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2 habitat

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26 **Abstract**

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

47

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

50

51

52 **Introduction**

53 Traditional conservation, habitat restoration and emerging Reduced Emissions from
54 Deforestation and Degradation (REDD+) projects all require monitoring protocols for
55 assessing the effectiveness of conservation action and the impact of habitat degradation and
56 restoration on biodiversity (Harrison et al. 2012). The challenge is understanding how flora
57 and fauna respond to land-use change and management, particularly in species-rich tropical
58 forests where the costs of undertaking comprehensive multi-species field studies normally
59 exceed typical budgetary limitations (Lawton et al. 1998). One approach is to determine the
60 occurrence or abundance of a small set of species that are sensitive to habitat disturbance,
61 previously described by Caro (2010) as ‘ecological-disturbance indicator species (EDIS)’ and
62 defined as ‘a species or group of species that demonstrate(s) the effects of environmental
63 change (such as habitat alteration and fragmentation and climate change) on biota or biotic
64 systems’ (McGeoch 2007). In terrestrial systems EDIS can be identified by comparing
65 presence/absence and abundance of multiple taxa across a gradient of disturbance to find
66 those that best characterise each stage. This approach has been the subject of considerable
67 research (Laurence & Peres 2006; Caro 2010;) with varying levels of success (Lawton et al.
68 1998; Rodrigues & Brooks 2007; Trindade & Loyola 2011). These studies provide invaluable
69 information to underpin effective management of biodiversity, but few quantify the costs
70 associated with detecting EDIS. Determining the return-on-investment when selecting
71 indicator species or taxonomic groups is important where careful allocation of funds is
72 paramount (Favreau et al. 2006). Taxa that have been selected following consideration of
73 cost-effectiveness rather than purely on their indicator value have previously been described
74 as ‘high performance indicator taxa’ (Gardner et al. 2008). Once a robust site-specific dataset
75 for a range of taxa exists the selection of these high performance indicator taxa generally
76 follows a three-stage process (Gardner et al. 2008). The first stage involves clearly defining

77 the conservation objective(s); the second comprises identification of ecologically meaningful
78 criteria for selection of EDIS; and the third stage requires measurement of the relative cost-
79 effectiveness of sampling different taxa under the various criteria to derive high performance
80 EDIS.

81 Our objective was to identify high performance EDIS for small vertebrates in tropical
82 Andean forests exhibiting differential anthropogenic disturbance. A range of ecologically
83 meaningful selection criteria have previously been used that are based on changes in species
84 richness, community composition and population size. Of these, change in population size is
85 considered the most sensitive as it can forewarn of localised extinction (Caro, 2010). A range
86 of approaches exist for assessing species sensitivity to disturbance, including k-dominance
87 curves, rarefaction techniques, correspondence analysis and probability-based indicators of
88 ecological disturbance (Magurran 2004; Howe et al. 2007; Halme et al. 2009;). However, the
89 most common selection method used to identify EDIS in previous studies in tropical forests
90 has been the indicator value method (IndVal) (Gardner et al. 2008; Kessler et al. 2011). This
91 screening method combines measurements of the degree of specificity of a species to an
92 ecological state (such as habitat type), and its fidelity within that state (Dufrene & Legendre
93 1997). Using IndVal, indicators (EDIS) can be identified from sets of sites under increasing
94 disturbance (Dufrene & Legendre 1997; De Caceres & Legendre 2009; De Caceres et al.
95 2012). IndVal identifies two types of EDIS: ‘characteristic species’, which are only present
96 in particular habitats (disturbance states), and ‘detector species’, found at different
97 abundances across a range of habitats (levels of disturbance). Characteristic species are more
98 likely to be vulnerable to habitat degradation, but detector species are suggested to be a more
99 sensitive measure for monitoring change over time than a single state variable, as they exhibit
100 lower specificity and span a range of ecological states (McGeoch et al. 2002). Although an
101 accessible and relatively simple method, the weakness of IndVal is that it cannot incorporate

102 potential covariates within habitat disturbance categories that might confound patterns of
103 species presence and abundance. For example, small mammals are structured by multiple
104 predictors such as altitude, microhabitat and temperature in mountain forests (Bateman et al.
105 2010). In this study we compare the efficacy of IndVal in identifying EDIS, as compared to a
106 generalized linear modelling (GL(M)M) approach, to explore the potential need to employ
107 greater statistical complexity to effectively identify indicators. With a focus on determining
108 statistically significant differences in abundance between habitat disturbance categories,
109 GL(M)M is expected to provide greater resolution than IndVal.

110 The final stage requires use of a cost-effectiveness method for sampling different taxa and
111 thereby detecting high performance EDIS. There is a rapidly growing body of work that has
112 incorporated cost-effectiveness analysis in identifying conservation priorities (Tulloch et al
113 2011; Somerville et al 2013; Halpern et al 2013). More specifically, a number of studies have
114 combined cost analysis with species accumulation curves to identify levels of sampling
115 required, and models (i.e. IndVal) to detect trends in species response to environmental
116 covariates such as disturbance or change (Gregory et al 2005; Gardner et al. 2008; Caro
117 2010; Kessler et al. 2011). The current study is the first to combine all three approaches to
118 provide real advice to those wishing to undertake monitoring of species in response to
119 environmental change.

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

126

127 **Methods**

128 **Field sites**

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

141

142 **Species survey methods**

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

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

158 We sampled small mammals from JCR during two field expeditions in 2010 using clusters of
159 Sherman live-traps deployed along line transects. A total of six transects of average length
160 175 m were distributed equally between primary and secondary forest at altitudes of between
161 1300 and 1900 m, with a total of 186 traps deployed, averaging 37 per transect. Silvopasture
162 habitat was not present in JCR. Traps were deployed for 8 consecutive nights, resulting in a
163 total of 1488 trap nights over an overall transect length of 1.48 km. We baited each trap daily
164 with a mixture of peanut butter, oats, vanilla essence and tinned tuna and checked traps every
165 morning.

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

173

174 **Data analysis**

175 **Identifying EDIS**

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

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

193

194 **Cost-effectiveness**

195 The resources for sampling biodiversity include monetary costs, time investment and
196 availability of adequate technical expertise. Consistent with previous studies, we quantified
197 monetary costs for taxa based on costs of field survey equipment and ‘time effort’ costs for
198 the minimum number of staff required to undertake fieldwork, species identification and
199 subsequent data management (Gardner et al. 2008; Kessler et al. 2011). Field scientists were

200 costed at 100 € per day, and field assistants at 20 € per day according to values used in a
201 recent study in the Amazon region (Kessler et al. 2011).

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

225 replication levels representing the least effectively-sampled group. We then re-ran the
226 GL(M)M models to determine how many EDIS remained at this lower sampling effort (and
227 cost) for each taxon. For taxa with more than one EDIS we randomly resampled the raw
228 datasets at reduced levels of replication and ran GL(M)M models to determine the
229 relationship between number of indicator species and effort/cost.
230 Where there was satisfactory fit (which we defined as $R^2 > 0.75$) we used the slope from
231 linear regression of number of indicator species against \log_{10} (costs) as an ‘ecological
232 disturbance indicator species (EDIS) cost-effectiveness metric’ to compare species groups.
233 This metric provides an indication of the number of EDIS generated for a 10-fold increase in
234 investment; a useful characteristic of a taxon as multiple indicators provide greater
235 confidence in correctly assessing forest status (De Caceres et al., 2012).

236

237 **Results**

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

244

245 **Small vertebrate EDIS**

246 For birds, a total of 10 significant indicator species were identified using IndVal with a single
247 indicator for primary forest, one for secondary and 8 for silvopasture (Table A2). For both
248 primary and secondary indicators, specificity (B_{ij} , proportion of habitat category sites in
249 which indicator is present) was low - at 46% for primary and 23% for secondary forest

250 indicators. Most of the silvopasture indicators had higher specificity but generally lower
251 fidelity (Aij, proportion of individuals in habitat category). No significant indicators were
252 identified for the other taxa using IndVal.

253 Indicators identified using the GL(M)M approach for each taxon are shown in tables 1 to 3.
254 Complete surveys of birds provide a total of 20 indicator species (14% of total recorded
255 richness), with both leaf litter-lizards and small mammals providing 2 indicator species each
256 (28% and 22% of total recorded richness respectively). Bats fail to provide a significant
257 indicator species for primary or secondary habitat (Table 3).

258 Seven bird species (15% of the total) were more abundant in primary forest sites than
259 secondary or silvopasture; three (7%) were more abundant in secondary than all other habitat
260 types; and ten (22%) were observed at highest densities in silvopasture (Table 1, Table A2).

261 The IndVal method did not identify any indicator species in common with the GL(M)M
262 approach for primary and secondary forest, although six indicator species were identified in
263 common by both approaches for the silvopasture habitats (Table A2).

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

267 **Cost effectiveness of selected taxa as EDIs**

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

275 Birds generate the cheapest single EDIS, with the Andean Solitaire (*Myadestes ralloides*)
276 identified as a detector species of primary forest at a survey cost of 204 €. EDIS for small
277 mammals represent 22% of total species richness of this group at absolute survey cost (Figure
278 2A). For standardised costs, where survey costs represent equal coverage of species richness
279 across taxa, EDIS for lizards represent 28% of the total richness of this group (Figure 2(b)).
280 However this, provides a biased view of numbers of indicators generated as when lower
281 numbers of indicator species at reduced survey effort are accounted for small mammal EDIS
282 again represent the greatest percentage of richness for least cost (Figure 2(c)).
283 No significant correlations were detected between percentage of indicator species and either
284 absolute (Fig. 2(a); Spearman's rank correlation, $r_s = 0.2$, $P > 0.05$) or standardised (Fig. 2(b);
285 Spearman's rank correlation, $r_s = 0.3$, $P > 0.05$) survey costs. However, plots of standardised
286 indicators against standardised costs (Fig. 2(c) and (d)) show a positive trend that approaches
287 significance (Spearman's rank correlation, $r_s = 0.95$, $P = 0.051$).
288 A positive correlation was detected between number of indicators, and total species richness
289 (Pearson's Correlation, $r_p=0.99$, $P < 0.01$), and number of indicators and total abundance
290 (Pearson's Correlation, $r_p=0.99$, $P < 0.01$). However, the relationship between proportion of
291 estimated species richness actually detected per taxon and number of indicator species was
292 non-significant (Spearman's rank correlation, $r_s = -0.2$, $P > 0.05$) partly reflecting adequate
293 sampling coverage of the majority of taxa, at over 67% of taxon richness sampled.
294 Fitting a logarithmic curve to the number of indicators against costs is optimal for birds (best
295 fit: Number of indicator species = $4.9 \ln [\text{Cost of survey}] - 23.6$, $R^2=0.964$) but sub-optimal
296 for small mammals (best fit: Number of indicator species = $0.4 \ln [\text{Cost of survey}] - 1.9$,
297 $R^2=0.56$) and leaf-litter lizards (best fit: Number of indicator species = $0.6 \ln [\text{Cost of survey}]$
298 $- 4.5$, $R^2=0.34$). Satisfactory fits for the EDIS cost-effectiveness metric was seen for small
299 mammals ($R^2 = 0.79$) and birds ($R^2 = 0.93$), generating values of 0.94 and 6.13 respectively.

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

302

303 **Discussion**

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

313 **Screening for indicator taxa**

314 Previous studies have used the indicator value (IndVal) metric (Dufrene & Legendre 1997) to
315 screen for EDIS in tropical forests (Gardner et al. 2008; Kessler et al. 2011), however this
316 method has a weakness in failing to explicitly incorporate covariates that can also structure
317 species presence and abundance (Ferrier 2002). By comparing IndVal to a more statistically
318 rigorous generalised linear modelling approach, we found that IndVal shows some merit in
319 screening for EDIS; for example it identified 75% of bird EDIS in common with GL(M)M.
320 The IndVal method also identified characteristic indicator species (species seen with high
321 fidelity and specificity within a particular disturbance state) for primary and secondary forests
322 that were not identified by GL(M)M . Three bird species are defined as characteristic EDIS
323 (McGeoch et al. 2002; Alves da Mata et al. 2008) of silvopasture, with all others considered
324 detector species (Table A2). The GL(M)M approach, with a focus on detecting statistically

325 significant differences in abundances between disturbance states, aids in identifying a greater
326 number of detector EDIS than IndVal in forest disturbance gradients co-structured by other
327 factors, such as altitude hence caution must be taken when solely applying the IndVal metrics
328 to such systems.

329 **Cost effectiveness of indicator species**

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

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

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

350 **Covariates of altitude**

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

363 **Outline method to identify indicator species**

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

374 resampling under different temporal or spatial conditions to ensure they act as robust habitat
375 management tools (McGeoch et al. 2002).

376 Long-term, local-based biodiversity monitoring programmes are vital for measuring and
377 arresting loss of biodiversity in the tropics and guidance is required to provide a cost effective
378 approach. The use of ecological disturbance indicator species provides a useful and relatively
379 simple measure of the effect of land-use change and management on biodiversity (Caro
380 2010). However, indicators need to be identified according to conservation objectives and on
381 a site-specific basis, particularly in regions with high beta diversity. Screening of indicators
382 requires more robust statistical analytical approaches where strong natural gradients are
383 thought to co-structure species presence and abundance and survey designs are unbalanced
384 and include repeated measures. These factors often coincide in long-term monitoring
385 programmes where repeated measures are inevitable and balanced designs are often
386 impossible. Such programmes, including ours, often depend on ‘citizen science’ to provide
387 the funds and manpower to generate datasets that extend beyond the timeframes of typical
388 research-funding cycles. In challenging environments, e.g. tropical mountain forests,
389 volunteers often find it difficult to survey more distant sample points. This leads to
390 unbalanced datasets, which require the additional statistical power of more complex
391 analytical methods, such as those used in this study. The design of scientifically robust, cost-
392 effective monitoring programs aimed at assessing the impacts of environmental and climatic
393 change gives the potential to integrate conservation, ecological research, environmental
394 education, capacity-building and income generation through scientific ecotourism. Such
395 programmes should be encouraged, established and supported (Sekercioglu 2012;
396 Sekercioglu et al. 2012).

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401

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514

515

	Mean count per point sample	% of Primary forest count	
		Secondary	Silvopasture
Primary Forest indicators			
516			
517			
518			
519			
520			
521			
522			
Secondary Forest indicators		% of Secondary forest count	
523		Primary	Silvopasture
524			
525			
526			
Silvopasture Forest indicators		% of Silvopasture count	
527		Primary	Secondary
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534			

535 Table 1 Bird species observed at significantly higher ($p < 0.05$) counts in primary forest habitat, showing counts and relative counts in
536 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 <i>(Transandinomys bolivaris)</i>	Secondary	0.36	39%	n/a	Count ~ Habitat + Altitude	Yes ** (40%)
Alfaro's Rice Rat <i>(Handleyomys alfaroi)</i>	Primary	0.38	n/a	37%	Count ~Habitat + Altitude	No

537

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

541

542

'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 (<i>Lepidoblepharis</i> sp.)	Primary	0.90	32%	16%	Count ~ Habitat + Altitude	No
			1			
Tropical Lightbulb Lizard (<i>Riama oculata</i>)	Primary	1.4	0%	61%	Count ~ Habitat + Altitude	No

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

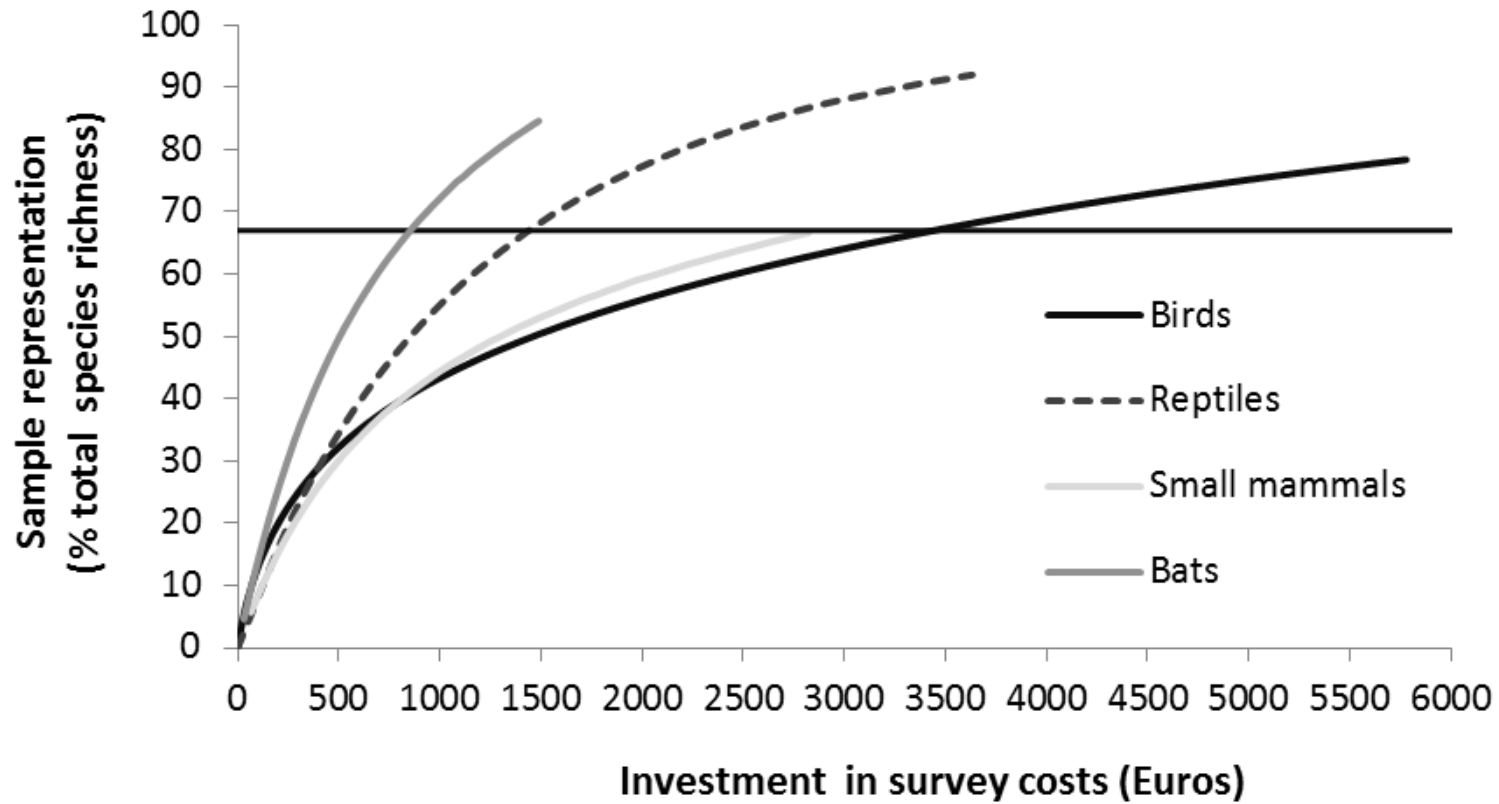
546 .

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	-

548

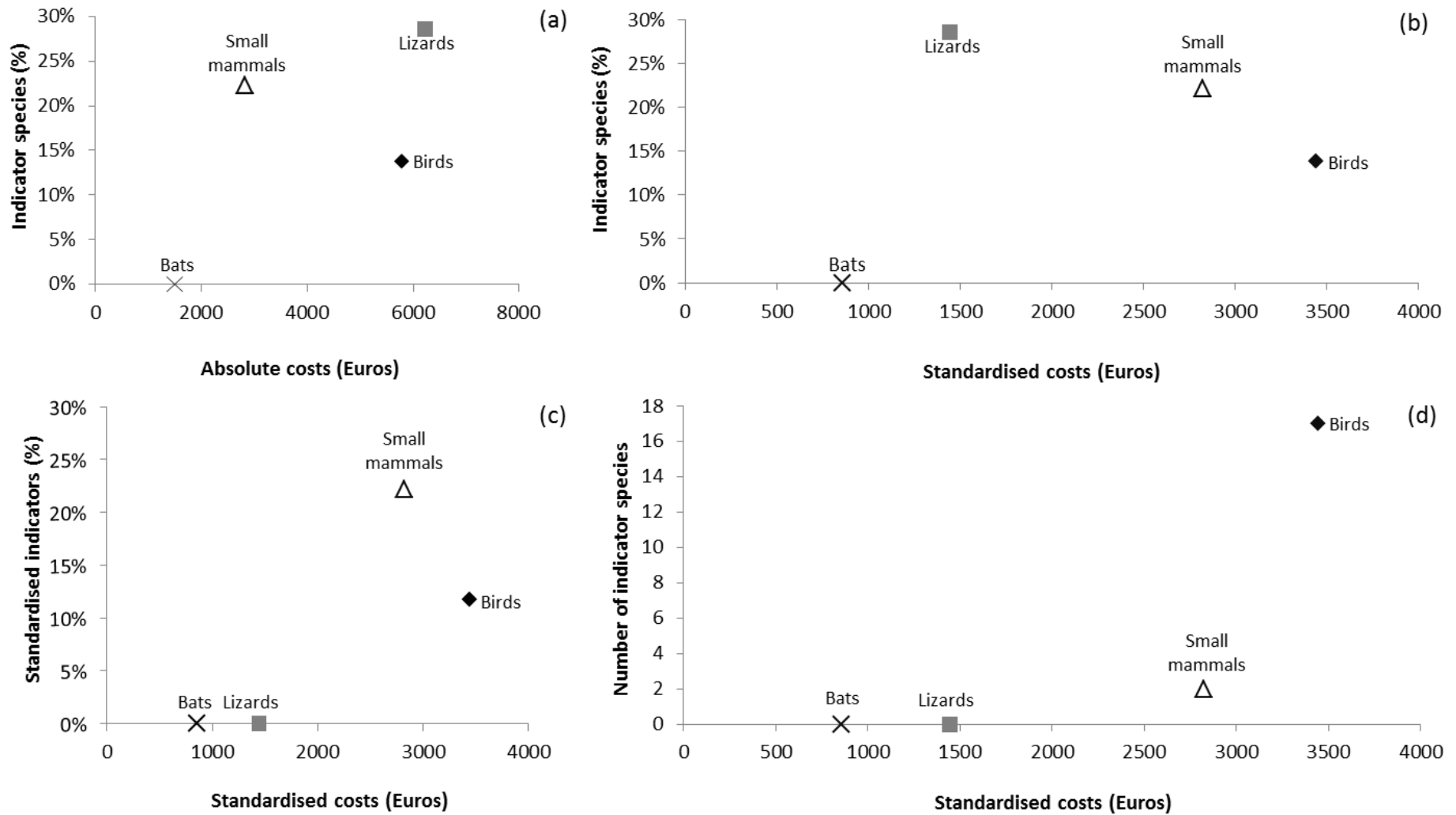
549 Table 4 Biodiversity datasets showing number of individuals sampled and species richness from full surveys for each taxon. Number and
550 percentage of indicator species from each habitat are shown for full surveys and at standardised costs.

551



552

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

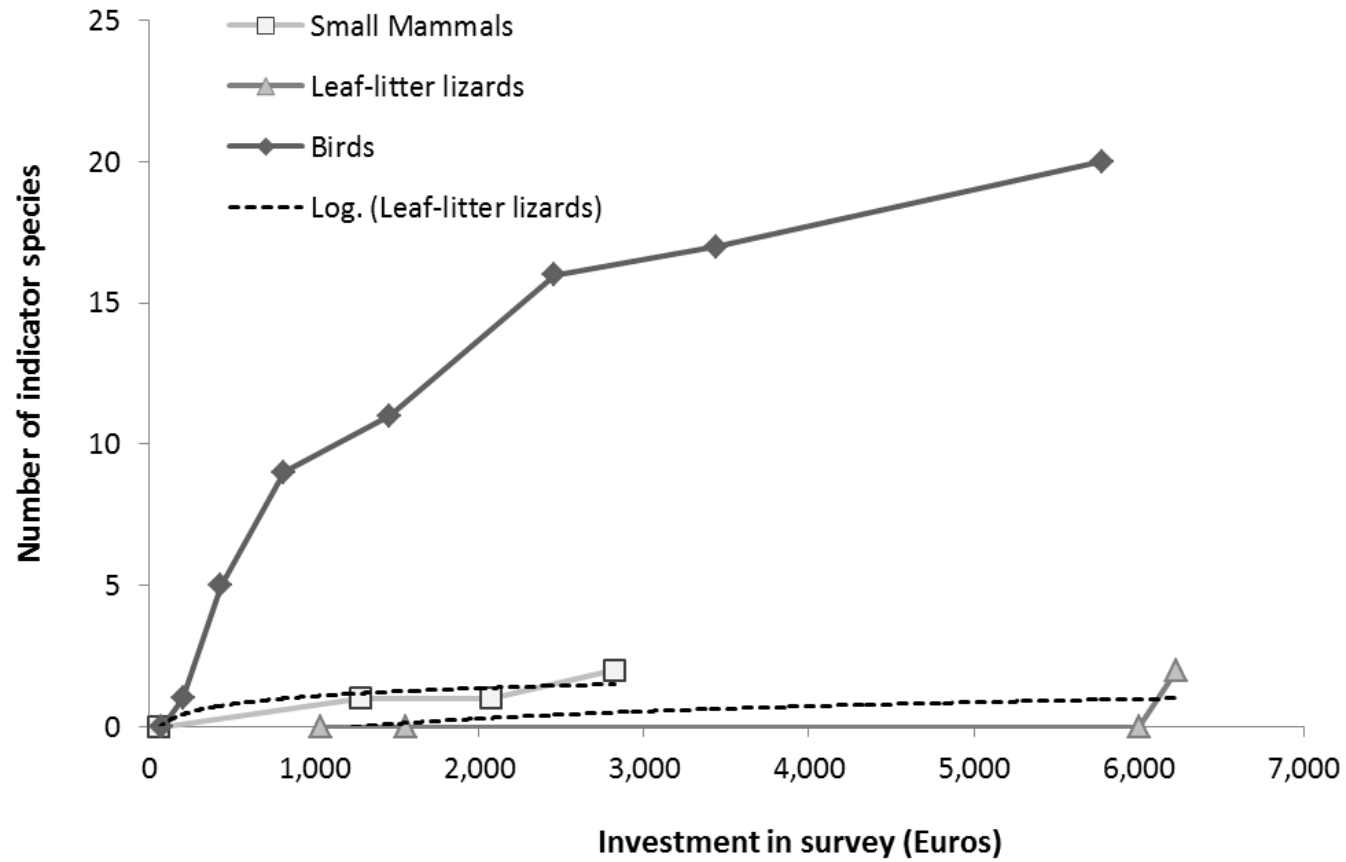


556

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

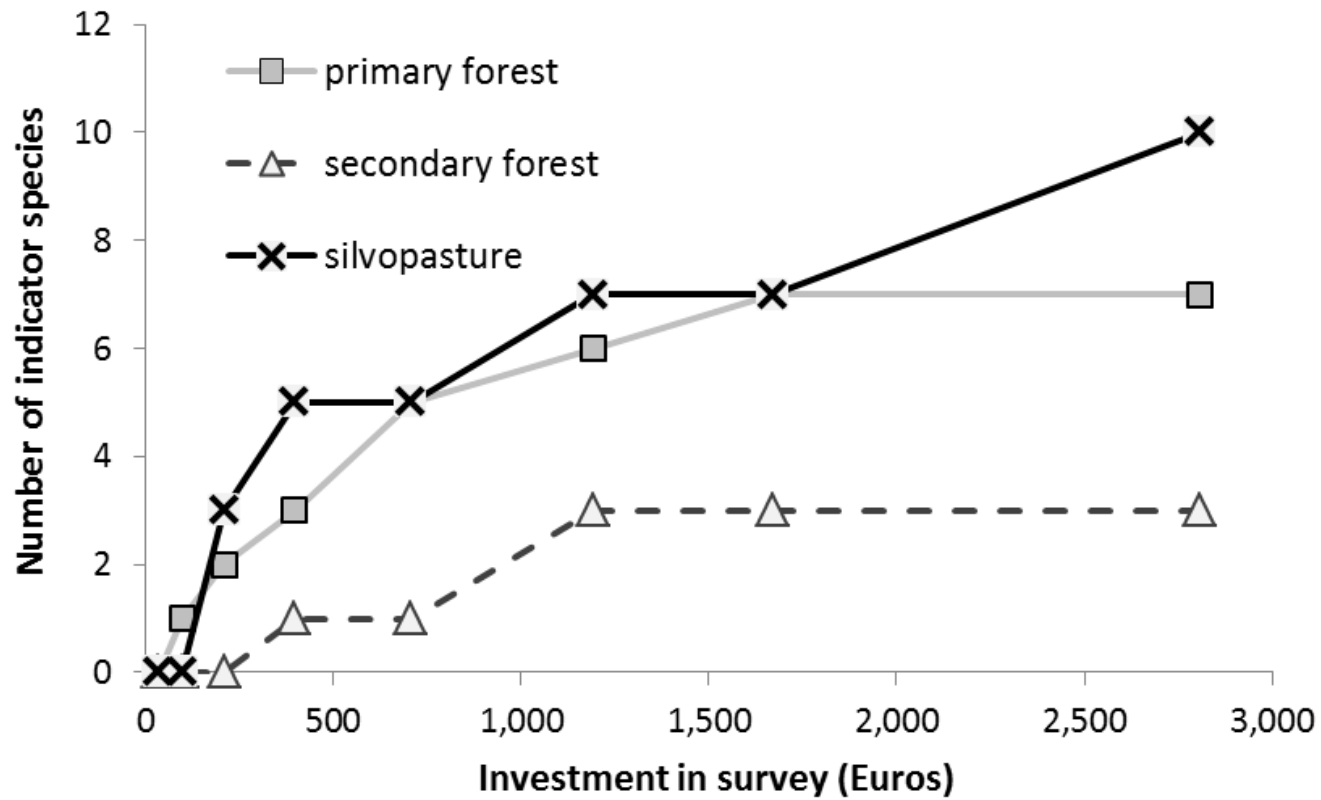
558 number (d) of standardised indicators against standardised costs.

559



560

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



563

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

565 habitat type.

566

567

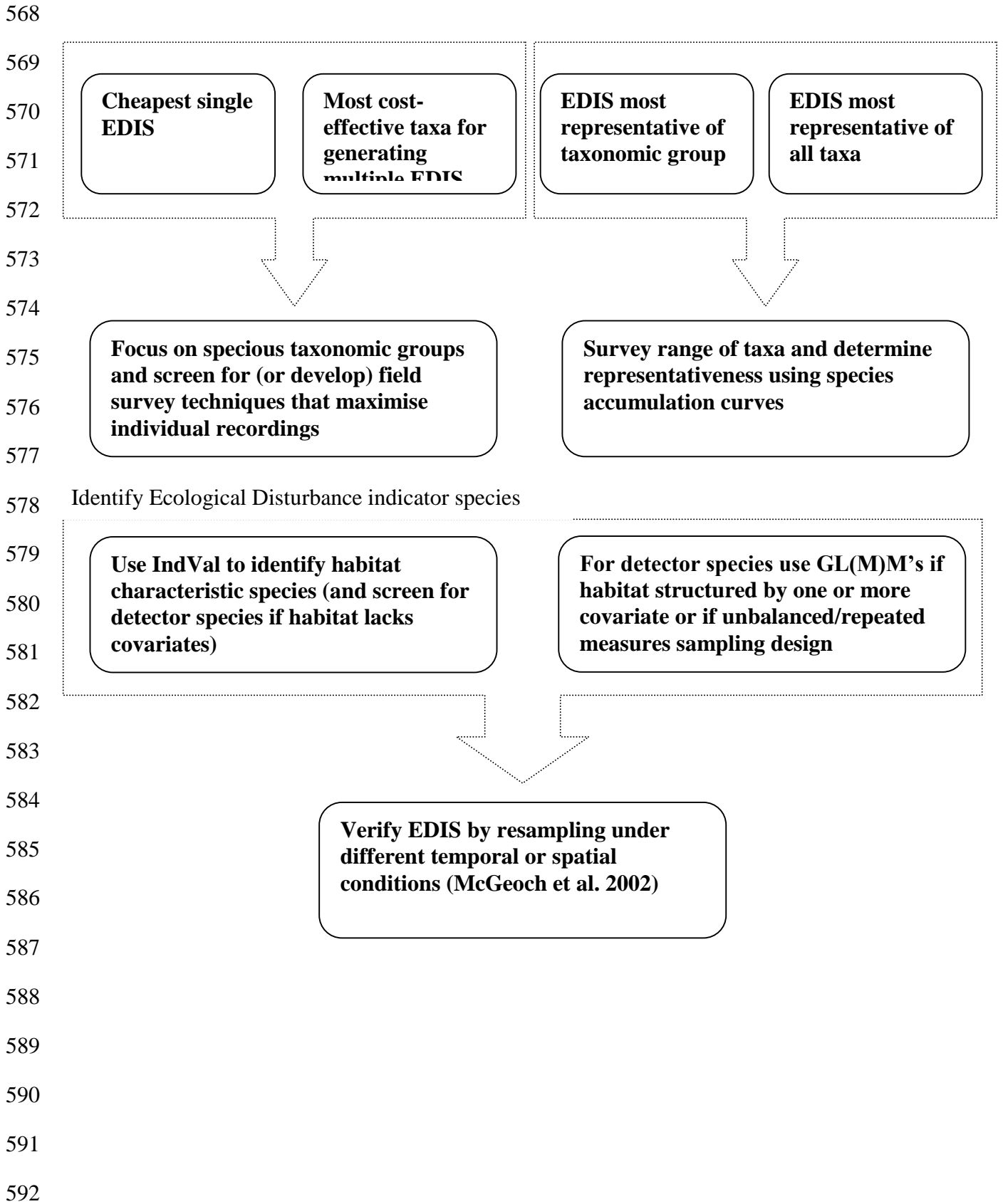


Fig. 5 Framework for identifying ecological disturbance indicator species.

594 **Supplementary material**

595

Species lists

Small Mammals

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

Birds (10 or more individuals)

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

Metallic-green Tanager
 Nariño Tapaculo
 Orange-bellied Euphonia
 Plate-billed Mountain-Toucan
 Plumbeous Pigeon
 Red-billed Parrot
 Red-headed Barbet
 Ruddy Foliage-gleaner
 Rufous-breasted Antthrush
 Russet-crowned Warbler
 Smoke-colored Pewee
 Sparkling Violetear
 Spillmann's Tapaculo
 Tawny-bellied Hermit
 Three-striped Warbler
 Toucan Barbet
 Violet-tailed Sylph
 White-sided Flowerpiercer
 White-tailed Tyrannulet

Tangara labradorides
Scytalopus vicini
Euphonia xanthogaster
Andigena laminirostris
Patagioenas plumbea
Pionus sordidus
Eubucco bourcierii
Automolus rubiginosus
Formicarius rufipectus
Basileuterus coronatus
Contopus fumigatus
Colibri coruscans
Scytalopus spillmanni
Phaethornis syrmatorphorus
Basileuterus tristriatus
Semnornis ramphastinus
Agelaiocercus coelestis
Diglossa albilatera
Mecocerculus poecilocercus

Lizards

Tropical lightbulb lizard
 Drab lightbulb lizard
 Unknown
 Unknown
 Brown Prionodactylus
 Unknown
 Unknown

Riama oculata
Riama unicolor
Riama sp.
Echinosaura brachycephala
Cercosaura vertebralis
Lepidoblepharis sp.
Alopoglossus festae

Bats

Rosenberg's fruit-eating bat
 Silky short-tailed bat
 Chestnut Short-tailed Bat
 Seba's short-tailed bat
 Little Big-eared Bat
 Highland Yellow-shouldered Bat
 Spectral bat
 Little black serotine
 Hairy-legged Myotis
 Black Myotis
 Riparian Myotis

Artibeus rosenbergii
Carollia brevicauda
Carollia castanea
Carollia perspicillata
Micronycteris megalotis
Stunira ludovici
Vampyrum spectrum
Eptesicus andinus
Myotis keaysi
Myotis nigricans
Myotis riparius

596

597 Table A1 Species used in analysis.

598

599

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

600

601

602

603

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)

604

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	-	-			
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

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