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Cost-Effectiveness of Using Small Vertebrates as Indicators of Disturbance

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Abstract: *In species-rich tropical forests, effective biodiversity management demands measures of progress, yet budgetary limitations typically constrain capacity of decision makers to assess response of biological communities to habitat change. One approach is to identify ecological-disturbance indicator species (EDIS) whose monitoring is also monetarily cost-effective. These species can be identified by determining individual species' responses to disturbance across a gradient; however, such responses may be confounded by factors other than disturbance. For example, in mountain environments the effects of anthropogenic habitat alteration are commonly confounded by elevation. EDIS have been identified with the indicator value (IndVal) metric, but there are weaknesses in the application of this approach in complex montane systems. We surveyed birds, small mammals, bats, and leaf-litter lizards in differentially disturbed cloud forest of the Ecuadorian Andes. We then incorporated elevation in generalized linear (mixed) models (GL(M)M) to screen for EDIS in the data set. Finally, we used rarefaction of species accumulation data to compare relative monetary costs of identifying and monitoring EDIS at equal sampling effort, based on species richness. Our GL(M)M generated greater numbers of EDIS but fewer characteristic species relative to IndVal. In absolute terms birds were the most cost-effective of the 4 taxa surveyed. We found one low-cost bird EDIS. In terms of the number of indicators generated as a proportion of species richness, EDIS of small mammals were the most cost-effective. Our approach has the potential to be a useful tool for facilitating more sustainable management of Andean forest systems.*

Keywords: disturbance gradients, ecological-disturbance indicator species, generalized linear modeling, IndVal, survey costs, tropical montane forest

Rentabilidad del Uso de Pequeños Vertebrados como Indicadores de Perturbaciones

Resumen: *En los bosques tropicales con gran riqueza de especies, el manejo efectivo de la biodiversidad exige medidas del progreso, sin embargo las limitaciones presupuestales típicamente restringen la capacidad de quienes toman las decisiones para evaluar la respuesta de las comunidades biológicas al cambio. Una estrategia consiste en identificar a las especies indicadoras de perturbaciones ecológicas (EIPE) cuyo monitoreo también es rentable. Estas especies pueden identificarse al determinar las respuestas individuales de las especies a las perturbaciones a lo largo de un gradiente; sin embargo, dichas respuestas pueden ser frustradas por otros factores que no son la perturbación. Por ejemplo, en los ambientes montañosos los efectos de la alteración antropogénica de hábitat son comúnmente frustrados por la elevación. Las especies indicadoras de perturbaciones ecológicas se han identificado con la medida del valor indicador (IndVal, en inglés), pero*

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hay debilidades en la aplicación de esta estrategia en los sistemas montañosos complejos. Censamos aves, mamíferos pequeños, murciélagos y lagartijas de hojarasca en bosques de niebla con diferentes perturbaciones en los Andes Ecuatorianos. Después usamos la elevación en modelos (mixtos) lineales generalizados (M(M)LG) para buscar EIPE en el juego de datos. Finalmente usamos la rarefacción de datos de acumulación de especies para comparar los costos monetarios relativos de la identificación y monitoreo de EIPE en un esfuerzo igual de muestreo, basado en la riqueza de especies. Nuestro M(M)LG generó un mayor número de EIPE, pero un menor número de especies características con relación al IndVal. En términos absolutos, las aves fueron el más rentable de los cuatro taxones censados. Encontramos un ave que fuera rentable y que funcionara como EIPE. En términos del número de indicadores generados como una proporción de la riqueza de especies, las EIPE que fueron mamíferos pequeños también fueron las más rentables. Nuestra estrategia tiene el potencial de ser una herramienta útil para facilitar un manejo más sustentable de los sistemas boscosos en los Andes.

Palabras Clave: bosque tropical de montaña, costo de censos, especies indicadoras de perturbaciones ecológicas, gradientes de perturbación, IndVal, modelado lineal generalizado

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 and absence and abundance of multiple taxa across a gradient of disturbance to find those that best characterize each stage. This approach has been the subject of considerable research (Laurence & Peres 2006; Caro 2010) and has been applied 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 when 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 (IndVal) have been described as high performance indicator taxa (Gardner et al. 2008).

Once a robust site-specific data set for a range of taxa exists the selection of these high performance indicator taxa generally follows a 3-stage process (Gardner et al. 2008). The first stage involves clearly defining the conservation objective(s); the second is 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 that are based on changes in species richness, community composition, and population size are in common use. Of these, change in population size is considered the most sensitive because it can forewarn of localized 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). The most common selection method used to identify EDIS in tropical forests is the IndVal method (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 levels of disturbance (Dufrene & Legendre 1997; De Caceres & Legendre 2009; De Caceres et al. 2012). IndVal identifies 2 types of EDIS: characteristic species, which are only present in particular disturbance states and detector species, which are found at different abundances across a range of levels of disturbance. Characteristic species are more likely to be vulnerable to habitat degradation, but detector species may be a more sensitive measure for monitoring change over time than a single state variable because 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 elevation, microhabitat and temperature in mountain forests (Bateman et al. 2010). We compared the efficacy of IndVal in identifying EDIS with that of a generalized linear (mixed effects) modeling (GL(M)M) approach to explore the potential need to use 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 of the approach outlined by Gardner et al. (2008) requires the 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; Sommerville et al. 2011; 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 used 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). We are the first to combine all 3 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 was novel because we compared EDIS generated by IndVal with more complex GL(M)M that incorporated additional environmental covariates and then assessed relative cost-effectiveness of the EDIS identified with rarefaction to compare cost per taxon at equal sampling of estimated species richness.

Methods

Field Sites

We conducted field surveys in 2 tropical Andean montane reserves, the Santa Lucía 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, northwestern Ecuador. The SLR spans an elevational range of 1400–2560 m and JCR ranges from 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 is composed of fragmented forest reserves surrounded by a matrix of cultivation and pasture lands. It lies within the Tropical Andes biodiversity hotspot (Myers et al. 2000) and exhibits 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; the average annual temperature is 16 °C (Rivas-Martinez & Navarro 1995).

Species Survey Methods

We surveyed avifauna in primary, secondary, and silvopasture sites (pasture planted with nitrogen-fixing Andean alder [*Alnus acuminata*]) in SLR using point-count sampling. We established 52 permanent point-count survey locations a minimum of 100 m apart to avoid spatial pseudo-replication. Of the 52 point-count locations, 24 were in primary forest, 17 in secondary forest, and 11 in silvopasture. To minimize records from boreal migrants, we conducted fieldwork between June and August over 4 field seasons from 2008 to 2011. Experienced ornithologists surveyed 8 locations daily from 0600 to 0900. They identified birds within a 50 m radius to species level through both visual and auditory cues. Each location was surveyed for 10 min following an initial 2-min acclimatization time.

We surveyed leaf-litter lizards during 5 field expeditions to SLR over 3 years (2008–2010). We deployed 21 pitfall traplines with drift-fence arrays equally across primary forest, secondary forest, and silvopasture. Each trapline measured 5 × 5 m and was constructed in a T formation of 5, 25-L plastic buckets buried at intervals of 2.5 m. We left traplines in situ for 10 days and checked them twice daily.

We used clusters of Sherman live-traps deployed along line transects to sample small mammals from JCR during 2 field expeditions in 2010. Six transects of average length 175 m were distributed equally between primary and secondary forest at elevations of 1300–1900 m. We deployed 186 traps, averaging 37/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. Four 200-m transects were deployed, each composed of 4, 6 × 2.6 m mist nets spaced 50 m apart. Nets were distributed equally between primary and secondary forest at elevations of 1300–1400 m and were positioned in microhabitats that would optimize capture. One to 2 transects were sampled per night, equating to 4–8 nets in situ for 3 h/night (from 1800 to 2100). We used taxonomic keys to identify chiropterans in the field (Albuja et al. 1980; Tirira 2007).

Data Analyses

For all taxa, we determined the ability of the IndVal metric to identify EDIS relative to more complex GL(M)M that allowed inclusion of potential environmental covariates. The IndVal metric generates a percentage IndVal for each species by multiplying measures of habitat specificity (based on abundance) and habitat fidelity (based on presence and 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 modeled by fitting GLM with Poisson error distributions, which included the fixed effects of habitat and elevation and the interaction between them. Because point-count survey locations were sampled repeatedly for birds, we determined the effect of habitat on abundance of bird species with 10 or more observations by fitting GLMM assuming a Poisson error distribution. Fixed effects included habitat, elevation, and interactions among habitat, elevation, and year. We incorporated the repeated measures temporal sampling of survey locations 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 in R (Version 2.13: R Foundation for Statistical Computing, Vienna, Austria).

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 cost 100 €/d, and field assistants cost 20 €/d according to values used in a recent study in the Amazon (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) with absolute survey costs and standardized 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 recalibration of the y-axis to represent proportion of the total number of species sampled, based on estimates of total species richness obtained with 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 when the least effectively sampled group is used 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 because statistical power to differentiate between disturbance levels (i.e., primary forest, secondary forest, silvopasture) is reduced. Kessler et al. (2011) attempted to account for this by modeling the loss of information via introducing a measure of residual survey costs. They assumed that a logarithmic relationship represents the increase in numbers of indicator species with increasing effort and 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 elevation, the relationship may not be logarithmic and may even include threshold-type responses.

To investigate this we took a different approach. We assessed effective indicator numbers for each species group at standardized cost and effort by randomly resampling habitat indicator species data sets at replication levels representing the least effectively sampled group. We then reran the GL(M)M 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 data sets at reduced levels of replication and ran GL(M)M to determine the relationship between number of indicator species and effort and 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 EDIS cost-effectiveness metric with which 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 because multiple indicators provide greater confidence in correctly assessing forest status (De Caceres et al. 2012).

Results

We recorded 172 small vertebrate species, 7 species of leaf-litter lizards, 9 species of small mammals, 11 species of bats (Supporting Information) and 145 species of birds. For the latter, 45 species were represented by 10 or more individual observations and were subsequently used in all analyses. We captured 78% of bird species, 100% of leaf-litter lizard species, 66% of small mammal species, and 85% of bat species.

Small Vertebrate EDIS

For birds, 10 significant indicator species were identified with IndVal (Supporting Information). One species

Table 1. Mean number of observations of bird species per point count for significant indicator species of each forest type, with relative observations per point for other forest types.

Type of habitat and indicator species	*Mean observations/point*	*Percent primary observations/point*	
		Secondary	*Silvopasture*
Primary forest			
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		Percent secondary observations/point	
		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		Percent silvopasture observations/point	
		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

was an indicator of primary forest, one of secondary forest, and 8 of silvopasture. For both primary and secondary indicators, specificity (B_{ij}, proportion of habitat category sites in which indicator is present) was low: 46% for primary and 23% for secondary forest indicators. Most of the silvopasture indicators had higher specificity but generally low fidelity (A_{ij}, proportion of individuals in habitat category). No significant indicators were identified for the other taxa with IndVal.

Complete surveys of birds provided 20 indicator species that represented 14% of total recorded richness (Table 1). Leaf litter-lizards and small mammals provided 2 indicator species each (28% and 22% of total recorded richness respectively; Supporting Information). Bats failed to provide a significant indicator species for primary or secondary forest.

Seven bird species (15% of the total) were more abundant in primary forest than secondary forest or silvopasture; 3 (7%) were more abundant in secondary forest than the other habitat types; and 10 (22%) were observed at highest densities in silvopasture (Table 1 & Supporting Information). The IndVal method did not identify any indicator species in common with the GLMM approach for primary or secondary forest, although 6 indicator species were identified in common by both approaches for silvopasture (Supporting Information).

At standardized sampling effort (67% of total richness), birds generated 17 indicators (9% of estimated total richness) and small mammals 2 (15% of total richness). Leaf-litter lizards and bats failed to generate any indicators at the lower standardized level of replication (Table 2).

Cost-effectiveness of selected taxa as EDIS

Total costs of surveys varied among taxa (range from 1490 € for bats to 6230 € for leaf-litter lizards) (Fig. 1; Supporting Information). The proportion of salary costs were 59% for bats, 97% for birds, 74% for small mammals, and 92% for leaf-litter lizards. For all taxa the surveys captured a significant proportion of estimated total species richness; rarefaction curves showed small mammals as the least-surveyed taxon with 67% of estimated total species richness represented (Fig. 2). Comparing taxa at standardized sampling effort for species richness, survey costs of taxa ranged from 857 € for bats to 3444 € for birds (Supporting Information). Birds generated the cheapest single EDIS; the Andean Solitare (*Myadestes ralloides*) was a detector species of primary forest at a survey cost of 204 €. The EDIS for small mammals represented 22% of total species richness of this group at absolute survey cost (Fig. 3a). For standardized costs, where survey costs represented equal coverage of species richness across taxa, EDIS for lizards represented 28% of the total richness of this group (Fig. 3b). This result, however, provides a biased view of numbers of indicators generated because when lower numbers of indicator species at reduced survey effort were accounted for, small mammal EDIS again represented the greatest percentage of species richness for the least cost (Fig. 3c).

No significant correlations were detected between percentage of indicator species and either absolute (Fig. 3a; Spearman's rank correlation, $r_s = 0.2$, $P > 0.05$) or standardized (Fig. 3b, and Spearman's rank correlation, $r_s = 0.3$, $P > 0.05$) survey costs. However, plots of standardized indicators against standardized costs (Fig. 3c and d) showed a positive trend that approached 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 not 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 was optimal for birds (best fit: number of indicator species = 4.9 ln [cost of survey] − 23.6, $R^2 = 0.964$) but suboptimal 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 were seen for small mammals ($R^2 = 0.79$) and birds ($R^2 = 0.93$). They had values of 0.94 and 6.13 respectively. Fewer bird EDIS were associated with secondary forest than either primary forest or silvopasture (Supporting Information).

Discussion

For decision makers engaged in habitat restoration, management, or sustainable forestry, 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 (Pearce & Venier 2005; Jones et al. 2009). Our study represents the first assessment of small vertebrates in tropical mountain forests, where biodiversity is often structured by elevation in addition to land cover (Sanchez-Cordero 2001; McCain 2005). Identifying cost-effective EDIS, or high performance indicator species, is a 3-stage process involving defining clear conservation objectives; use of a method to screen for suitable indicator species; and assessment of costeffectiveness.

Screening for indicator taxa

Previous studies have used the IndVal metric (Dufrene & Legendre 1997) to screen for EDIS in tropical forests (Gardner et al. 2008; Kessler et al. 2011); however, this method fails to explicitly incorporate covariates that can also structure species presence and abundance (Ferrier 2002). By comparing IndVal to a more statistically rigorous GLMM approach, we found that IndVal showed some merit in screening for EDIS. For example, it identified 75% of bird EDIS in common with GLMM. 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; all other species are considered detector species (Supporting Information). The GL(M)M approach, with a focus on detecting

Table 2. **Number of individuals sampled, species richness, and number of species that are indicators of primary, secondary, and silvopasture forest for nonstandardized survey effort and for survey effort standardized to represent equal sampling of species richness across taxonomic groups.**

Group	*Number of individuals*	*Recorded species*	*Estimated species richness (Chao 2)*	*Number of indicator species from nonstandardized 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	–

statistically significant differences in abundances between disturbance states, aids in identifying a greater number of detector EDIS than IndVal in forest disturbance gradients costructured by other factors, such as elevation; 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 determine the single most cost-effective indicator species, to identify taxa that generate the greatest

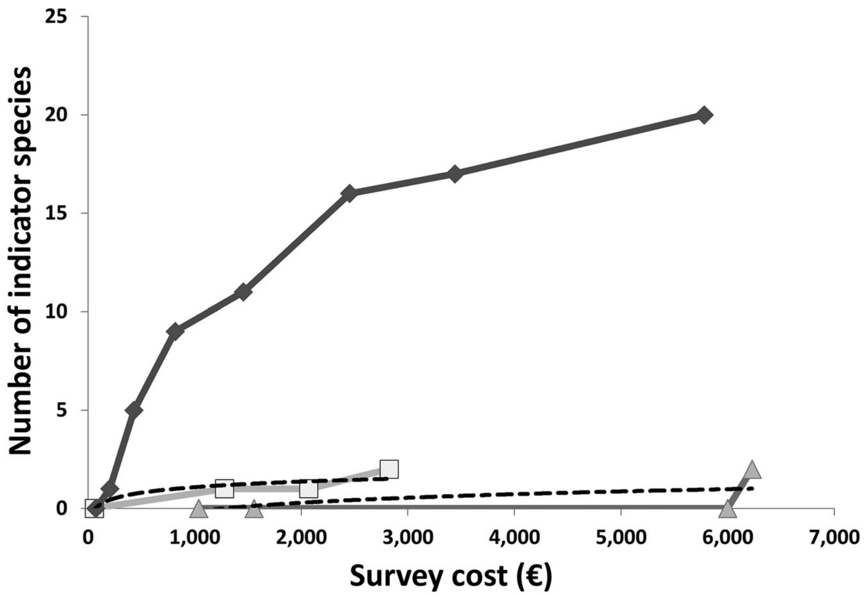

Figure 1. Return-on-investment curves for surveys of indicator species against investment (€) for birds (diamonds), leaf-litter lizards (triangles), and small mammals (squares). Shows number of indicator species at given levels of investment and a logarithmic trend-line fitted for small mammals and leaf-litter lizards.

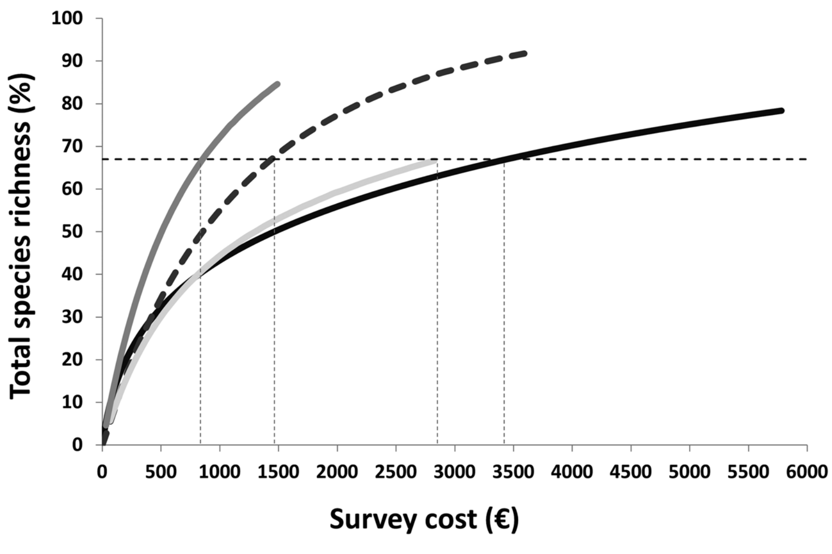

Figure 2. Rarefaction curves for percentage of total estimated species richness sampled against costs of sampling for 4 taxonomic groups (solid black curve, birds; dashed black curve, reptiles; light grey curve, small mammals; medium grey curve, bats; horizontal dashed line, least effectively sampled group as the reference level; vertical lines, indication of costs for other taxa at a standardized estimate of total species richness for each group).

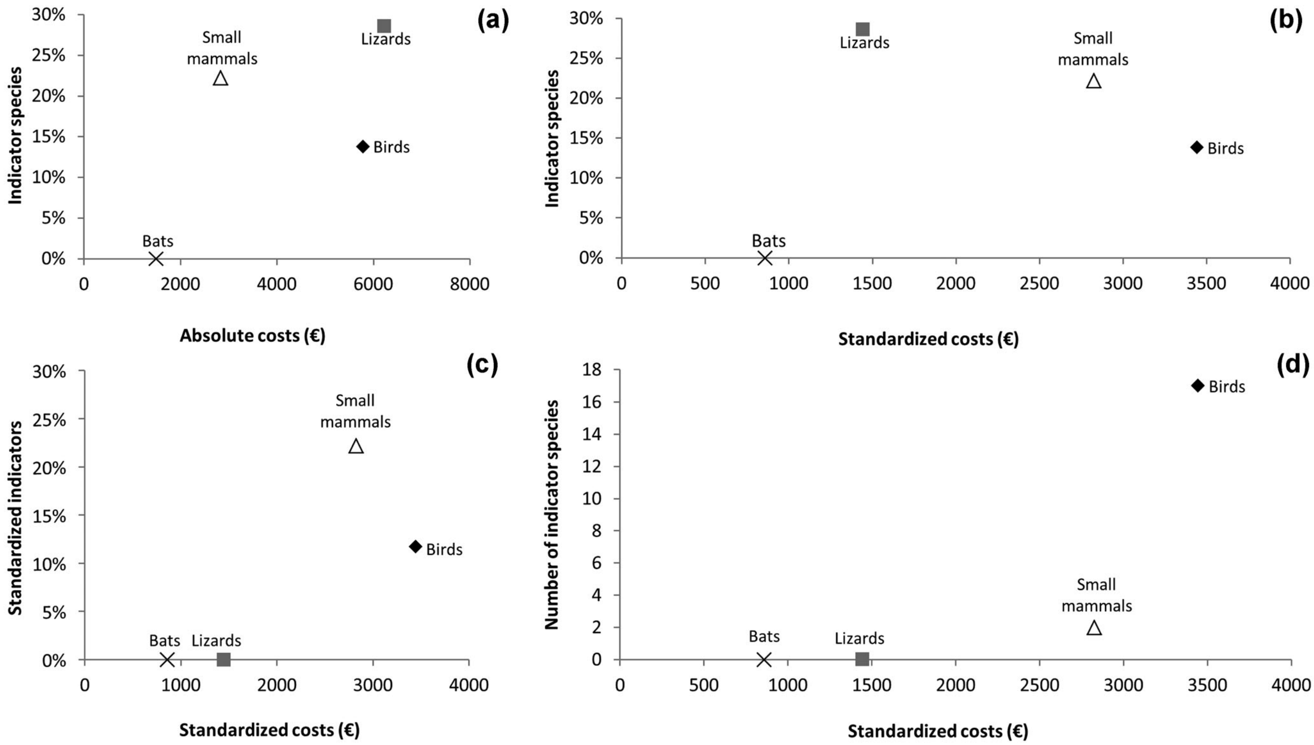

Figure 3. Percentage of indicator species against total cost of survey for each (a) taxon, (b) standardized survey costs and (c) percentage and (d) number of standardized indicators against standardized costs.

number of indicators for investment (De Caceres et al. 2012), or to screen for indicators that are most representative of their own and other taxa (e.g., surrogates [Caro 2010]).

Our results show that birds not only generate the cheapest EDIS, but also generate the most EDIS per given level of investment. This is important because recent work reports that the use of multiple EDIS increases confidence in correctly assigning disturbance status (De Caceres et al. 2012). Because 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 identified via GLMM reflects diminishing return on investments and is consistent with the residual survey costs method used 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 across taxa indicators generated with cost.

Covariates of elevation

Spatial autocorrelation associated with measuring change across gradients complicates development of indicators; species-elevation relationships play 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 confounding (Menezes et al. 2006). The majority (79%) of indicator species predicted by our GL(M)M models included elevation as a significant covariate of abundance, highlighting the difficulties of identifying generic habitat indicators for mountainous areas. Sensitivity to elevation also highlights the potential impact of climate change, with scenarios predicting elevational 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).

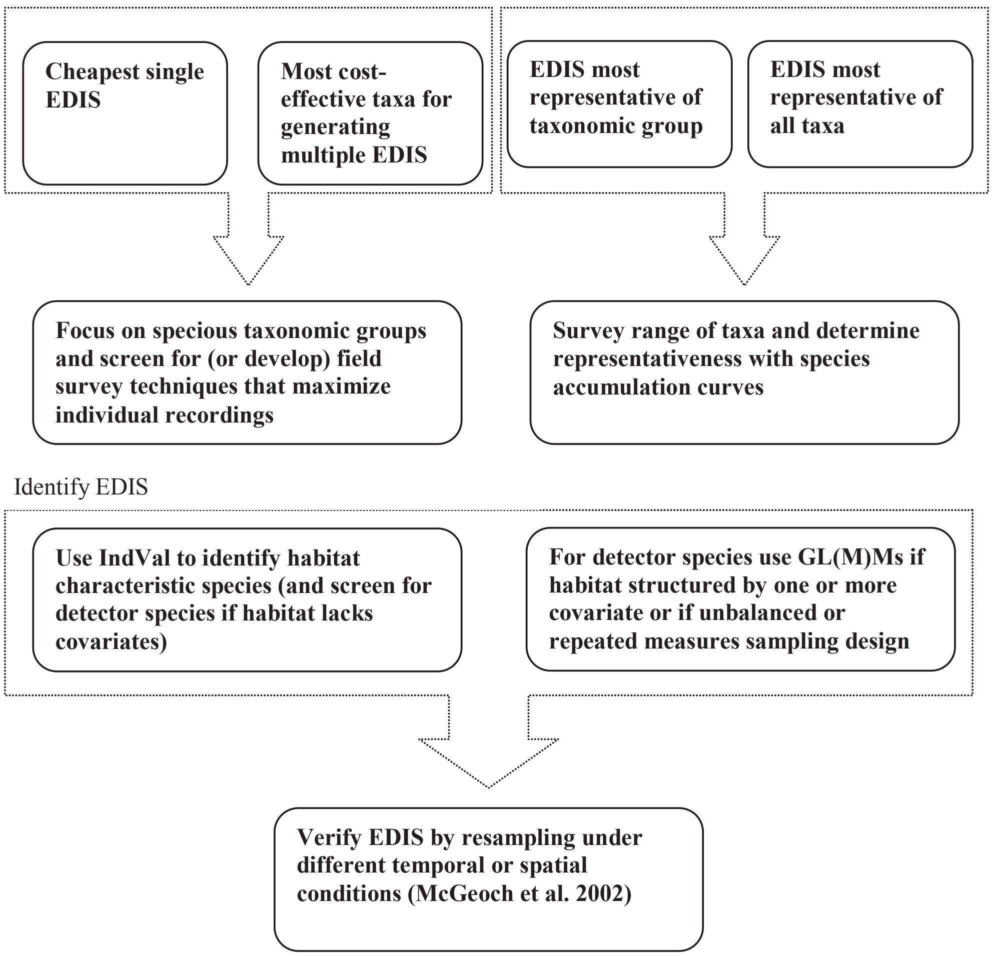

Figure 4. Framework for identifying ecological-disturbance indicator species (EDIS) based on indicator requirements with an indicator value (IndVal) or GL(M)M approach.

Outline method to identify indicator species

We devised a stepwise approach to identifying EDIS (Fig. 4). 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 fulfill 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 maximize 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 or with 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 that identify detector EDIS. 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 programs 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 EDIS 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 costructure species presence and abundance and survey designs are unbalanced and include repeated measures. These factors often coincide in long-term monitoring programs where repeated measures are inevitable and balanced designs are often impossible. Such programs, including ours, often depend on citizen science to provide the funds and manpower to generate data sets that extend beyond the time frames of typical research-funding cycles. In challenging environments (e.g., tropical mountain forests), volunteers often find it difficult to survey more distant locations. This leads to unbalanced data sets that require the additional statistical power of more complex analytical methods, such as we used here. The design of scientifically robust, cost-effective monitoring programs aimed at assessing the impacts of environmental and climatic change offers the potential to integrate conservation, ecological research, environmental education, capacity-building, and income generation through scientific ecotourism. Such programs should be encouraged, established, and supported (Sekercioglu 2012; Sekercioglu et al. 2012).

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Supporting Information

A list of species used in analyses (Appendix S1) and of species identified as significant IndVal indictors (Appendix S2), cost estimates for field surveys (Appendix S3), list of species with significantly different abundances among land covers (Appendix S4), list of leaf-litter lizards with significantly different abundances among land covers (Appendix S5), and number of bird indicator species relative to survey cost are available on-line. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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