Title: Cost-effectiveness of using small vertebrates as indicators of habitat

Running title: Cost-effective habitat indicators

Word Count: 4957

Corresponding author: Mika Robert Peck, JMS Building, University of Sussex, Falmer, Brighton BN1 9QJ, UK. Email: m.r.peck@sussex.ac.uk. Tel: 01273 877332, Fax: 01273 877586

Simon T. Maddock, Department of Zoology, Natural History Museum, London SW7 5BD, UK.

Jorge Noe Morales, Santa Lucía Cloud Forest Reserve, Barrio La Delicia, Nanegal, Ecuador.

Hugolino Oñate, Santa Lucía Cloud Forest Reserve, Barrio La Delicia, Nanegal, Ecuador.

Paola Mafla-Endara, Escuela de Ciencias Biológicas**,** Pontificia Universidad Católica del Ecuador (PUCE), Quito, Ecuador.

Vanessa Aguirre Peñafiel, Escuela de Ciencias Biológicas**,** Pontificia Universidad Católica del Ecuador (PUCE), Quito, Ecuador.

Omar Torres-Carvajal, Escuela de Ciencias Biológicas**,** Pontificia Universidad Católica del Ecuador (PUCE), Quito, Ecuador.

Wilmer E. Pozo-Rivera, Departamento Ciencias de la Vida, Carrera de Ciencias Agropecuarias (IASA I), Escuela Politécnica del Ejército (ESPE), PO Box 171-5-231-B, Sangolquí, Ecuador.

Xavier A. Cueva-Arroyo, Departamento Ciencias de la Vida, Carrera de Ciencias Agropecuarias (IASA I), Escuela Politécnica del Ejército (ESPE), PO Box 171-5-231-B, Sangolquí, Ecuador.

Bryony A. Tolhurst, University of Brighton, Cockcroft Building, Lewes Road, Brighton, Sussex, BN2 4GJ, UK.

Abstract

In species-rich tropical forests, effective biodiversity management demands measures of progress, yet budgetary limitations typically constrain capacity of conservation decision-makers to assess response of biological communities to habitat change. One approach is to identify 'ecological-disturbance indicator species' (EDIS) that are additionally cost-effective in monetary terms. EDIS can be identified by determining individual species responses across a disturbance gradient, however these may be confounded by additional factors; for example in mountain environments the effects of anthropogenic habitat alteration are commonly confounded by altitude. Previous studies have identified EDIS using the IndVal metric, but there are weaknesses in the application of this approach to complex montane systems. We surveyed birds, small mammals, bats, and leaf-litter lizards in differentially disturbed cloud-forest of the Ecuadorian Andes. We then employed a novel statistical approach that incorporates altitude as a covariate using generalised linear mixed models GL(M)M, to screen for EDIS in the dataset. Finally, we used rarefaction of species accumulation data to compare relative monetary costs of the EDIS identified, at equal sampling effort, based on species richness. Our GL(M)Ms generated greater numbers of detector species, but fewer numbers of characteristic species relative to IndVal. In absolute terms birds were the most cost-effective of the four taxa surveyed, with a single, low-cost EDIS detected. However, in terms of the number of indicators generated as a proportion of species richness, EDIS of small mammals were the most cost-effective.. We discuss how our approach could be used as a tool for more sustainable management of Andean forest systems.

Keywords: Ecological disturbance indicator species, disturbance gradients, altitude, survey costs, tropical montane forest, IndVal, Generalised linear modelling

Introduction

Traditional conservation, habitat restoration and emerging Reduced Emissions from Deforestation and Degradation (REDD+) projects all require monitoring protocols for assessing the effectiveness of conservation action and the impact of habitat degradation and restoration on biodiversity (Harrison et al. 2012). The challenge is understanding how flora and fauna respond to land-use change and management, particularly in species-rich tropical forests where the costs of undertaking comprehensive multi-species field studies normally exceed typical budgetary limitations (Lawton et al. 1998). One approach is to determine the occurrence or abundance of a small set of species that are sensitive to habitat disturbance, previously described by Caro (2010) as ‘ecological-disturbance indicator species (EDIS)’ and defined as ‘a species or group of species that demonstrate(s) the effects of environmental change (such as habitat alteration and fragmentation and climate change) on biota or biotic systems’ (McGeoch 2007). In terrestrial systems EDIS can be identified by comparing presence/absence and abundance of multiple taxa across a gradient of disturbance to find those that best characterise each stage. This approach has been the subject of considerable research (Laurence & Peres 2006; Caro 2010;) with varying levels of success (Lawton et al. 1998; Rodrigues & Brooks 2007; Trindade & Loyola 2011). These studies provide invaluable information to underpin effective management of biodiversity, but few quantify the costs associated with detecting EDIS. Determining the return-on-investment when selecting indicator species or taxonomic groups is important where careful allocation of funds is paramount (Favreau et al. 2006). Taxa that have been selected following consideration of cost-effectiveness rather than purely on their indicator value have previously been described as ‘high performance indicator taxa’ (Gardner et al. 2008). Once a robust site-specific dataset for a range of taxa exists the selection of these high performance indicator taxa generally follows a three-stage process (Gardner et al. 2008). The first stage involves clearly defining the conservation objective(s); the second comprises identification of ecologically meaningful criteria for selection of EDIS; and the third stage requires measurement of the relative cost-effectiveness of sampling different taxa under the various criteria to derive high performance EDIS.

Our objective was to identify high performance EDIS for small vertebrates in tropical Andean forests exhibiting differential anthropogenic disturbance. A range of ecologically meaningful selection criteria have previously been used that are based on changes in species richness, community composition and population size. Of these, change in population size is considered the most sensitive as it can forewarn of localised extinction (Caro, 2010). A range of approaches exist for assessing species sensitivity to disturbance, including k-dominance curves, rarefaction techniques, correspondence analysis and probability-based indicators of ecological disturbance (Magurran 2004; Howe et al. 2007; Halme et al. 2009;). However, the most common selection method used to identify EDIS in previous studies in tropical forests has been the indicator value method (IndVal) (Gardner et al. 2008; Kessler et al. 2011). This screening method combines measurements of the degree of specificity of a species to an ecological state (such as habitat type), and its fidelity within that state (Dufrene & Legendre 1997). Using IndVal, indicators (EDIS) can be identified from sets of sites under increasing disturbance (Dufrene & Legendre 1997; De Caceres & Legendre 2009; De Caceres et al. 2012). IndVal identifies two types of EDIS: ‘characteristic species’, which are only present in particular habitats (disturbance states), and ‘detector species’, found at different abundances across a range of habitats (levels of disturbance). Characteristic species are more likely to be vulnerable to habitat degradation, but detector species are suggested to be a more sensitive measure for monitoring change over time than a single state variable, as they exhibit lower specificity and span a range of ecological states (McGeoch et al. 2002). Although an accessible and relatively simple method, the weakness of IndVal is that it cannot incorporate potential covariates within habitat disturbance categories that might confound patterns of species presence and abundance. For example, small mammals are structured by multiple predictors such as altitude, microhabitat and temperature in mountain forests (Bateman et al. 2010). In this study we compare the efficacy of IndVal in identifying EDIS, as compared to a generalized linear modelling (GL(M)M) approach, to explore the potential need to employ greater statistical complexity to effectively identify indicators. With a focus on determining statistically significant differences in abundance between habitat disturbance categories, GL(M)M is expected to provide greater resolution than IndVal.

The final stage requires use of a cost-effectiveness method for sampling different taxa and thereby detecting high performance EDIS. There is a rapidly growing body of work that has incorporated cost-effectiveness analysis in identifying conservation priorities (Tulloch et al 2011; Somerville et al 2013; Halpern et al 2013). More specifically, a number of studies have combined cost analysis with species accumulation curves to identify levels of sampling required, and models (i.e. IndVal) to detect trends in species response to environmental covariates such as disturbance or change (Gregory et al 2005; Gardner et al. 2008; Caro 2010; Kessler et al. 2011). The current study is the first to combine all three approaches to provide real advice to those wishing to undertake monitoring of species in response to environmental change.

We used standard field survey techniques to compare the cost-effectiveness of EDIS for birds, bats, small mammals, and leaf-litter lizards in Andean forest systems. Our approach is novel in that: a) we compare EDIS generated using IndVal with a more complex GL(M)M that incorporates additional environmental covariates; b) we then assess relative cost-effectiveness of the EDIS identified using rarefaction to compare cost for each taxon at equal sampling of estimated species richness.

Methods

Field sites

We conducted field surveys within two tropical Andean montane reserves, the Santa Lucia Cloud Forest Reserve (SLR, 0°07′30″N, 78°40′30″W) and the Junin Community Reserve (JCR, 0°17′00″N, 78°38′00″W), situated on the Western (Pacific) slopes of the Andes in the provinces of Pichincha and Imbabura, North-western Ecuador. SLR spans an altitudinal range of 1400 – 2560 m and JCR 1200 to 1900 m. The forest in the study area is lower montane rain forest (Holdridge et al. 1971), commonly referred to as cloud forest. The area has a humid subtropical climate (Cañadas-Cruz 1983) and comprises fragmented forest reserves surrounded by a matrix of cultivation and pasture-lands. It lies within the Tropical Andes biodiversity hotspot (Myers et al. 2000) exhibiting high plant species endemism and diversity. Topography is defined by steep-sloping valley systems of varying aspect. Annual rainfall ranges from 1500 to 2800 mm with average annual temperature of 16 °C (Rivas-Martinez & Navarro 1995).

Species survey methods

We surveyed avifauna in primary, secondary and silvopasture sites (Comprising of pasture planted with nitrogen-fixing Andean Alder - *Alnus acuminata)* in SLR using point-count sampling. We established 52 permanent point survey locations a minimum of 100 m apart to avoid spatial pseudo-replication. Of the 52 points, 24 were in primary forest, 17 in secondary forest and 11 in silvopasture. We conducted fieldwork between June and August over four field seasons from 2008 to 2011 to minimise records from boreal migrants. Experienced ornithologists surveyed 8 points daily between 6 and 9am, identifying birds to within a 50 m radius to species level using both visual and auditory cues. Each point was surveyed for a standardised period of 10 minutes following an initial 2-minute acclimatization time.

We surveyed leaf-litter lizards during five field expeditions to SLR over a period of three years (2008 - 2010). We deployed a total of 21 pitfall trap-lines with drift-fence arrays equally across three habitat types; primary forest, secondary forest and silvopasture. Each trap-line measured 5 m by 5 m constructed in a 'T' formation comprising five 25 L plastic buckets buried at intervals of 2.5 m. We left trap-lines *in situ* for a ten-day sampling period checking them twice daily.

We sampled small mammals from JCR during two field expeditions in 2010 using clusters of Sherman live-traps deployed along line transects. A total of six transects of average length 175 m were distributed equally between primary and secondary forest at altitudes of between 1300 and 1900 m, with a total of 186 traps deployed, averaging 37 per transect. Silvopasture habitat was not present in JCR. Traps were deployed for 8 consecutive nights, resulting in a total of 1488 trap nights over an overall transect length of 1.48 km. We baited each trap daily with a mixture of peanut butter, oats, vanilla essence and tinned tuna and checked traps every morning.

Mist-netting surveys of bats along line transects were conducted in JCR, concurrently with small mammal sampling. A total of four 200 m transects were deployed, each comprising four 6 m x 2.6 m mist nets spaced 50 m apart. Nets were distributed equally between primary and secondary forest at altitudes of between 1300 and 1400 m and positioned in microhabitats considered to optimise capture. One to two transects were sampled per night, equating to four to eight nets *in situ* for three hours per night (from 6 to 9pm). Chiropterans were identified in the field using existing taxonomic keys (Albuja et al. 1980; Tirira 2007).

Data analysis

Identifying EDIS

For all taxa we determined the ability of the Indicator Value (IndVal) metric to identify EDIS against more complex generalized linear models that allow inclusion of potential environmental covariates. The IndVal metric generates a percentage indicator value for each species by multiplying measures of habitat specificity (based on abundance) and habitat fidelity (based on presence/absence). Significance is tested using the random reallocation of sites within site groups (Dufrene & Legendre 1997).

For lizards, bats and small mammals, individual species abundances were then modelled by fitting generalized linear models (GLM) with Poisson error distributions, which included the fixed effects of Habitat and Altitude and the interaction between them. Because survey points were sampled repeatedly for birds, we determined the effect of habitat on abundance of bird species with 10 or more observations, by fitting generalized linear mixed effects models (GLMM) assuming a Poisson error distribution. Fixed effects included Habitat, Altitude (m) and interactions between Habitat, Altitude, and Year. We incorporated the repeated measures temporal sampling of survey points within the random component of the model. For the best-fit model for each species, EDIS were identified as those that showed a significant difference in abundance between habitat types at the 5% level. All analyses were computed using R (Version 2.13: R Foundation for Statistical Computing, Vienna, Austria).

Cost-effectiveness

The resources for sampling biodiversity include monetary costs, time investment and availability of adequate technical expertise. Consistent with previous studies, we quantified monetary costs for taxa based on costs of field survey equipment and 'time effort' costs for the minimum number of staff required to undertake fieldwork, species identification and subsequent data management (Gardner et al. 2008; Kessler et al. 2011). Field scientists were costed at 100 € per day, and field assistants at 20 € per day according to values used in a recent study in the Amazon region (Kessler et al. 2011).

We compared the number of species showing significant differences in abundance between the habitat types (e.g. EDIS) for species groups (birds, lizards, bats, small mammals) against *absolute survey costs* and s*tandardized survey costs* as defined by Gardner et al. (2008). *Standardized survey costs* were determined by generating individual-based rarefaction curves for each vertebrate taxon with subsequent re-calibration of the y-axis to represent proportion of total number of species sampled, based on estimates of total species richness obtained using Chao2 (Chao 2005) in EstimateS (Gardner et al. 2008; Colwell 2009;). The x-axis was recalibrated to represent cumulative cost of sampling for each taxon. Finally, rarefaction of the data allows comparison of costs at equal levels of sampling effort based on species richness, using the least effectively sampled group as the reference level. However, as highlighted by Kessler et al. (2011), a weakness of *standardized survey costs* is that this rarefaction process does not take into consideration the loss of biological information associated with reduced effort. The reduced sampling effort should result in a loss of indicator species within a taxon as statistical power to differentiate between disturbance levels (i.e. primary, secondary forest, silvopasture) is reduced. Kessler et al. (2011) attempted to account for this by modelling the loss of information by introducing a measure of *residual survey costs*. They assumed a logarithmic relationship would represent the increase in numbers of indicator species with increasing effort/cost. This might hold within homogenous habitat (disturbance) categories. However, in more complex environments such as Andean forest systems with species structured by both habitat and altitude, the relationship may not be logarithmic, and might even include threshold-type responses. To investigate this we took a different approach. We assessed *effective indicator numbers* for each species group at standardised cost/effort by randomly resampling habitat indicator species datasets at replication levels representing the least effectively-sampled group. We then re-ran the GL(M)M models to determine how many EDIS remained at this lower sampling effort (and cost) for each taxon. For taxa with more than one EDIS we randomly resampled the raw datasets at reduced levels of replication and ran GL(M)M models to determine the relationship between number of indicator species and effort/cost.

Where there was satisfactory fit (which we defined as $R^2 > 0.75$) we used the slope from linear regression of number of indicator species against $\log_{10}$ (costs) as an 'ecological disturbance indicator species (EDIS) cost-effectiveness metric' to compare species groups. This metric provides an indication of the number of EDIS generated for a 10-fold increase in investment; a useful characteristic of a taxon as multiple indicators provide greater confidence in correctly assessing forest status (De Caceres et al., 2012).

Results

We recorded a total of 172 small vertebrate species. The number of species per taxon ranged from 7 for leaf-litter lizards, through to 9 for small mammals, 11 for bats (Table A1) and 145 for birds. For the latter, 45 species were represented by ten or more individual observations and were subsequently used in all analyses (Table A1). Using Chao2 to estimate total richness, our field survey captured 78% of bird species, 100% of leaf-litter lizards, 66% of small mammals and 85% of bats.

Small vertebrate EDIS

For birds, a total of 10 significant indicator species were identified using IndVal with a single indicator for primary forest, one for secondary and 8 for silvopasture (Table A2). For both primary and secondary indicators, specificity (B_{ij}, proportion of habitat category sites in which indicator is present) was low - at 46% for primary and 23% for secondary forest indicators. Most of the silvopasture indicators had higher specificity but generally lower fidelity (Aij, proportion of individuals in habitat category). No significant indicators were identified for the other taxa using IndVal.

Indicators identified using the GL(M)M approach for each taxon are shown in tables 1 to 3. Complete surveys of birds provide a total of 20 indicator species (14% of total recorded richness), with both leaf litter-lizards and small mammals providing 2 indicator species each (28% and 22% of total recorded richness respectively). Bats fail to provide a significant indicator species for primary or secondary habitat (Table 3).

Seven bird species (15% of the total) were more abundant in primary forest sites than secondary or silvopasture; three (7%) were more abundant in secondary than all other habitat types; and ten (22%) were observed at highest densities in silvopasture (Table 1, Table A2). The IndVal method did not identify any indicator species in common with the GL(M)M approach for primary and secondary forest, although six indicator species were identified in common by both approaches for the silvopasture habitats (Table A2).

At standardised sampling effort (67% of total richness) birds generated 17 indicators (9% of estimated total richness) and small mammals two (15% of total richness). Leaf-litter lizards and bats failed to generate any indicators at the lower standardized level of replication.

Cost effectiveness of selected taxa as EDIs

Total costs of surveys varied between taxa, ranging from 1490 € for bats to 6230 € for leaf-litter lizards (Table A3). The proportion of salary costs ranged from 59% for bats to 97% for birds, with 74% for small mammals and 92% for leaf-litter lizards. For all taxa the surveys capture a significant proportion of estimated total species richness, with rarefaction curves showing small mammals as the least-surveyed taxon with 67% of estimated total species richness represented (Fig. 1). Comparing taxa at standardized sampling effort for richness, we found that survey costs of taxa ranged from 857 € for bats to 3444 € for birds (Table 3A).

Birds generate the cheapest single EDIS, with the Andean Solitare (*Myadestes ralloides*) identified as a detector species of primary forest at a survey cost of 204 €. EDIS for small mammals represent 22% of total species richness of this group at absolute survey cost (Figure 2A). For standardised costs, where survey costs represent equal coverage of species richness across taxa, EDIS for lizards represent 28% of the total richness of this group (Figure 2(b)). However this, provides a biased view of numbers of indicators generated as when lower numbers of indicator species at reduced survey effort are accounted for small mammal EDIS again represent the greatest percentage of richness for least cost (Figure 2(c)).

No significant correlations were detected between percentage of indicator species and either absolute (Fig. 2(a); Spearman's rank correlation, $r_s = 0.2$, $P > 0.05$) or standardised (Fig. 2(b); Spearman's rank correlation, $r_s = 0.3$, $P > 0.05$) survey costs. However, plots of standardised indicators against standardised costs (Fig. 2(c) and (d)) show a positive trend that approaches significance (Spearman's rank correlation, $r_s = 0.95$, $P = 0.051$).

A positive correlation was detected between number of indicators, and total species richness (Pearson's Correlation, $r_p=0.99$, $P < 0.01$), and number of indicators and total abundance (Pearson's Correlation, $r_p=0.99$, $P < 0.01$). However, the relationship between proportion of estimated species richness actually detected per taxon and number of indicator species was non-significant (Spearman's rank correlation, $r_s = -0.2$, $P > 0.05$) partly reflecting adequate sampling coverage of the majority of taxa, at over 67% of taxon richness sampled.

Fitting a logarithmic curve to the number of indicators against costs is optimal for birds (best fit: Number of indicator species = 4.9 ln [Cost of survey] – 23.6, $R^2=0.964$) but sub-optimal for small mammals (best fit: Number of indicator species = 0.4 ln [Cost of survey] – 1.9, $R^2=0.56$) and leaf-litter lizards (best fit: Number of indicator species = 0.6 ln [Cost of survey] – 4.5, $R^2=0.34$). Satisfactory fits for the EDIS cost-effectiveness metric was seen for small mammals ($R^2 = 0.79$) and birds ($R^2 = 0.93$), generating values of 0.94 and 6.13 respectively.

Fewer bird EDIS were associated with secondary forest than either primary forest or silvopasture (Fig. 4).

Discussion

For decision makers engaged in habitat restoration, management or sustainable forestry, ‘ecological-disturbance indicator species (EDIS)’ that reflect the effects of environmental change on biota or biotic systems (McGeoch 2007) are a useful tool for assessing success or failure of conservation management (Pearce & Venier 2005; Jones et al. 2009). The current study represents the first assessment for small vertebrates in tropical mountain forests where biodiversity is often structured by altitude in addition to habitat (Sanchez-Cordero 2001; McCain 2005). Identifying cost-effective EDIS, or ‘high performance indicator species’ is a three-stage process involving: defining clear conservation objectives; use of a method to screen for suitable indicator species; and assessment of cost-effectiveness.

Screening for indicator taxa

Previous studies have used the indicator value (IndVal) metric (Dufrene & Legendre 1997) to screen for EDIS in tropical forests (Gardner et al. 2008; Kessler et al. 2011), however this method has a weakness in failing to explicitly incorporate covariates that can also structure species presence and abundance (Ferrier 2002). By comparing IndVal to a more statistically rigorous generalised linear modelling approach, we found that IndVal shows some merit in screening for EDIS; for example it identified 75% of bird EDIS in common with GL(M)M. The IndVal method also identified characteristic indicator species (species seen with high fidelity and specificity within a particular disturbance state) for primary and secondary forests that were not identified by GL(M)M . Three bird species are defined as characteristic EDIS (McGeoch et al. 2002; Alves da Mata et al. 2008) of silvopasture, with all others considered detector species (Table A2). The GL(M)M approach, with a focus on detecting statistically significant differences in abundances between disturbance states, aids in identifying a greater number of detector EDIS than IndVal in forest disturbance gradients co-structured by other factors, such as altitude hence caution must be taken when solely applying the IndVal metrics to such systems.

Cost effectiveness of indicator species

Selection of the most cost-effective EDIS is highly dependent on the conservation objective, which may vary from the need to i) determine the single most cost-effective indicator species, ii) identify taxa that generate the greatest number of indicators for investment (De Caceres et al. 2012), or iii) screen for indicators that are most representative of their own and other taxa e.g. surrogates (Caro 2010).

Our study shows that birds not only generate the cheapest EDIS but also generate the most EDIS per given level of investment. This is important as recent work reports that the use of multiple EDIS increases confidence in correctly assigning disturbance status (De Caceres et al. 2012). As the number of EDIS generated in our study was positively correlated with both total species richness and abundance of each taxon, we recommend that screening for new EDIS in other environments should first target species-rich groups. Where the goal is to find EDIS that best represent the greatest percentage of within- taxon species richness, we found small mammals to be the most parsimonious group. However, this may simply reflect low overall richness for this group.

The logarithmic relationship we report between bird EDIS and costs using GL(M) M reflects diminishing return on investments and is consistent with the '*residual survey costs*' method employed by Kessler et al. (2011). As such it lends support for the use of the IndVal indicator screening method in combination with logarithmic regression to estimate numbers of indicators against cost. This result also suggests that our 'cost-effective EDIS' metric is an appropriate measure for comparing indicators generated with cost, across taxa.

Covariates of altitude

Spatial autocorrelation associated with measuring change across gradients complicates development of indicators, with species-altitude relationships playing a strong role in structuring species distribution in montane environments (Herzog et al. 2011;Sanders & Rahbek 2012). However, spatial autocorrelation is not unique to mountains; gradients in the depth of the sea bed, and dynamic salinity in estuaries may be similarly confounded (Menezes et al., 2006). The majority (79%) of indicator species predicted by our GL(M)M models include altitude as a significant covariate of abundance, highlighting the difficulties of identifying generic habitat indicators for mountainous areas. Sensitivity to altitude also highlights the potential impact of climate change, with scenarios predicting altitudinal shifts in species distributions in mountain environments (Sekercioglu et al., 2012). As a result, elevational connectivity of protected areas is likely to play a major role in determining survival and extinction for many species (Herzog et al. 2011).

Outline method to identify indicator species

A stepwise approach to identifying EDIS is outlined in figure 5. The first step requires clear articulation of the monitoring requirements. A review of any existing site-specific species lists will then help provide guidance in choosing taxa that fulfil the goals. Species-rich groups, with known taxonomy, are likely to generate higher numbers of EDIS if used in conjunction with field survey methods that maximise capture of individuals from the full range of forest microhabitats. The actual method used to screen for EDIS depends on both forest type and survey design. Studies in complex environments, structured by multiple gradients and/or using survey designs that include unbalanced and repeated measures, are all likely to benefit from the greater statistical power offered by the GL(M)M approaches to identify detector EDIS. It should be noted that potential EDIS will still need to be verified by resampling under different temporal or spatial conditions to ensure they act as robust habitat management tools (McGeoch et al. 2002).

Long-term, local-based biodiversity monitoring programmes are vital for measuring and arresting loss of biodiversity in the tropics and guidance is required to provide a cost effective approach. The use of ecological disturbance indicator species provides a useful and relatively simple measure of the effect of land-use change and management on biodiversity (Caro 2010). However, indicators need to be identified according to conservation objectives and on a site-specific basis, particularly in regions with high beta diversity. Screening of indicators requires more robust statistical analytical approaches where strong natural gradients are thought to co-structure species presence and abundance and survey designs are unbalanced and include repeated measures. These factors often coincide in long-term monitoring programmes where repeated measures are inevitable and balanced designs are often impossible. Such programmes, including ours, often depend on ‘citizen science’ to provide the funds and manpower to generate datasets that extend beyond the timeframes of typical research-funding cycles. In challenging environments, e.g. tropical mountain forests, volunteers often find it difficult to survey more distant sample points. This leads to unbalanced datasets, which require the additional statistical power of more complex analytical methods, such as those used in this study. The design of scientifically robust, cost-effective monitoring programs aimed at assessing the impacts of environmental and climatic change gives the potential to integrate conservation, ecological research, environmental education, capacity-building and income generation through scientific ecotourism. Such programmes should be encouraged, established and supported (Sekercioglu 2012; Sekercioglu et al. 2012).

Acknowledgements

We would like to thank all the Earthwatch volunteers for their hard work in sample collection and preparation. MP and BT thank the Holly Hill Trust and Earthwatch for funding the projects, STM thanks the RGS for support for reptile surveys.

References

Albuja, L., M. Ibarra, J. Urgiles, and R. Barriga 1980. Estudio Preliminar de los Vertebrados Ecuatorianos. Escuela Politecnica Nacional, Quito, Ecuador.

Alves da Mata, R., M. McGeoch, and R. Tidon. 2008. Drosophilid assemblages as a bioindicator system of human disturbance in the Brazilian Savanna. Biodiversity and Conservation **17**:2899-2916.

Bateman, B. L., A. S. Kutt, E. P. Vanderduys, and J. E. Kemp. 2010. Small-mammal species richness and abundance along a tropical altitudinal gradient: an Australian example. Journal of Tropical Ecology **26**:139-149.

Cañadas-Cruz, L. 1983. El mapa bioclimático y ecológico del Ecuador. Ministerio de Agricultura y ganadería, Programa Nacional de regionalización Agraria, Banco Central del Ecuador, Quito.

Caro, T. M. 2010. Conservation by proxy: Indicator, umbrella, keystone, flagship, and other surrogate species. Island Press, Washington DC.

Chao, A. 2005. Species richness estimation. Pages 7909-7916 in N. Balakrishnan, C. B. Read, and B. Vidakovic, editors. Encyclopedia of Statistical Sciences. Wiley, New York.

Colwell, R. K. 2009. EstimateS: Statistical estimation of species richness and shared species from samples. Available from http://purl.oclc.org/estimates (last accessed December 2013).

De Caceres, M., and P. Legendre. 2009. Associations between species and groups of sites: indices and statistical inference. Ecology **90**:3566-3574.

De Caceres, M., P. Legendre, S. K. Wiser, and L. Brotons. 2012. Using species combinations in indicator value analyses. Methods in Ecology and Evolution **3**:973-982.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

Favreau, J. M., C. A. Drew, G. R. Hess, M. J. Rubino, F. H. Koch, and K. A. Eschelbach. 2006. Recommendations for assessing the effectiveness of surrogate species approaches. Biodiversity and Conservation **15**:3949-3969.

Ferrier, S. 2002. Mapping spatial pattern in biodiversity for regional conservation planning: Where to from here? Systematic Biology **51**:331-363.

Fu, C. Z., J. X. Wang, Z. C. Pu, S. L. Zhang, H. L. Chen, B. Zhao, J. K. Chen, and J. H. Wu. 2007. Elevational gradients of diversity for lizards and snakes in the Hengduan Mountains, China. Biodiversity and Conservation **16**:707-726.

Gardner, T. A., et al., 2008. The cost-effectiveness of biodiversity surveys in tropical forests. Ecology Letters **11**:139-150.

Halpern, B.S., Klein, C.J., Brown, C.J., Beger, M., Grantham, H.S. Mangubhai, S., Ruckelshaus, M., Tulloch, V.J., Watts, M., White, C., and Possingham, H.P., 2013. Achieving the triple bottom line in the face of inherent trade-offs among social equity, economic return, and conservation. Proceedings of the National Academy of Sciences **110:** 6229-6234

Halme, P., M. Monkkonen, J. S. Kotiaho, A.-L. Ylisirnio, and A. Markkanen. 2009. Quantifying the Indicator Power of an Indicator Species. Conservation Biology **23**:1008-1016.

Harrison, M. E., Boonman, A., Cheyne, S. M., Husson, S. J., Marchant, N. C., and Struebig M. J.. 2012. Biodiversity monitoring protocols for REDD+: can a one-size-fits-all approach really work? Tropical Conservation Science **5**:1-11.

Herzog, S. K., R. Martínez, P. M. Jørgensen, and H. Tiessen 2011. Climate Change and Biodiversity in the Tropical Andes. Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE).

Holdridge, L. R., W. C. Grenke, W.H.Hatheway, T. Liang, and J. A. Tosi. 1971. Forest environments in tropical life zones: a pilot study. Pergamon Press, Oxford.

Howe, R. W., R. R. Regal, G. J. Niemi, N. P. Danz, and J. M. Hanowski. 2007. Probability-based indicator of ecological condition. Ecological Indicators **7:**793-806.

Jankowski, J. E., S. K. Robinson, and D. J. Levey. 2010. Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. Ecology **91**:1877-1884.

Jones, G., D. S. Jacobs, T. H. Kunz, M. R. Willig, and P. A. Racey. 2009. Carpe noctem: the importance of bats as bioindicators. Endangered Species Research **8**:93-115.

Kessler, M. 2001. Patterns of diversity and range size of selected plant groups along an elevational transect in the Bolivian Andes. Biodiversity and Conservation **10**:1897-1921.

Kessler, M., S. Abrahamczyk, M. Bos, D. Buchori, D. D. Putra, S. R. Gradstein, P. Hohn, J. Kluge, F. Orend, R. Pitopang, S. Saleh, C. H. Schulze, S. G. Sporn, I. Steffan-Dewenter, S. S. Tjitrosoedirdjo, and T. Tscharntke. 2011. Cost-effectiveness of plant and animal biodiversity indicators in tropical forest and agroforest habitats. Journal of Applied Ecology **48**:330-339.

Laurence, W. F., and C. A. Peres, editors. 2006. Emerging Threats to Tropical Forests. University of Chicago Press, Chicago.

Lawton, J. H., D. E. Bignell, B. Bolton, G. F. Bloemers, P. Eggleton, P. M. Hammond, M. Hodda, R. D. Holt, T. B. Larsen, N. A. Mawdsley, N. E. Stork, D. S. Srivastava, and A. D. Watt. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature **391**:72-76.

Magurran, A. E. 2004. Measuring Biological Diversity. Blackwell, Malden, MA.

McCain, C. M. 2005. Elevational gradients in diversity of small mammals. Ecology **86**:366-372.

McGeoch, M. A. 2007. Insects and bioindication: theory and progress. Page 144 in A. J. A. Stewart, T. R. New, and O. T. Lewis, editors. Insect conservation biology. The Royal Entomological Society, London.

McGeoch, M. A., B. J. Van Rensburg, and A. Botes. 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. Journal of Applied Ecology **39**:661-672.

Menezes, Salomé, Soares, Amadeu M V M, Guilhermino, Lúcia and Peck, Mika R (2006) Biomarker responses of the estuarine brown shrimp *Crangon crangon L*. to non-toxic stressors: temperature, salinity and handling stress effects. Journal of Experimental Marine Biology & Ecology **335:** 114-122.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature **403**:853-858.

Pearce, J., and L. Venier. 2005. Small mammals as bioindicators of sustainable boreal forest management. Forest Ecology and Management **208**:153-175.

Rivas-Martinez, S., and G. Navarro. 1995. Bioclimatic Map of South America: Bioclimates. Scale 1:22,000,000. Cartographic Service, University of Leon, Spain.

Rodrigues, A. S. L., and T. M. Brooks. 2007. Shortcuts for biodiversity conservation planning: The effectiveness of surrogates. Pages 713-737. Annual Review of Ecology Evolution and Systematics. Annual Reviews, Palo Alto.

Sanchez-Cordero, V. 2001. Elevation gradients of diversity for rodents and bats in Oaxaca, Mexico. Global Ecology and Biogeography **10**:63-76.

Sanders, N. J., and C. Rahbek. 2012. The patterns and causes of elevational diversity gradients. Ecography **35**:1-3.

Sekercioglu, C. H. 2012. Promoting community-based bird monitoring in the tropics: Conservation, research, environmental education, capacity-building, and local incomes. Biological Conservation **151**:69-73.

Sekercioglu, C. H., R. B. Primack, and J. Wormworth. 2012. The effects of climate change on tropical birds. Biological Conservation **148**:1-18.

Sommerville, M. M., Milner-Gulland, E. J., Jones J. P.G. (2011).The challenge of monitoring biodiversity in payment for environmental service interventions. Biological Conservation **144:** 2832–284.

Tulloch, A., Possingham, H.P., Wilson, K., 2011. Wise selection of an indicator for monitoring the success of management actions. Biological Conservation **144:** 141-154

Tirira, D. 2007. Mamiferos del Ecuador, guia de Campo. Ediciones Murcielago Blanco. Publicacion Especial 6, Quito.

Trindade, J., and R. D. Loyola. 2011. Performance and Consistency of Indicator Groups in Two Biodiversity Hotspots. Plos One **6**.

Primary Forest indicators	Mean count per point sample	% of Primary forest count	
		Secondary	Silvopasture
Gorgeted Sunangel *(Heliangelus strophianus)*	0.13	3%	-
Three-striped Warbler (*Basileuterus tristriatus*)	0.1	3%	-
Plate-billed Mountain Toucan (*Andigena laminirostris*)	0.09	52%	-
Gray-breasted Wood-Wren (*Henicorhina leucophrys*)	0.83	86%	31%
Orange-bellied euphonia (*Euphonia xanthogaster*)	0.47	48%	48%
Andean Solitaire (*Myadestes ralloides*)	0.42	51%	29%
Buff-tailed Coronet (*Boissonneaua flavescens*)	0.34	3%	9%
Secondary Forest indicators		% of Secondary forest count	
		Primary	Silvopasture
Violet-tailed Sylph (*Aglaiocercus coelestis*)	0.32	75%	71%
Russet-crowned warbler (*Basileuterus coronatus*)	0.36	62%	24%
Brown inca (*Coeligena wilsoni*)	0.11	93%	77%
Silvopasture Forest indicators		% of Silvopasture count	
		Primary	Secondary
Beryl-spangled Tanager (*Tangara nigroviridis*)	0.73	45%	48%
Booted Racket-tail (*Ocreatus underwoodii*)	0.66	86%	96%
Sparkling Violetear (*Colibri coruscans)*	0.47	36%	65%
Red-billed Parrot (*Pionus sordidus*)	0.43	14%	52%
Smoke-colored Pewee (*Contopus fumigatus*)	0.23	3%	20%
Flame-faced Tanager (*Tangara parzudakii*)	0.21	14%	43%
Brown-capped Vireo (*Vireo leucophrys*)	0.19	24%	35%
Azara's spinetail (*Synallaxis moesta*)	0.19	-	5%
White-sided Flowerpiercer (*Diglossa albilatera*)	0.13	12%	22%
Club-winged Manakin (*Machaeropterus deliciosus*)	0.11	13%	32%

Table 1 Bird species observed at significantly higher ($p<0.05$) counts in primary forest habitat, showing counts and relative counts in silvopasture and secondary habitats and minimum sampling of species richness needed for species to act as indicators ($p<0.05$).

‘Indicator’ species	Habitat	Mean count per trap cluster (in corresponding indicator habitat)	% Primary count	% Secondary count	Best fit GLM Model	Indicator at standardised richness (% richness as significant indicator)
Long-whiskered Rice Rat (*Transandinomys bolivaris*)	Secondary	0.36	39%	n/a	Count ~ Habitat + Altitude	Yes ** (40%)
Alfaro's Rice Rat (*Handleyomys alfaroi*)	Primary	0.38	n/a	37%	Count ~Habitat + Altitude	No

Table 2 Small mammal species recorded at significantly different ($p<0.05$) abundances between primary, secondary and silvopasture habitats, and their best-fit generalized linear model (GLM), final column shows whether species is still a significant indicator at standardised survey costs (*$p<0.05$, **$p<0.01$) and minimum sampling of species richness needed for species to act as indicators ($p<0.05$).

'Indicator' species	Habitat	Mean count per trap-line (in corresponding indicator habitat)	% Secondary count	% Silvopasture count	Best fit GLM Model	Indicator at standardised richness (% richness as significant indicator)
Scaly-eyed Gecko (*Lepidoblepharis* sp.)	Primary	0.90	32%	16%	Count ~ Habitat + Altitude	No
Tropical Lightbulb Lizard (*Riama oculata*)	Primary	1.4	1 0%	61%	Count ~ Habitat + Altitude	No

Table 3 Leaf-litter lizard species recorded at significantly different ($p<0.05$) abundances between primary, secondary and silvopasture habitats, and their best-fit generalized linear model (GLM), final column shows whether species is still a significant indicator at standardised survey costs (*$p<0.05$, **$p<0.01$) and minimum sampling of species richness needed for species to act as indicators ($p<0.05$).

.

547

Group	Number of individuals	Recorded species	Estimated species richness (Chao 2)	Number of indicator species from full survey (%)			Number of indicator species at standardized sampling effort (%)		
				Primary	Secondary	Silvopasture	Primary	Secondary	Silvopasture
Birds	2808	145	185	7 (4.8%)	3 (2.1%)	10 (6.9%)	7 (4.8%)	3 (2.1%)	7 (2.7%)
Lizards	61	7	7	2 (28%)	0	0	0	0	0
Small mammals	48	9	13.5	1 (11%)	1 (11%)	-	1 (11%)	1 (11%)	-
Bats	37	11	13	0	0	-	0	0	-

Table 4 Biodiversity datasets showing number of individuals sampled and species richness from full surveys for each taxon. Number and percentage of indicator species from each habitat are shown for full surveys and at standardised costs.

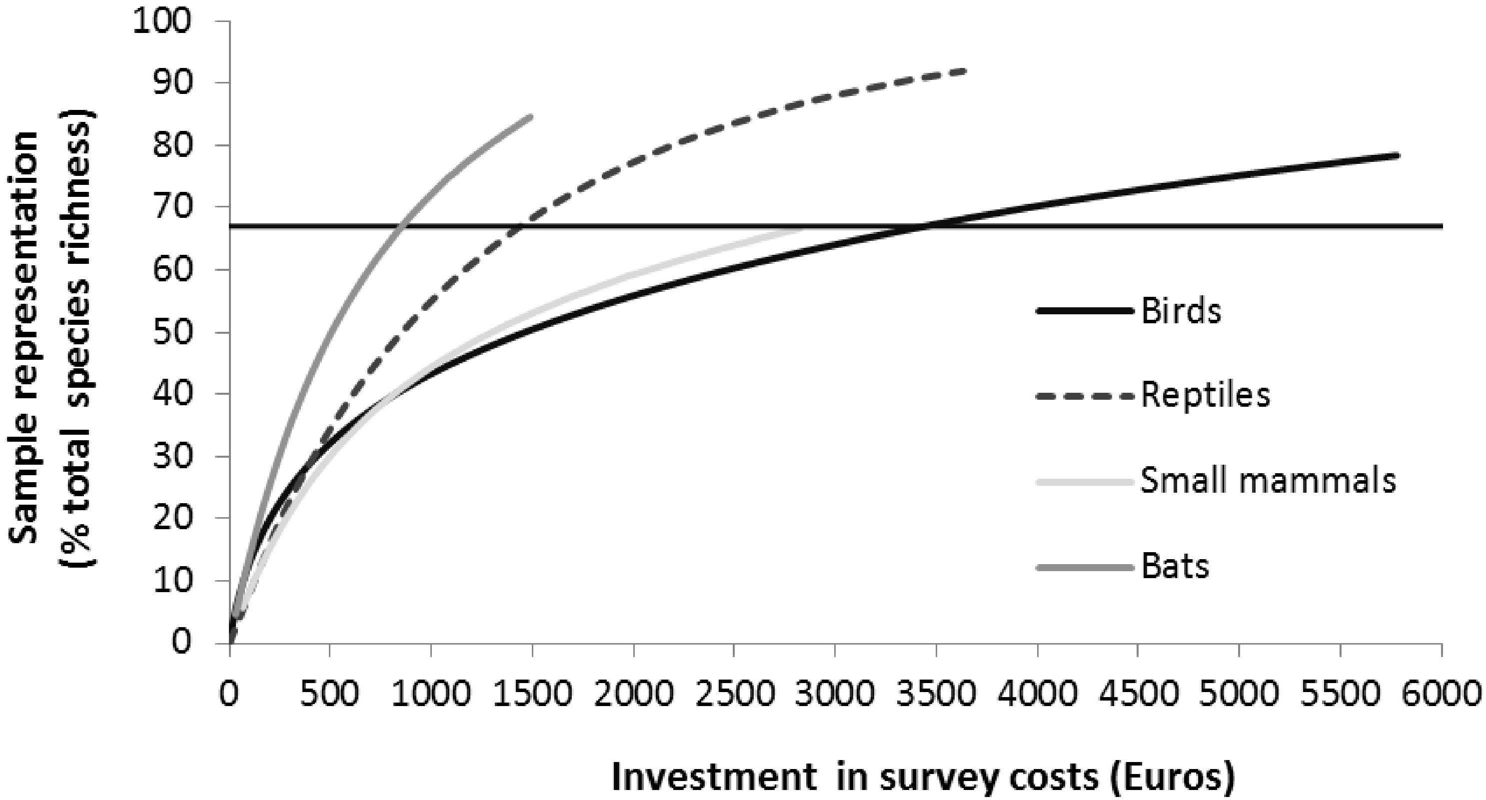

Fig1 Rarefaction curves for percentage of total estimated richness sampled against costs for each taxon. Horizontal dotted line represents the least effectively sampled group as the reference level with vertical bars providing an indication of costs for other taxa at standardised estimate of total richness for each species group.

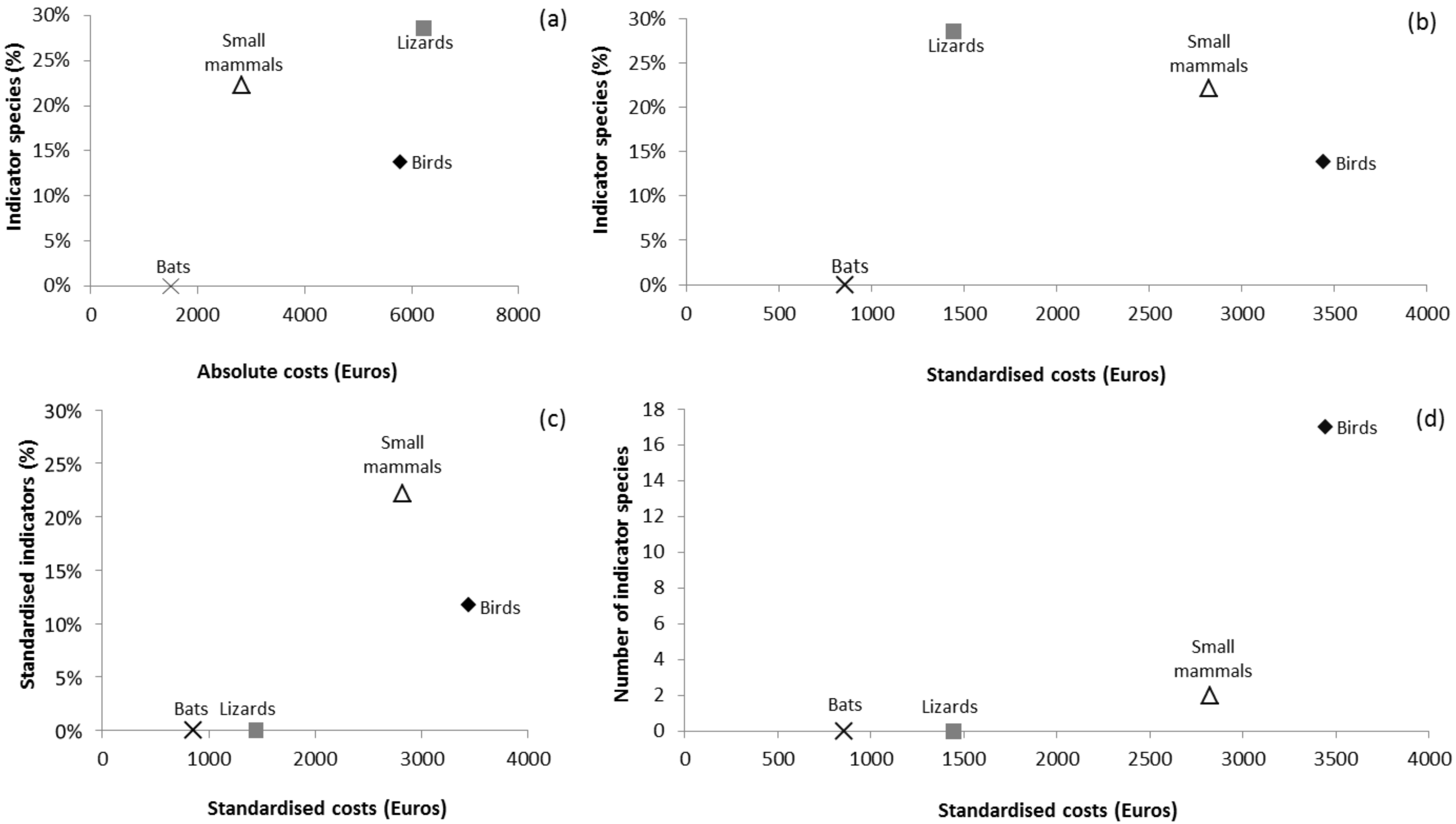

Fig 2 Percentage of indicator species against total cost of survey for each taxon (a), against standardised survey costs (b) and Percentage (c) and number (d) of standardised indicators against standardised costs.

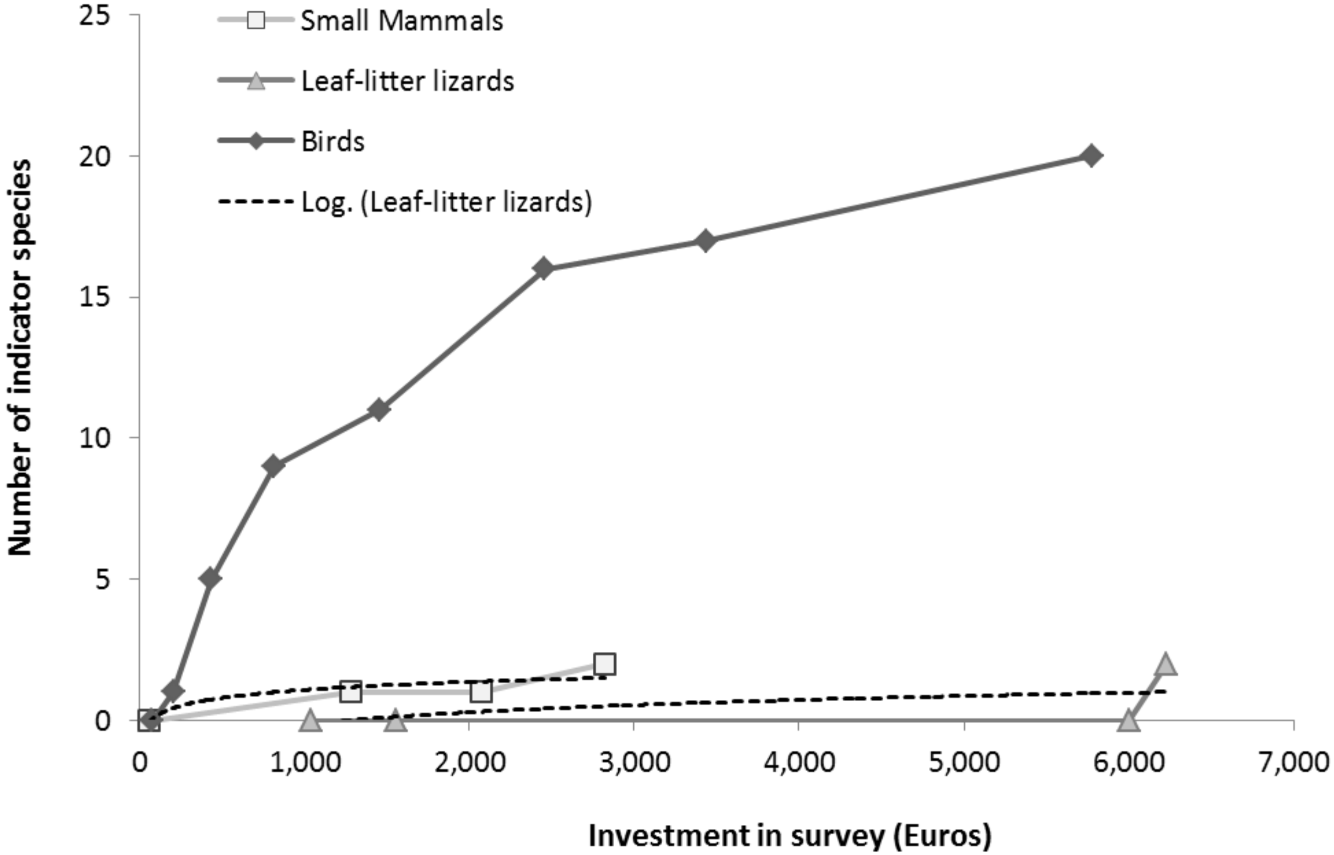

Fig 3 Return-on-investment curves for birds, leaf-litter lizard, and small mammals, showing number of indicator species yielded at a given level of investment with a logarithmic trend-line fitted for small mammals and birds.

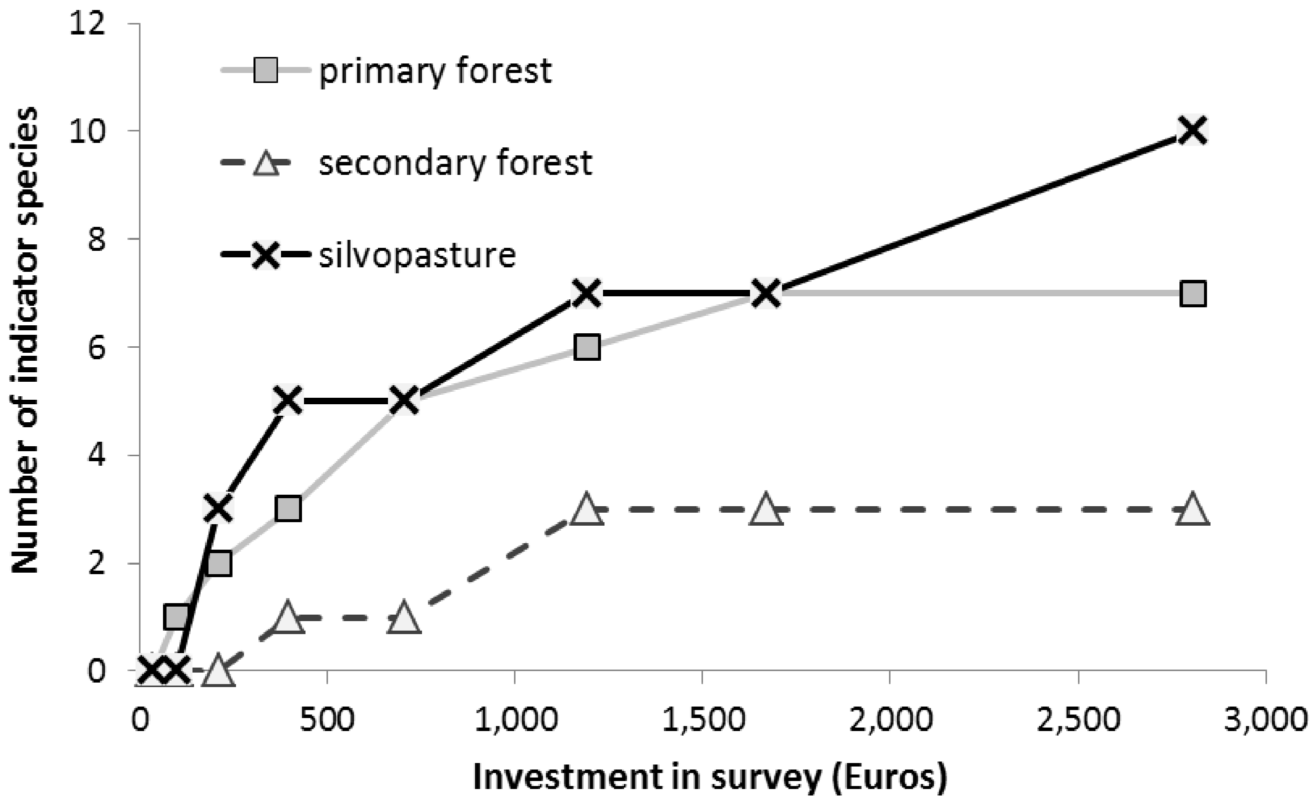

Fig 4 Return-on-investment curve for bird indicator species, showing number of indicators yielded at a given level of investment, for each habitat type.

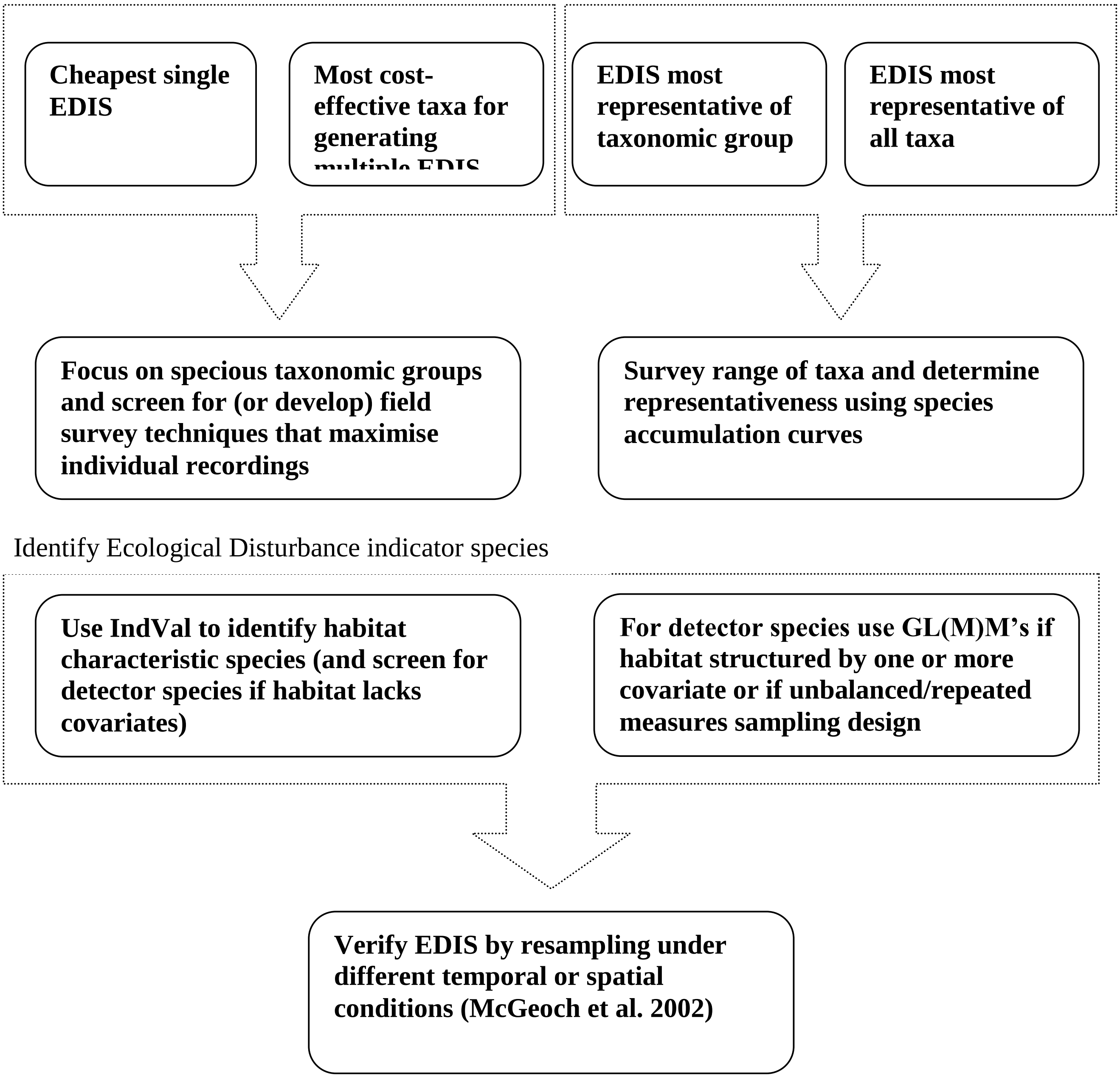

Fig. 5 Framework for identifying ecological disturbance indicator species.

Supplementary material

Species lists

Small Mammals

Alfaro's Rice Rat	*Handleyomys alfaroi*
Dusky Rice Rat	*Melanomys caliginosus*
Tomes's Rice Rat	*Nephelomys albigularis*
Bicolored Arboreal Rice Rat	*Oecomys bicolor*
unknown	*Reithrodontomys soderstromi*
Long-whiskered Rice Rat	*Transandinomys bolivaris*
Talamancan Rice Rat	*Transandinomys talamancae*
unknown	*Microrizomys altissimus*
Tschudi's Slender Opossum	*Marmosops impavidus*

Birds (10 or more individuals)

Andean Solitaire	*Myadestes ralloides*
Azara's Spinetail	*Synallaxis azarae*
Band-tailed Pigeon	*Patagioenas fasciata*
Beryl-spangled Tanager	*Tangara nigroviridis*
Blue-grey Tanager	*Thraupis episcopus*
Blue-winged Mountain-Tanager	*Anisognathus somptuosus*
Booted Racket-tail	*Ocreatus underwoodii*
Brown Inca	*Coeligena wilsoni*
Brown Violetear	*Colibri delphinae*
Brown-capped Vireo	*Vireo leucophrys*
Buff-tailed Coronet	*Boissonneaua flavescens*
Club-winged Manakin	*Machaeropterus deliciosus*
Crimson-rumped Toucanet	*Aulacorhynchus haematopygus*
Dusky Bush-Tanager	*Chlorospingus semifuscus*
Flame-faced Tanager	*Tangara parzudakii*
Glossy-black Thrush	*Turdus serranus*
Golden Tanager	*Tangara arthus*
Golden-crowned Tanager	*Iridosornis rufivertex*
Golden-headed Quetzal	*Pharomachrus auriceps*
Golden-naped Tanager	*Tangara ruficervix*
Golden-winged Manakin	*Masius chrysopterus*
Gorgeted Sunangel	*Heliangelus strophianus*
Gray-breasted Wood-Wren	*Henicorhina leucophrys*
Green-and-black Fruiteater	*Pipreola riefferii*
Masked Flowerpiercer	*Diglossa cyanea*
Masked Trogon	*Trogon personatus*

Metallic-green Tanager	*Tangara labradorides*
Nariño Tapaculo	*Scytalopus vicinior*
Orange-bellied Euphonia	*Euphonia xanthogaster*
Plate-billed Mountain-Toucan	*Andigena laminirostris*
Plumbeous Pigeon	*Patagioenas plumbea*
Red-billed Parrot	*Pionus sordidus*
Red-headed Barbet	*Eubucco bourcierii*
Ruddy Foliage-gleaner	*Automolus rubiginosus*
Rufous-breasted Antthrush	*Formicarius rufipectus*
Russet-crowned Warbler	*Basileuterus coronatus*
Smoke-colored Pewee	*Contopus fumigatus*
Sparkling Violetear	*Colibri coruscans*
Spillmann's Tapaculo	*Scytalopus spillmanni*
Tawny-bellied Hermit	*Phaethornis syrmatophorus*
Three-striped Warbler	*Basileuterus tristriatus*
Toucan Barbet	*Semnornis ramphastinus*
Violet-tailed Sylph	*Aglaiocercus coelestis*
White-sided Flowerpiercer	*Diglossa albilatera*
White-tailed Tyrannulet	*Mecocerculus poecilocercus*
Lizards	
Tropical lightbulb lizard	*Riama oculata*
Drab lightbulb lizard	*Riama unicolor*
Unknown	*Riama sp.*
Unknown	*Echinosaura brachycephala*
Brown Prionodactylus	*Cercosaura vertebralis*
Unknown	*Lepidoblepharis sp.*
Unknown	*Alopoglossus festae*
Bats	
Rosenberg's fruit-eating bat	*Artibeus rosenbergii*
Silky short-tailed bat	*Carollia brevicauda*
Chestnut Short-tailed Bat	*Carollia castanea*
Seba's short-tailed bat	*Carollia perspicillata*
Little Big-eared Bat	*Micronycteris megalotis*
Highland Yellow-shouldered Bat	*Stunira ludovici*
Spectral bat	*Vampyrum spectrum*
Little black serotine	*Eptesicus andinus*
Hairy-legged Myotis	*Myotis keaysi*
Black Myotis	*Myotis nigricans*
Riparian Myotis	*Myotis riparius*

Table A1 Species used in analysis.

Significant IndVal indicators	IndVal	Aij	Bij	p value	Identified by GLMM
Primary Forest indicators					
Blue tanager (*Tangara vassorii*)	0.65	0.91	0.46	0.02	No
Secondary forest indicators					
Scale-crested Pygmy Tyrant (*Lophotriccus pileatus*)	0.48	1	0.23	0.05	No
Silvapasture Forest Indicators					
Smoke-colored Pewee (*Contopus fumigatus*)	0.87	0.89	0.86	0.001	Yes
Flame-faced tanager (*Tangara parzudakii*)	0.79	0.73	0.86	0.002	Yes
Club-winged manakin (*Machaeropterus deliciosus*)	0.76	0.81	0.71	0.002	Yes
Azara's spinetail (*Synallaxis azarae*)	0.7	0.86	0.57	0.002	Yes
White-sided flowerpiercer (*Diglossa albilatera*)	0.62	0.68	0.57	0.015	Yes
Montane woodcreeper (*Lepidocolaptes lacrymiger*)	0.6	0.84	0.43	0.01	No
Brown-capped vireo (*Vireo leucophrys*)	0.6	0.62	0.57	0.016	Yes
Tricolored brush-finch (*Atlapetes tricolor*)	0.51	0.61	0.43	0.043	No

Table A2 Species identified as significant ($p<0.05$) using the Indicator value (IndVal) metric. Underlined species are considered characteristic indicator species and others as detector species (McGeoch et al. 2002)

Group	Postdoc (days)				Field assistant (days)				Materials (euro)	Total expend (euro)	Standardized survey costs (euro)
	fieldwork	processing in the field	processing in the lab/ID	data management /other	fieldwork	processing in the field	processing in the lab/ID	data management /other			
Birds	39	-	-	9.5	39	-	-	-	150	5780	3444
Leaf- litter lizards	25	5	10	5	55	5	0	2	490	6230	1445
Small mammals	5	1	-	2	50	2	10	2	745	2825	2825
Bats	2	2	-	-	10	2	10	2	610	1490	857

Table A3. Costs estimates for field surveys for the range of taxa surveyed.