicator value was not related to the pattern of biodiversity indicator value ($r = 0.5$, $P = 0.1$, Fig. 2). With respect to biodiversity indicator value, although some taxa performed better than others (Fig. 2b), no single taxonomic group was clearly superior in reflecting the response patterns of all other taxa; e.g. the maximum average correlation coefficient was 0.57 (butterflies; this pattern was similar whether using abundance or presence–absence-based community data; Barlow *et al.* 2007). However, these analyses include the very weak associations with certain taxa that appear to have unique response patterns (notably, leaf-litter amphibians, small mammals, bats and orchid bees; Barlow *et al.* 2007).

Identifying high-performance indicator taxa

There was a significantly negative relationship between standardized survey cost and ecological indicator value across taxa was for all forest types (primary forest, $r = -0.53$, $P = 0.05$; secondary forest, $r = -0.55$, $P = 0.04$; plantations, $r = -0.57$, $P = 0.05$, Fig. 3a–c): taxa that were particularly inexpensive to survey were often the most effective ecological indicators (most notably birds and dung beetles), while those that were relatively expensive to survey were relatively poor at discriminating differences in structural integrity (e.g. moths and small mammals; Fig. 3). Some taxa were outliers to the general pattern (scavenger flies and
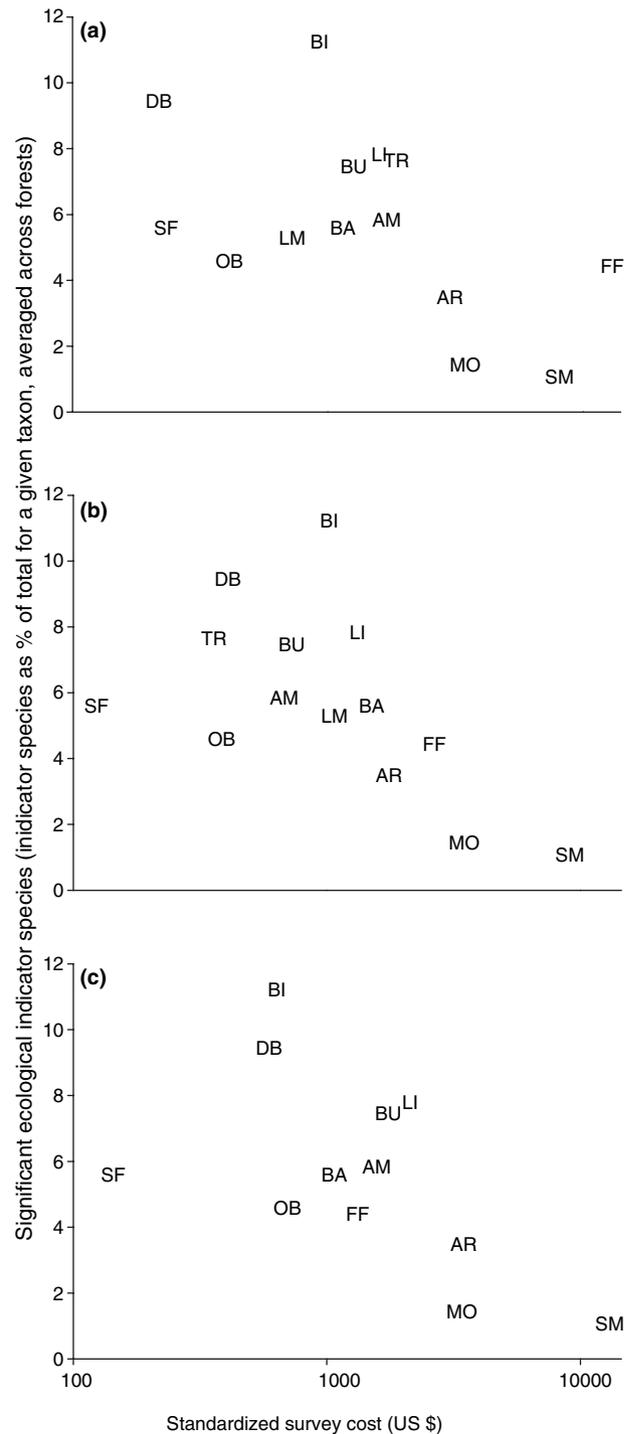
Figure 3 Cost-effectiveness of surveying 14 higher taxa in the Brazilian Amazon. The relationship between the standardized cost and ecological indicator value of a variety of focal taxa sampled in primary, secondary and plantation forests (a–c, respectively) in the Brazilian Amazon. Note the log-scale on the x axis. Taxa are labelled as two letter species codes on each plot (see Figure 2 for interpretation of codes). See text for a complete description of each taxon.

orchid bees) in that they could be surveyed inexpensively, yet performed only moderately well as ecological indicators (Fig. 3a–c). There was no significant relationship across all taxa between standardized survey cost and biodiversity indicator value ($P > 0.61$ in all forest types), although birds and dung beetles (the highest performing ecological indicators) were also above average indicators of biodiversity (see Fig. 2b and Barlow *et al.* 2007).

DISCUSSION

Very few studies have quantitatively evaluated the efficiency of sampling different taxa, and previous attempts have assumed equal survey time and cost for different taxa (Rohr *et al.* 2007). By explicitly accounting for differences in the cost of sampling and identification, we provide the first quantitative evaluation of the cost of surveying different higher taxa in a tropical forest landscape.

The high cost of biodiversity research in tropical forests is well recognized (Lawton *et al.* 1998). However, a particularly striking result from our study was the magnitude of the variability in investment necessary to survey different higher taxa to an equal standard, with standardized costs in primary forest varying by up to three orders of magnitude (e.g. *c.* $200 for dung beetles to *c.* $13 000 for fruit flies). Certain taxa therefore hold a distinct advantage in terms of the level of investment required for effective research in our study area (Pawar 2003). While it is possible that some of the observed variability in sampling costs can be attributed to intrinsic differences in rarity or habitat specialization, it is more likely that this variability is due to differences in the suitability and effectiveness of taxon-specific sampling methods and ease of identification (Pawar 2003). Contrary to expectation (Lawton *et al.* 1998), there was no systematic relationship between the cost of processing specimens (or species records) and body size. For example, although the smallest and largest bodied higher taxa were, respectively, the most expensive (fruit flies, often requiring genital dissection) and cheapest (large mammals, all identified in the field) to identify, many plants and a number of vertebrate taxa (e.g. rodents and marsupials, leaf-litter amphibians and lizards) often required intensive processing for species identification. In addition to cost, the second significant factor determining the feasibility of surveying different taxa was the availability of relevant expert taxonomists and the availability of taxonomic monographs and reference collections. The global-scale disparity between the areas of highest biodiversity and the locations of most of the world's taxonomists is well known (Gaston & May 1992). Nevertheless, our results emphasize that in Brazil, as for many of the world's most biodiverse countries, taxonomic research remains chronically under-funded.

Identifying high-performance indicator taxa for monitoring and evaluating biodiversity in Brazilian Amazonia

The limited financial resources available to conservation research (Balmford & Whitten 2003) demand that money invested in biodiversity surveys is spent as effectively as possible. However, the majority of conservation studies do not explicitly evaluate costs and benefits, partly because most conservation benefits cannot be quantified in monetary terms. Nevertheless, it is often possible to identify cost-effective options by comparing a standardized monetary cost with an objective measure of benefit expressed in its original ecological units (Naidoo *et al.* 2006). The lack of such a framework in tropical forest management systems for the selection of cost-effective indicator taxa has led to much confusion and frustration among managers and scientists alike (Hagan & Whitman 2006), providing a major barrier to the implementation of effective monitoring and evaluation programmes in sustainable forest management initiatives (UNFF 2004; Dudley *et al.* 2005; Hagan & Whitman 2006). In this study, marked differences in both the standardized survey cost and the ecological indicator value exhibited by different taxa enabled us to make a relatively robust identification of high-performance indicator taxa for monitoring and evaluating forest management systems in our study region. Both birds (Bibby 1999) and dung beetles (Spector 2006) have been widely recommended as suitable ecological indicator taxa, and together they integrate many structural and functional aspects of the forest ecosystem, such that information on changes in the number of individuals and species predictably reflect wider changes in habitat integrity (e.g. McGeoch *et al.* 2002). However, this is the first time that the practical indicator performance of both groups has been empirically evaluated across a variety of higher taxa using objective cost and benefit criteria.

The dilemma facing biodiversity research in tropical forests

Biodiversity research needs to be effective and meaningful or it risks losing the support of increasingly disillusioned conservation practitioners and funding bodies (Cleary 2006). However, there is concern that the strategic allocation of limited resources towards the collection of data on a priority set of high-performance indicator taxa carries the inevitable consequence of diverting research effort away from other poorly understood taxa that are less cost-effective to study, thus amplifying the existing taxonomic biases in tropical forest biodiversity research (Pawar 2003). Resolving this dilemma can be achieved most effectively by recognizing the importance of setting clear objectives in biodiversity research, and by doing so maximizing the information value

of taxa selected to evaluate a particular conservation problem. We have shown that evaluating the ecological consequences of changes in structural habitat integrity within tropical forest management systems in our study area can be made more effective by adopting an objective method to selecting groups of high-performance indicator taxa. This approach departs significantly from a commonly adopted selection process based on anecdotal evidence and personal experience that is almost guaranteed to fail (Pullin *et al.* 2004). However, the effective adoption of the framework we present requires an explicit recognition of its limitations: taxa that are particularly effective at discriminating gradients of structural habitat integrity (high ecological indicator value) comprise only a small fraction of the total biological and functional diversity of an area, and are not necessarily effective at discriminating patterns of diversity in other taxa (Fig. 2b and see Barlow *et al.* 2007), or other types of stressor. Consequently, the specific criteria identified here will not necessarily suffice in the case of biodiversity surveys designed to solve other problems; e.g. selecting high-priority conservation areas, or resolving taxon-specific threats that also urgently require targeted research in their own right (Lindenmayer *et al.* 2000).

We therefore caution strongly against an over-simplistic interpretation of these results for wider biodiversity research in tropical forests. First, biologists studying higher taxa that lack effective sampling methodologies and easily visible identification traits are faced with a disproportionate challenge. Higher investment of time and resources may provide a disincentive to study these taxa, and polarize research towards taxonomic groups that are easier to survey (Pawar 2003). Underinvestment in such disadvantaged taxa will in turn lead to increasingly poor levels of representation in field projects, slowing progress in taxonomic research and our understanding of biodiversity in general, and encouraging a culture of 'taxonomic chauvinism' (Pawar 2003). Second, our results represent a snapshot in time and space, and it is possible that the relative rankings of cost-effectiveness may shift as sampling methods improve, further taxon-specific survey experience is gained (especially for currently disadvantaged taxa), and identification characters become better understood. Moreover, as demonstrated here, economies of scale in combining sampling techniques for several groups can reduce survey costs, and consequently improve cost-effectiveness. Finally, there is an urgent need to replicate our study in other tropical forest regions both within and outside Brazil to gain a wider understanding of the cost-effectiveness of sampling different higher taxa in multiple regions. Geographical variability in taxon-specific sampling costs will vary not only with differences in species-abundance distributions, but also differences in the availability and cost of taxonomic expertise and research facilities.

Nevertheless, while such caveats are important we believe it is irresponsible to use them as excuses for inactivity or maintaining the status quo (attempting to sample many taxa inadequately in the absence of clear objectives – unfortunately something that is too often the case), as evidence-based conservation action is urgently needed in forest landscapes worldwide (Sheil 2001). The case study we present to highlight the indicator-selection framework in this paper provides clear advice on the choice of high-performance indicator taxa for managers and researchers concerned with evaluating forest management systems in the Brazilian Amazon. In making this choice, it is necessary to remember the intractable complexity of biodiversity, and that where funds permit other taxa should also receive attention.

CONCLUSION

By not explicitly considering the cost-effectiveness of their studies, many researchers concerned with monitoring and evaluating biodiversity to improve habitat management programmes are failing to ensure the strategic allocation of scarce resources (Cleary 2006), and are currently missing out on many conservation opportunities (Naidoo *et al.* 2006).

Conservation biology needs to better adopt the tools of decision-making that take into account constraints, trade-offs and uncertainties to deliver the best possible long-term outcome in the real-world (Possingham 2001). Unless society recognizes the true value of effective conservation and readjusts global spending priorities accordingly (James *et al.* 1999), management-oriented biodiversity research can gain significant benefits from adopting a more cost-effective approach, accompanied by a clearer recognition of both the underlying objectives and limitations. In developing a generic framework for evaluating the cost-effectiveness of indicator taxa, our study provides an example of such an approach with respect to improving monitoring and evaluation programmes for forest management systems in the Brazilian Amazon. This indicator-selection framework complements other recent efforts to adopt a more business-like approach to biodiversity surveys that can make monitoring more meaningful (e.g. Field *et al.* 2007; Franco *et al.* 2007; Garden *et al.* 2007). We are only just beginning to understand the consequences of habitat change and alternative management strategies in species-rich tropical forests. We hope this paper will improve this situation by encouraging similar efforts elsewhere in the near future.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix 1 Field data collection.
Figure S1 Map of study site.
Figure S2 Sensitivity of cost-effectiveness comparisons to the inclusion of fixed laboratory capital costs.
Figure S3 Total survey costs for 14 higher taxa in the Brazilian Amazon.
Figure S4 Total time investment to survey 14 higher taxa in the Brazilian Amazon.

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