Cheap carbon and biodiversity co-benefits from forest regeneration in a hotspot of endemism

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Supplementary Methods

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Supplementary Methods

Details of study areas

The Tropical Andes, spanning parts of Bolivia, Colombia, Ecuador, Perú and Venezuela, have

seen widespread conversion of natural habitats to agriculture, particularly in northern areas[1]

(Supplementary Fig. S1). Our study sites were located within the departments of Antioquia,

Risaralda and Chocó, Colombia, each comprising a mix of primary forest, naturally regenerating

secondary forests and agricultural matrix dominated by pasture (Supplementary Fig. S2 & Table

S1). Study areas spanned an altitudinal range of 1,290-2,680 m above sea level, a zone supporting

one of the highest global diversities of threatened and endemic taxa, and characterised by

widespread agricultural development. Levels of proportionate forest cover and paved roads

access in the study municipalities were similar to those found across the wider Colombian Andes

(see Supplementary Fig. S7).

Cattle farming is the primary land-use throughout the Tropical Andes (Supplementary Table

S3) and the only major agricultural activity within our study areas (Supplementary Table S1). In

our study areas, pasture habitats typically included some primary and secondary forest fragments,

as well as a limited cover of other crops (<10 hectares in total, primarily maize and orchards of

tamarillo *Solanum betaceum*). We visually mapped the proportionate cover of wooded habitats

within a 100 m radius surrounding each pasture sampling point, using this as an index of farming

intensity in each sampled area.

Carbon assessments

We sampled non-soil carbon stocks in 43 squares (see Supplementary Table S1). In each 15 x 5

m plot, we measured diameter at breast height (dbh) for all trees >5 cm dbh, and measured wood

specific gravity (density) using tree cores extracted with an increment borer (two threads, 5.15

46   mm diameter; Haglöf, Sweden). Where core extraction was not possible, we applied the local

47   mean wood specific gravity calculated from all cores collected from the same plot. To estimate

48   tree biomass, we used our measured values of dbh and woods specific gravity to apply a range of

49   allometric equations from harvested tree studies. For primary forest trees, we used the following:

50   Chave 'Type II wet forest'[2], Feldpauch 'Western Amazonia'[3], 'Feldpauch Pantropical'[3], Alvarez

51   'Lower montane wet forest model I.3'[4] and Sierra 'primary forest'[5]. For secondary forest trees,

52   we used the following: Sierra 'secondary forest'[5], van Breugel 'model 2'[6], and Ketterings

53   'secondary forest'[7]. We used the mean value as the final aboveground biomass estimate for each

54   tree (see Supplementary Table S2). We estimated root biomass for each tree using the global

55   mean upland forest root:shoot ratio of 0.26 (refs 8,9).

56   For deadwood, we estimated the biomass for all standing dead trees >5 cm d.b.h. within each

57   plot using equations from ref (2), applying the average wood density for deadwood of 0.31 g cm^{-3}

58   calculated for Andean forests[9,10]. We also calculated the volume of all coarse woody debris >5

59   cm diameter, estimating total biomass by multiplying by 0.31. The biomass of vines was

60   estimated for all vines >2 cm in diameter up to 1 m from the long edges of the plot (i.e. a sampled

61   area of 15 m^2 x 2 for each plot) and using an equation developed in Colombian montane forest[5].

62   Lastly, we collected all leaf litter, grass and small plants (<0.5 m in height) from 4 x 0.25 m^2

63   quadrats within each plot. These quadrats were combined into one sample per plot, weighed to

64   the nearest 0.1g and a subsample of 10-20% of the total mass was retained. Subsamples were

65   oven-dried to a constant mass, re-weighed to the nearest 0.01g and the fresh:dry weight ratio of

66   the subsample was used to estimate the dry mass of the original sample[11]. Biomasses were

67   summed for the plot and multiplied by 0.474, a value derived from a meta-analysis of studies in

68   the tropics[12], to give an estimate of total carbon stock.

69   We used a large number of relatively small plots (215 in total) to better capture the small-

70   scale heterogeneity in land-use history typical of the Tropical Andes[5]. Although soil carbon is

71   also a substantial component of ecosystem carbon stocks, studies across a range of land-uses in

72   the tropics suggest variation in soil carbon with land-use change is minor relative to non-soil

73   carbon pools[9,13,14].

74

75   <u>Data analysis</u>

76   *Economic parameter estimation*

77   To estimate the net present value of cattle pasture, we used government datasets to derive

78   values for cattle stock density, meat yield per head, market price and the costs of raising cattle to

79   market, including labour, medicine, dietary supplements and transport costs. We used data

80   compiled at the department and municipality level, shown in Supplementary Table S6. From

81   these values, we estimated the net present value (NPV) of one hectare of existing pasture thus[15]:

82     $$NPV = \sum_{1}^{n} \frac{(y * p) - c}{(1 + r)^n}$$

83   Equation (1)

84   where y is the annual yield of a hectare of pasture (metric tons produced for market); p is the

85   market price for a metric ton of cattle; c is annual cost of bringing the yield to market (US $ per

86   hectare); r is the discount rate and n is the time horizon. To account for uncertainty in our

87   economic data, we assigned uniform distributions to each parameter, in each case bounded by the

88   highest and lowest values taken from all data sources (see Supplementary Table S6). To reflect

89   uncertainty, we also assigned a uniform distribution for discount rate bounded by 0.04 and 0.12.

90   We then calculated 10,000 estimates of NPV by sampling across these distributions, generating a

91   mean and 95% credible interval for cattle pasture NPV within the study region.

92   Next, we estimated the costs involved in implementing, monitoring and managing a PES

93   scheme for natural forest regeneration. To account for management costs (e.g. cattle exclusion

94   fencing, guard salaries), we assigned a precautionary uniform distribution bounded by a lower

95   limit of US$0.50 and an upper limit of US$17 ha^{-1} yr^{-1}, the upper value being the highest found in

96   the literature (cost for managed secondary forests in North-western Ecuador[16]). For

97   implementation and monitoring costs of a PES scheme, we again assigned a uniform distribution

98   based on values reported in the literature, with a lower limit of US$ 0.37 ha^{-1} yr^{-1} (from ref. 17)

99   and an upper limit of US$ 3.01 ha^{-1} yr^{-1} (from ref. 18). We adjusted all economic values for

100   inflation to 2013 US$ levels.

101   To find the carbon price that offsets the opportunity costs of farming (NPV) and

102   implementation/management costs of establishing a PES, we calculated the break-even market

103   CO_2 price E (US$ t^{-1} CO_2) using two accounting methods long-term Certified Emission

104   Reductions (lCERs) and temporary Certified Emission Reductions (tCERs)[16, 19-22]. Both methods

105   assume that carbon credits are issued at five year intervals during a 30 year project. Under lCER

106   accounting, each credit lasts until the end of the 30 year horizon and cannot be re-issued. For

107   tCERS, by contrast, each credit expires at the end of each five year interval, but can be re-issued

108   in the next interval until the 30 year horizon is reached. As such, tCERs are issued for the total

109   cumulative carbon sequestered at the end of each interval, relative to the baseline at the start of

110   the project, such that the break-even price E is calculated thus:

111
$$E = \frac{R_{n,r} + C_{n,r}}{\sum_{1}^{n} tCER \cdot (1+r)^{-n}}$$

112   Equation (2)

113   where *R* is the net present value of pastoral agriculture ($ ha^{-1}) and *C* is the summed cost of

114   implementing, managing and monitoring the PES, both calculated over the full time horizon (*n* =

115   30 years) applying discount rate *r* which is assigned a diffuse uniform distribution bounded by

116   0.04 and 0.12. The denominator reflects the discounted number of tCER credits to be issued over

117   the life of the scheme, calculated thus:

118
$$\sum_{1}^{n} tCER \cdot (1+r)^{-n} = \frac{3.67 * Z_5}{(1+r)^5} + \frac{3.67 * Z_{10}}{(1+r)^{10}} + ... + \frac{3.67 * Z_{30}}{(1+r)^{30}}$$

119   Equation (3)

120   where $Z_5 ... Z_{30}$ are the net cumulative totals of carbon stored by the project at the end of

121   each five year interval (tons C ha^{-1}) relative to a pasture baseline, and 3.67 converts metric tons of

122   carbon into metric tons of CO_2[15]. We assigned a normal distribution for Z with mean and

123   standard deviation taken from the slope term of a linear mixed model predicting carbon stocks as

124   a function of secondary forest age. This model accounts for potential spatial autocorrelation by

125   including sampling square as a random effect. We applied discount rate *r* to carbon storage which

126   is again assigned a diffuse uniform distribution bounded by 0.04 and 0.12. We then generated

127   10,000 estimates of the required carbon market price *E* for tCERs, sampling across all parameter

128   distributions.

129   Break-even prices under the lCER approach are calculated in a similar way, but the

130   denominator in Equation 2 is replaced by the following expression:

131
$$\sum_{1}^{n} lCER \cdot (1+r)^{-n} = \frac{3.67 * Z_5}{(1+r)^5} + \frac{(3.67 * Z_{10}) - (3.67 * Z_5)}{(1+r)^{10}} + ... + \frac{(3.67 * Z_{30}) - (3.67 * Z_{25})}{(1+r)^{30}}$$

132   Equation (4)

133   Hence, lCER credits are only issued for the additional carbon stored within each five year time

134   interval, rather than the cumulative total stored since the start of the project. Again, we generated

135   10,000 estimates of the required lCER market price using a uniform distribution to reflect

136   uncertainty in discount rates ($r \sim U(0.04-0.12)$), and a normal distribution for carbon

137   accumulation Z based on the slope term of the linear mixed model relating carbon stocks to

138   secondary forest age.

139   Under carbon-based PES schemes such as REDD+, the additionality of carbon payments is

140   assessed relative to a baseline rate of carbon loss (deforestation, degradation, improved forest

141   management) or gain (regeneration under carbon enhancements). In the case of carbon

142   recuperation via natural forest regeneration, an appropriate baseline is a business-as-usual

143   scenario whereby existing land-uses are assumed to remain unchanged in the absence of PES[16,19-

144   22]. However, evidence suggests that some agricultural abandonment is currently occurring in the

145   Colombian Andes, even in the absence of carbon-based PES interventions[23]. We incorporated

146   this non-assisted farm abandonment into our assessment by assuming that farmers will abandon

147   their land whenever the NPV of pasture falls below zero. We therefore excluded randomisations

148   where NPV values were negative (approximately 9% of cases) from calculations of break-even

149   carbon price. We effectively assume, therefore, that PES payments will not be additional

150   whenever farming is uneconomical; excluding these cases ensures that our carbon price estimates

151   reflect genuine additionality.

152   To examine how incorporating leakage mitigation measures might influence break-even

153   carbon prices, we re-ran the analysis for both accounting methods incorporating an additional

154   cost equivalent to double the NPV of pasture. Previous research suggest that leakage prevention

155   costs can be *equal* to the opportunity costs of agriculture[24]; assuming a cost of *double* the pasture

156   NPV (i.e., double the opportunity cost of cattle farming) therefore reflects a highly conservative

157   estimate of likely leakage costs.

158

159 *Relaxing forest age assumptions*

160 As the ages of older secondary forest stands (>15 years) were estimated from interviews and

161 hence not known with certainty, we also conducted a precautionary re-analysis relaxing

162 assumptions about forest age certainty and carbon accumulation rates. To do this we pooled all

163 secondary forest plots, considering them to represent a random sample of carbon stocks in

164 secondary forests after a 30-year time horizon for regeneration. We excluded plots from younger

165 stands where age was known with certainty (<15 years, see Methods). We took the mean and

166 standard deviation from this pooled sample as parameters for a normal distribution that we used

167 to represent the total carbon sequestered per hectare over a 30-year time horizon. For both tCER

168 and lCER accounting methods, we sampled this normal distribution for Z to generate 10,000

169 carbon market price estimates (see Equations 2 & 3). This represents a conservative reanalysis,

170 because it applies a blanket assumption that all secondary forests in the pooled sample had been

171 accruing carbon for 30 years, when in reality most were considerably younger.

172

173 *Examining sensitivity to market change*

174 To examine how required carbon market prices might vary with future market changes, we

175 conducted a sensitivity analysis for yield, beef market price and production costs, allowing them

176 to vary over a wider range of values. We multiplied our mean data-derived values by an elasticity

177 index, drawn from a uniform distribution ranging from 1 to 3 (i.e. up to triple the mean observed

178 value). Again, we generated NPV estimates for 10,000 randomizations using Eq. (1), and

179 calculated break even carbon prices for both tCER and lCER accounting methods, incorporating

180 variation in discount rate (4% to 12%) and uncertainty in carbon accumulation rates. The relative

181 contribution of each parameter to variation in required carbon market price was inferred from the

182 slopes of linear regressions fitted to the randomization outputs.

183

Modelling biodiversity variation across habitats

185   To examine variation in species richness and occupancy probability across habitat types, we

186   modelled species-specific occupancy dynamics in a hierarchical community-modelling

187   framework[25-27]. Traditional methods for estimating species richness and community

188   characteristics are limited in their ability to account for imperfect detection of species[28], either

189   ignoring detection variability or assuming that every species is present at every sample location[26-

190   28]. The hierarchical community modeling approach has the advantage of allowing species-level

191   heterogeneity to be directly linked to habitat features whilst controlling for detection probability,

192   where species-level effects are naturally aggregated within higher-level effects across the

193   community as a whole[25]. This facilitates simultaneous broad- and fine-scale inferences and

194   allowing more precise estimates for infrequently observed species.

195   We estimate the probability of detecting a species, given that it is present at that location, by

196   modeling heterogeneity in detections over repeated visits to that location. Data are provided to

197   the model in the form of an observation matrix x_{ij} indicating the number of times species i was

198   detected at location j over a fixed number of visits (K). These data are used to estimate a

199   partially-observed matrix of true occurrences $z_{i,j}$, which are binary indicators of whether or not

200   species i was in fact present at site j. This formulation allows us to model variation in occurrence

201   probability for each species ($i = 1,2,\ldots,N$) across all sites ($j = 1,2,\ldots,J$) as a function of habitat

202   variables, and also simplifies the calculation of species accumulation curves and other

203   community metrics (e.g., similarity in species composition) by allowing us to integrate across

204   sources of uncertainty (nuisance variables such as altitude) and control for variation in detection

205   probability. By modeling the underlying distribution of true occurrences $z_{i,j}$, we are able to make

206 predictions about the distribution of each species with respect to habitat variation in the

207 landscape.

208   True occupancy is specified as a Bernoulli trial where $\psi_{i,j}$ is the probability that species i

209 occurs at site j:

210 $$z_{i,j} \sim Bern(\psi_{i,j})$$

211   Equation (5)

212 The parameter $\psi_{i,j}$ is then estimated from observations of species i at site j over K visits,

213 specifying the observed data $x_{i,j}$ as the sum of K Bernoulli trials where $\theta_{i,j,k}$ is the probability of

214 detecting species i at site j on visit k if species i is present at that site (i.e. $z_{i,j} = 1$):

215 $$x_{i,j,k} \sim Bern(\theta_{i,j,k} *_{z_{i,j}})$$

216   Equation (6)

217 Thus, if species i is not detected at site j (i.e., $x_{i,j} = 0$), species i is either absent (with probability

218 $(1 - \psi_{i,j})$) or present but undetected (with probability $\psi_{i,j} (1 - \theta_{i,j,k})^k$).

219 Both $\psi_{i,j}$ and $\theta_{i,j,k}$ are modeled as functions of covariates of interest by specifying either species-

220 or site-specific effects on the logit scale. As we are primarily interested in how species respond to

221 habitat variation (between primary forest, regenerating secondary forests and cattle pastures), we

222 modeled occupancy probability $\psi_{i,j}$ as a linear function of species-level responses to habitat types.

223 Because many species occupy restricted altitudinal ranges, we also included altitude as a centered

224 and standardized covariate, giving the following function:

225   Logit $(\psi_{i,j}) = u_i + \alpha 1_i \cdot$ ysecondary$_j + \alpha 2_i \cdot$ advsecondary$_j + \alpha 3_i \cdot$ lowgrass$_j + \alpha 4_i \cdot$ highgrass$_j$

226                                    $+ \alpha 5_i \cdot$ altitude$_j + \varepsilon_{i,s}$

227   Equation (7)

228 where 'ysecondary', 'advsecondary', 'lowgrass' and 'highgrass' are binary indicators of habitat

229 type at site j: secondary forest (<15 years), advanced secondary forest (>15 years), lower-

230   intensity pastoral matrix (>30% wooded habitat cover) or higher-intensity pastoral matrix (<30%

231   wooded habitat cover) respectively. Thus, the back-transformed logit of u_i gives the occurrence

232   probability for species i in primary forest at a given altitude. To account for potential sources of

233   spatial autocorrelation in species distributions, we added an additional random effect ε to

234   Equation 6 indexed by species i and sampling square s, assigning it a zero-mean normal

235   distribution with variance estimated from the data.

236   For birds, we assumed that detection probabilities vary across species and also in relation to

237   the timing of each visit, as most birds are easier to detect at times closer to dawn. We therefore

238   modeled detection probabilities θ for each species i, sampling point j and sampling occasion k

239   using a logit function:

240                    $$\text{Logit}\,(\theta_{i,j,k}) = \lambda_i + \beta_i \cdot \text{time}_{j,k}$$

241   Equation (8)

242   Because abundance and detection probability are likely to be related, we specified an underlying

243   correlation between occurrence likelihood and detection by allowing u_i and λ_i share a joint

244   bivariate normal distribution[25,28]:

245                    $$[u_i, \lambda_i \,|\, \Sigma] \sim N(0,\Sigma)$$

246   Equation (9)

247   where (σ^2_u, σ^2_v) are the variance components among species for occurrence and detection,

248   respectively, and σ_{uv} is the covariance of the 2 · 2 matrix Σ (refs 24 & 26). For dung beetles,

249   where sampling was continuous over each trap day, detection probabilities were simply modeled

250   as a function of species-level effects on the logit scale.

251   The model is made hierarchical at the community level by assuming that species-level and

252   site-level parameters are random effects, with values drawn from community-level 'hyper-

253   parameter' distributions. Thus, species-specific coefficients linking occurrence to habitat types

254 ($α1$, $α2$ etc.) are drawn from drawn from community-wide distributions, for example parameter

255 $α1$ for species i:

256
$$α1_i \sim N(u_{a1}, σ_{a1})$$

257 <div align="right">Equation (10)</div>

258 where u_{a1} is the community mean and $σ_{a1}$ is the standard deviation (inverse gamma distributed)

259 across all species in the community[29].

260

261 *Accounting for undetected species*

262 To estimate the species richness of communities occupying each habitat in the study area, we

263 derived species-accumulation curves to predict the number of species present within a given

264 habitat type as a function of area sampled. This involves computing spatially-independent

265 predictions of species accumulation that are robust to species-level variation in detection and

266 occurrence probabilities[26,27]. A key component of accumulation-based richness prediction is to

267 account for the presence of undetected species within the study area. To do this, we estimate the

268 true species richness N for a given area of habitat, based on the observed species richness n, using

269 a data augmentation approach[25,26] where the observed richness n is assumed to be drawn from a

270 'super-community' S which includes many more species than the true community N. The super-

271 community effectively represents the largest theoretical assemblage of species that might be

272 expected to occur within the region, and is given a value well above the expected true number of

273 species N.

274   We estimate N by augmenting the data matrix $x_{i,j}$ with a large number (S-n) of all-zero rows,

275 where each row represents an undetected species that might have been present in the study

276 region. The occurrence of these undetected species is modeled by incorporating a latent indicator

277 variable w_i which takes the value 1 if species i is a member of the community available to be

278   sampled and 0 otherwise. We then assume that w_i are independent Bernoulli-distributed random

279   variables, with probability determined by a new parameter Ω. Values of w_i are known for all

280   species detected within the survey (i.e. $I = 1,2…n$), but is unknown otherwise. Our estimate of N

281   is then derived by estimating Ω as a latent process within the model, with inference based on the

282   community-wide posterior distributions of occurrence and detection probabilities estimated from

283   the observed data[26,27].

284   *Prior distributions and parameter estimation*

285   We assign mutually independent prior distributions for all parameters[27-29]. In each case we use

286   diffuse, non-informative priors to ensure that posterior parameter distributions reflect the data

287   rather than model assumptions. We assume a uniform (0,1) priors for Ω and species-level hyper-

288   parameter means, and inverse-gamma (0.1, 10) priors for hyper-parameter variances[27]. For site-

289   level random effects, we assign zero-mean normal priors with inverse-gamma (0.1, 10) variances.

290   We estimated model parameters using Bayesian methods in WinBUGS version 1.4 (ref 30), using

291   a Markov Chain Monte Carlo (MCMC) simulation to estimate parameters via Gibbs sampling.

292   We sampled the posterior distribution of each parameter for 50,000 iterations, following a burn-in

293   of 20,000 iterations. This burn-in length was chosen after using the Gelman-Rubin diagnostic[31] to

294   assess convergence of three chains in an initial run.

295

296   *Computing habitat-specific species accumulation curves as a function of species occurrence*

297   We used fitted occupancy models to generate species accumulation curves for each habitat class,

298   allowing for full integration across possible sources of uncertainty in estimating N, the total

299   species richness for a given area of habitat. This is achieved by sampling the posterior-predictive

300   distribution of the species accumulation curve using the model-derived species occupancy

301   parameters[25,26]. First, we generate a pool of random draws from the posterior distributions

302 (normally distributed) of species-level occupancy parameters ψ_i, specific to a given habitat type

303 (e.g. young secondary forest). For each draw, we apply fitted versions of Equation 7 to calculate

304 a value of logit(ψ_i) specific to the habitat type in question, sampling across altitudinal uncertainty

305 by drawing a random altitude value from a uniform distribution with limits corresponding to the

306 altitudinal range of our study areas. The resulting value is then transformed to give a predicted

307 occupancy ψ_i probability for species i at a single site in that habitat. Repeated draws allow us to

308 derive occupancy probability estimates spanning the full range of uncertainty inherent in the data.

309 Using single random draws for each species in the super-community S, we generate a predicted

310 occurrence matrix $\check{Z}$ with dimensions $S \cdot L$, where L is a number of hypothetical sampling units

311 within the habitat in question. Each element of $\check{Z}$ is computed as a single Bernoulli trial with ψ_i,

312 the random draw for that species in that habitat type. The number of species occurring in L sites

313 is then the sum of all elements of $\check{Z}$ for a single set of random draws. We repeat these calculations

314 to generate 1,000 random samples of $\check{Z}$ across a range of values of L for each habitat type,

315 producing a posterior-predictive sample of habitat-specific species accumulation curves, from

316 which medians and 95% confidence intervals are derived[26,27].

317

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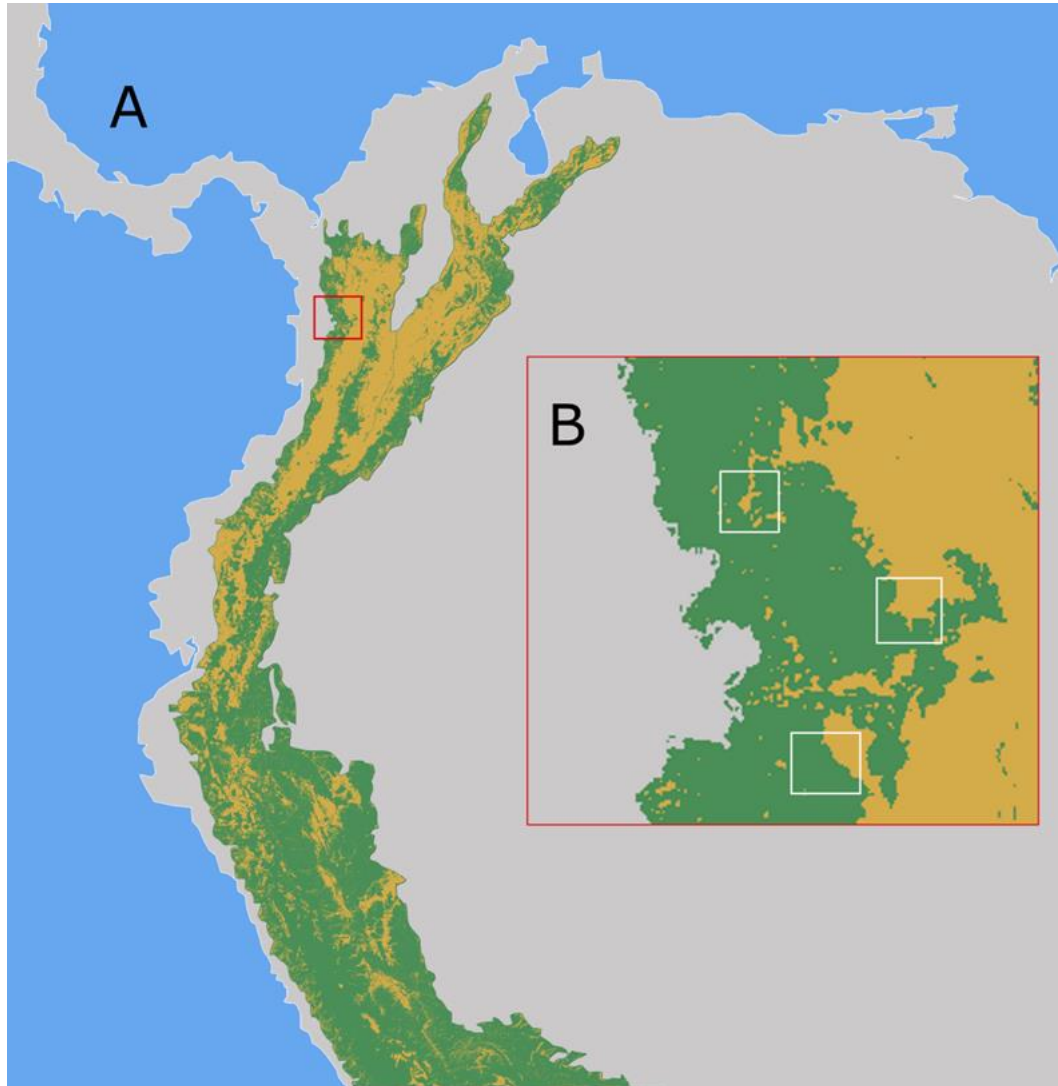
Figure S1. Map showing the extent of habitat conversion in the Tropical Andes zone (A) and

within our study region (red box, B), with the three study sites denoted by white boxes. Colors

represent areas with extant natural vegetation (dark green) and areas transformed to agriculture or

other land uses (pale orange), adapted from an analysis of 2000-2008 satellite imagery[1].

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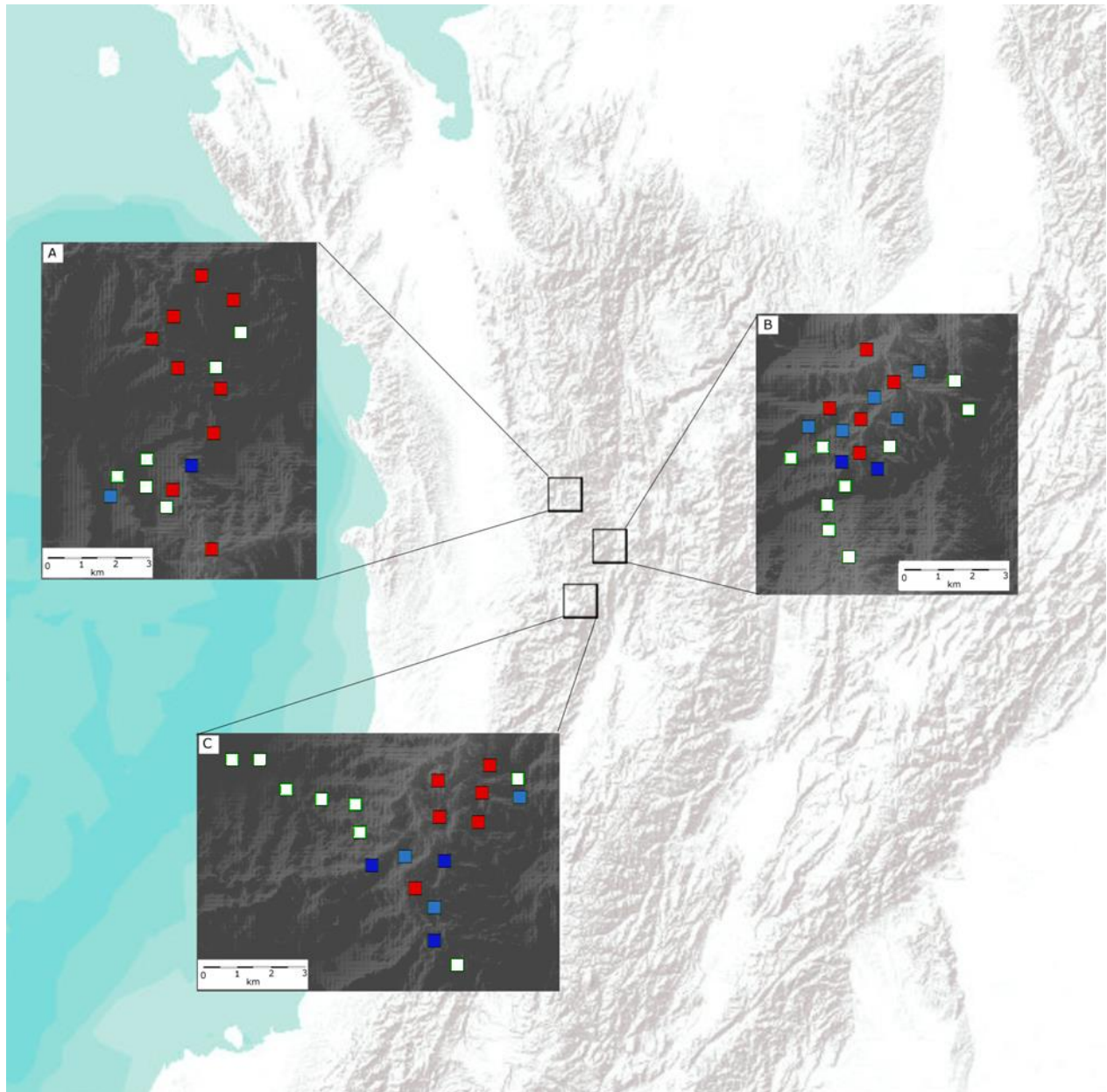
Figure S2. Map showing study areas in the Western Andes of Colombia. Inset maps show the

individual study sites (A = Reserva Tangaras, B = Reserva Mesenia-Paramillo, C = Cerro

Montezuma). Points show locations of 400x400m sampling squares, within which data were

sample from sets of evenly spaced points (see Methods for details of each dataset). Squares are

labelled according to the main habitat type present: cattle pasture (including both higher- and

lower-intensity points, red), young secondary forest (<15 years, light blue), advanced secondary

406 forest (>15 years, dark blue) and primary forest (white). Relief shows ASTER GEM data, a

407 product of METI and NASA.

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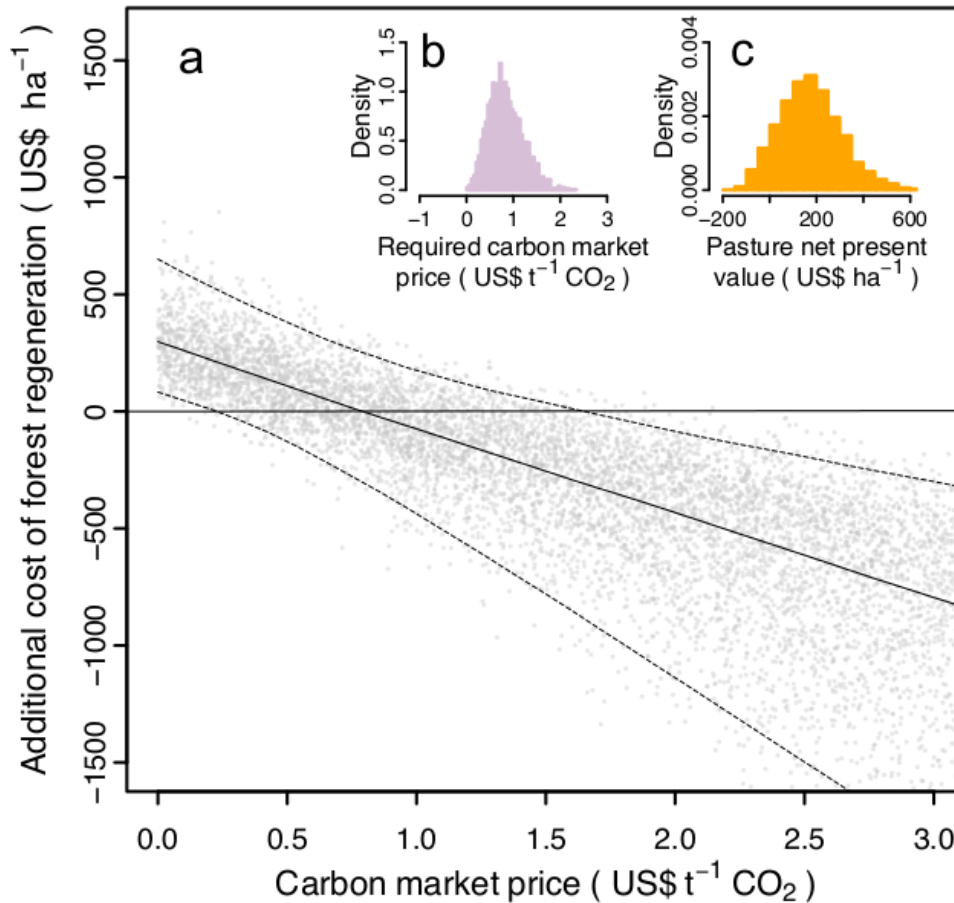
Figure S3. Predicted costs of natural secondary forest regeneration under a temporary credit

scheme (tCER). The cost of secondary forest regeneration (a) is the additional one-off payment

required to offset the net present value (NPV) of cattle pasture, accounting for uncertainty in

economic values, management/implementation costs and carbon storage levels, across a range of

possible carbon market prices (points show 3,000 model runs; lines show median and 95% CI).

Insets show the probability distribution of break-even carbon market prices required to make

secondary forest regeneration cost-effective (b), given the uncertainty in NPV values for pasture

(c).

Figure S4. Predicted costs of natural secondary forest regeneration, relaxing assumptions about certainty of forest age. The cost of secondary forest regeneration (A) is the additional payment required to offset the net present value (NPV) of cattle pasture, accounting for uncertainty in economic values, management/imple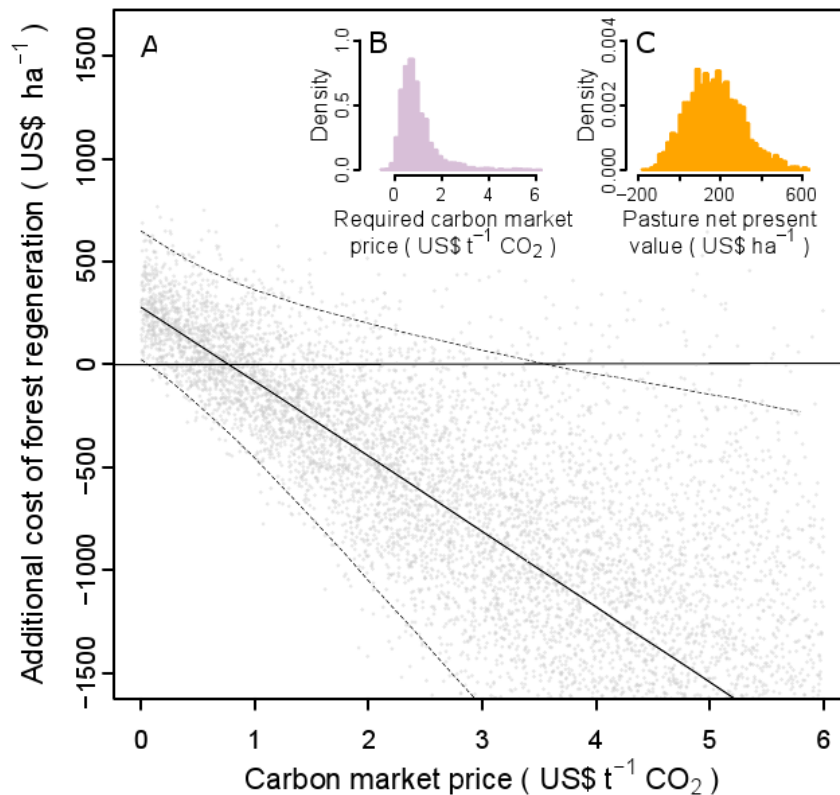mentation costs and carbon storage levels, across a range of possible carbon market prices (points show 3,000 model runs for tCER prices; lines show median and 95% CI). In these simulations, carbon storage estimates are drawn from a normal distribution with mean and standard error derived from the whole sample, making no assumptions about forest age (but excluding young plots where age was known with certainty). Insets show the probability distribution of tCER carbon market prices required to make secondary forest regeneration cost-effective (B), given the uncertainty in NPV values for pasture (C).
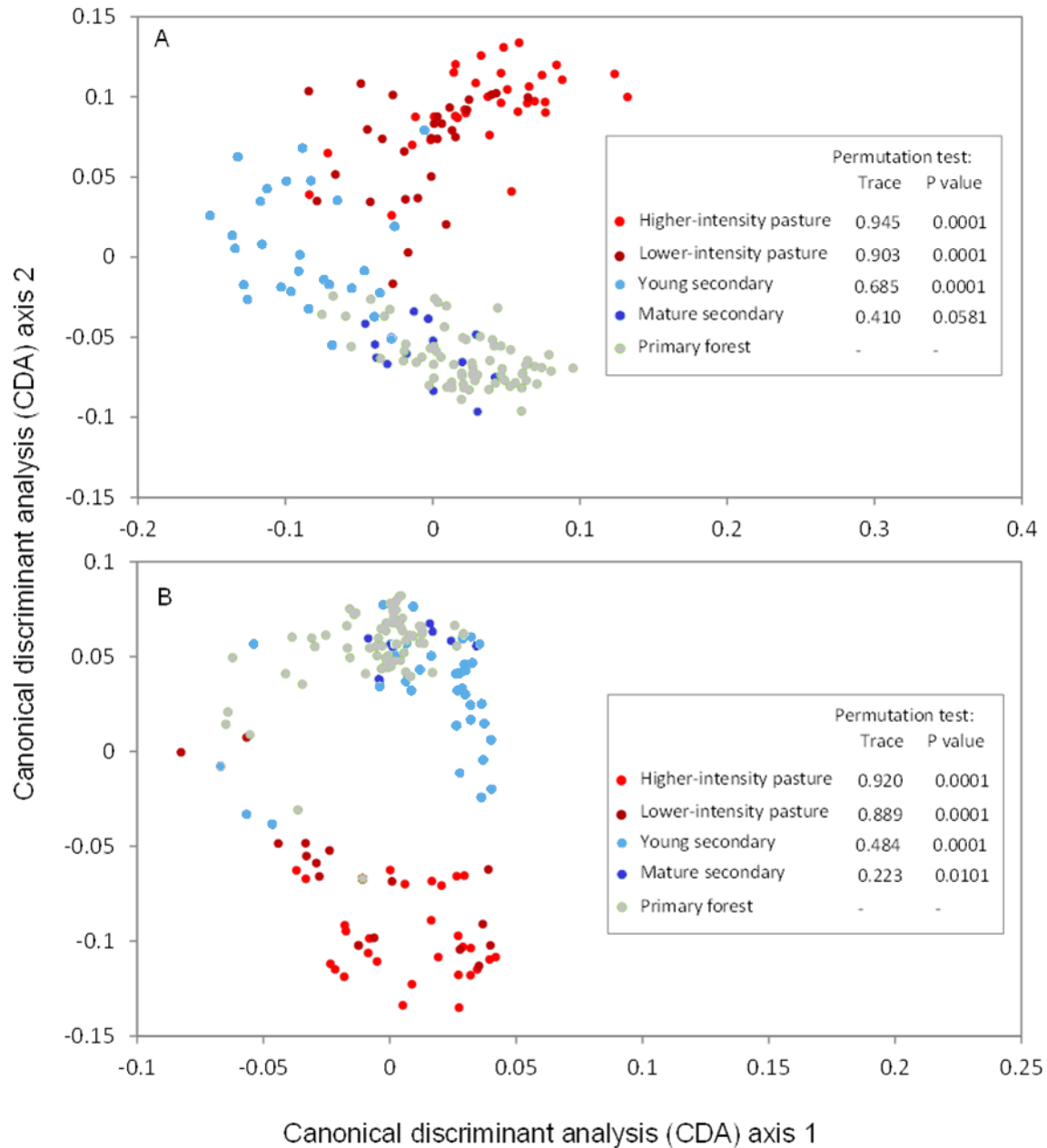
Figure S5. Canonical discriminant analysis (CDA) of principal components to assess community similarity for birds (A) and dung beetles (B) across habitats in the Tropical Andes. The first two CDA axes explain 80.4% (birds) and 73.2% (dung beetles) of variation in the principal components, and correctly classify 78.5% (birds) and 70.2% (dung beetles) of points within habitat groups in leave-one-out analysis[1]. Permutation test statistics are provided (insets) for
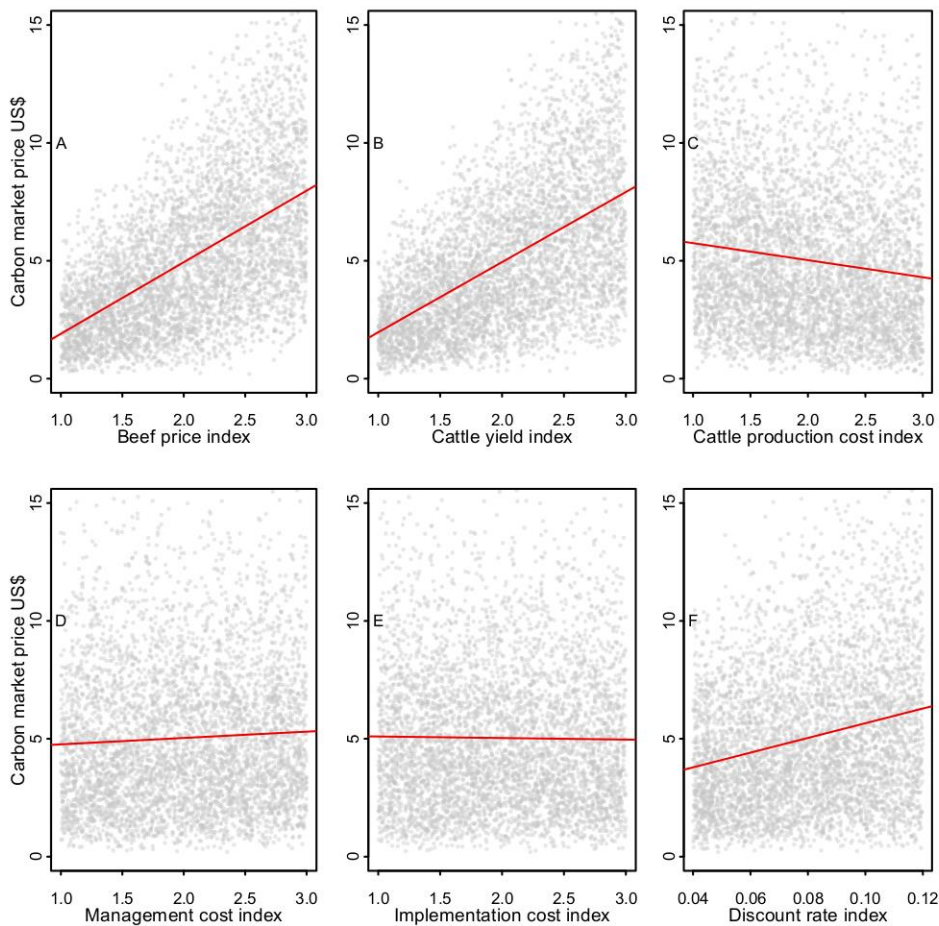
437 contrasts between each habitat type and primary forest, as indicators of statistical support for

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442 constrained ordination for ecology. *Ecology* **84**, 511-524 (2003).

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Figure S6. Economic sensitivity analysis examining the factors influencing cost-effectiveness of secondary forest regeneration. The median break-even tCER market price required for forest regeneration (i.e. to exceed the net present value of cattle pasture plus project management and implementation costs) is US$ 0.80 t^{-1} CO$_2$ (95% CI range = US$ 0.25 to US$ 1.67, see main article). Sensitivity of this value is shown for the following parameters: the beef market price (A), cattle yield per hectare (B), agricultural production costs (C), PES project management costs (D), PES implementation/monitoring costs (E) and discount rate (F). Variation in each parameter is generated by multiplying observed values by an index drawn a uniform distribution ranging from

453   1 to 3 (i.e. up to triple the mean observed value). Points show individual randomizations

454   (n=10,000 in each case) whilst trend line slopes indicate the relative contribution of each

455   parameter to variation in required carbon market price.

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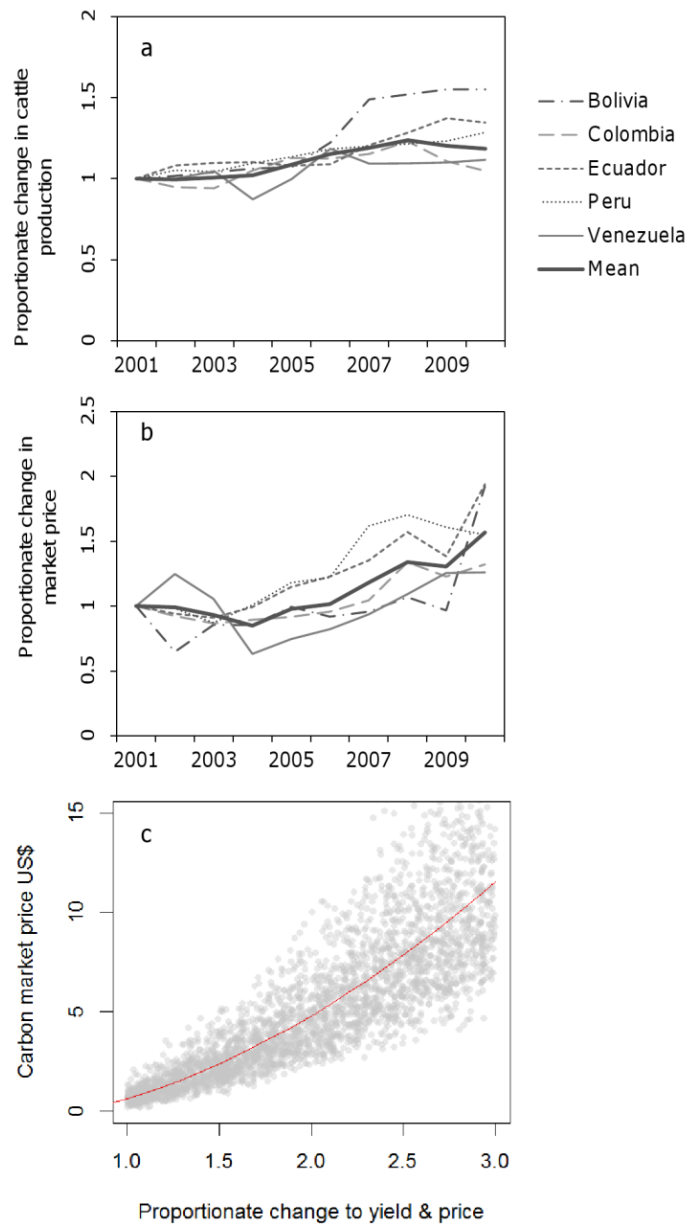
Figure S7 Trends in cattle production and beef market prices, and predicted response of break-even carbon market prices to future change. Trends in the total annual production of cattle (a) and mean market price for whole live animals (b) are shown for the nations in the Tropical Andes region (data from http://faostat.fao.org/). Trends are shown as proportionate change relative to the start year (2001). We also conducted a simulation analysis in which we

463   examined how increases in beef yield from our study areas (measured as tonnes brought to

464   market per hectare per year) and market prices influence the break-even carbon price for natural

465   forest regeneration (c, for tCER calculations without leakage mitigation). To do this we

466   multiplied our observed yield and price values by a value drawn from a uniform distribution

467   bounded by 1 and 3 (i.e. up to 300% increase).

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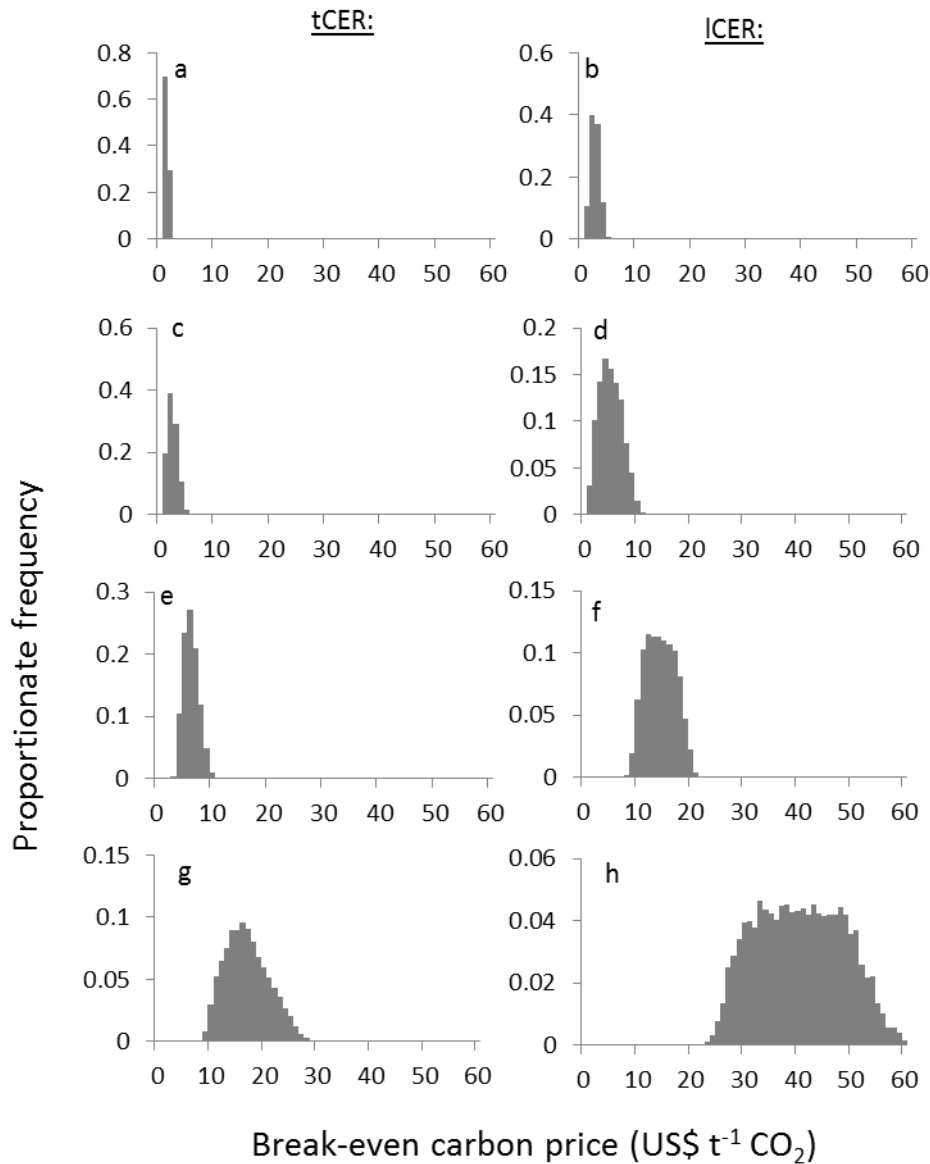
Supplementary Figure S8. Predicted break-even carbon market prices for a range of cost and market scenarios. Prices reflect the minimum required to make natural forest regeneration affordable under a PES scheme (i.e. accounting for agricultural opportunity costs, as well as scheme implementation and management costs). Each panel shows the proportionate frequency of break-even prices from 10,000 randomizations.The upper four panels (a-d) show estimates based on current economic data, either excluding leakage mitigation costs (tCER = a, lCER = b)

476   or incorporating a conservative leakage cost equivalent to double the agricultural opportunity cost

477   (tCER= c, lCER = d). The lower four panels (e-h) show estimates based on a hypothetical future

478   scenario in which beef yield and market prices are simultaneously doubled. Again, panels show

479   calculations excluding leakage mitigation costs (tCER = e, lCER = f) or incorporating leakage

480   costs (tCER = g, lCER = h).

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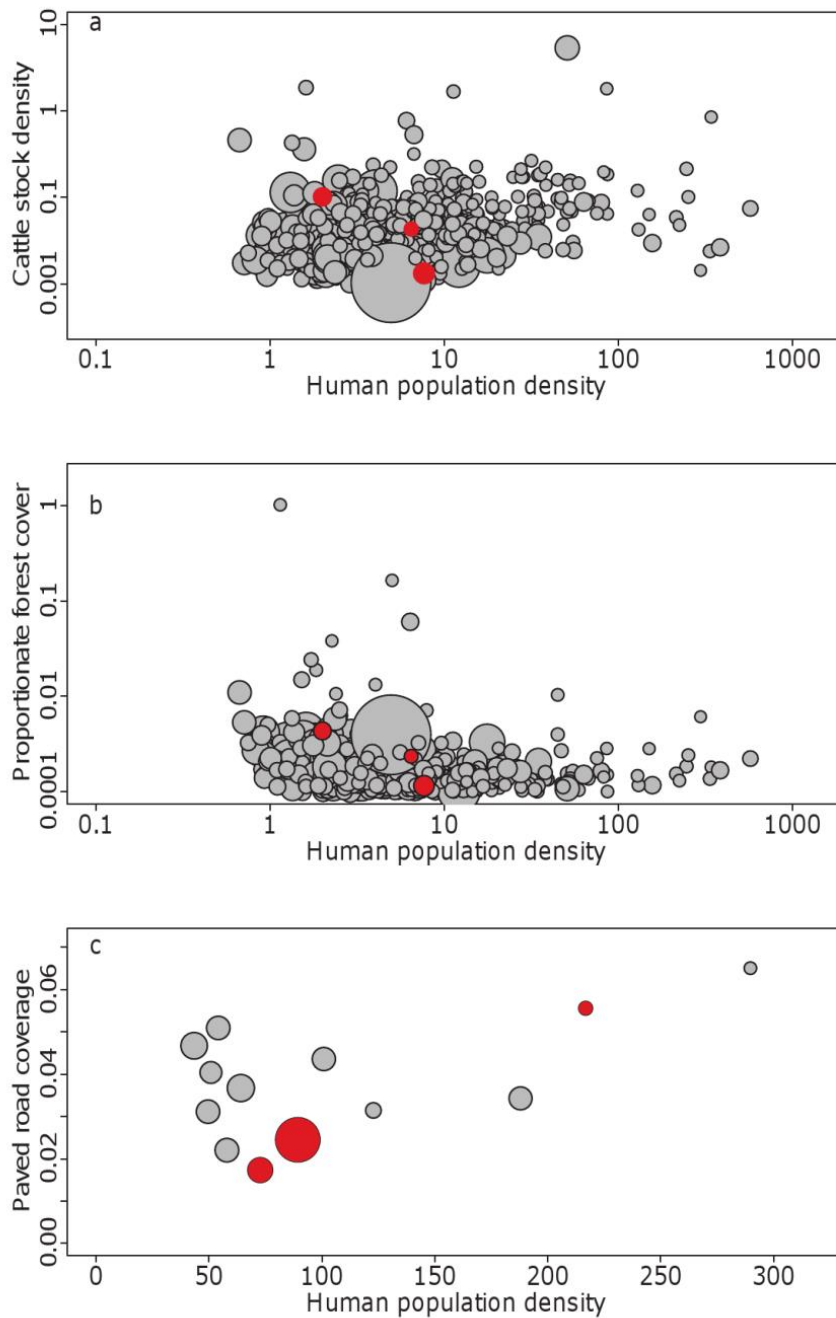
Figure S9. Socioeconomic and environmental characteristics of municipalities and departments across the Colombian Andes, in comparison to our study areas. Panels show human population densities (per km^2) plotted against cattle stock density (a, municipality-level), proportionate contiguous forest cover (b, municipality-level) and coverage of paved roads (c,

486   department level). All points are scaled by land area; red circles indicate municipalities and

487   departments where our field data were collected, whilst grey circles are other municipalities and

488   departments. All data are taken from the Colombian Sistema de Información Geográfica para la

489   Planeacion y el Ordenamiento Territorial (SIGOT), http://sigotn.igac.gov.co/sigotn/, for the year

490   2006.

491

492 **Supplementary Table S1. Study site details and sampling effort in the Western Andes of**

493 **Colombia.** Site areas were calculated as polygons bounded by the most distance sampling points

494 in each site. Pastures were classed as lower-intensity if non-pasture habitats (e.g. forest

495 fragments) covered more than 30% of the area within a 100m radius surrounding the sampling

496 point. Secondary forests were classed as advanced at 15 years and older. Sampling points were

497 located along transects within randomized squares (see Methods, Supplementary Fig. S1 for

498 details).

Site	Mesenia-Paramillo	Cerro Montezuma	Las Tangaras
Municipality	Jardin	Pueblo Rico	El Carmen
Department	Antioquia	Risaralda	Chocó
Midpoint (long, lat)	-75.8895, 5.4950	-76.0825, 5.2396	-76.1763, 5.8251
Size (ha)	3294.7	1742	1737.3
Altitudinal range	2055-2683	1315-2539	1291-2144
Bird sampling points:			
Primary forest	27	24	18
Advanced secondary forest	5	8	2
Young secondary forest	15	9	4
Lower-intensity pastoral matrix	8	10	10
Higher-intensity pastoral matrix	8	9	17
Dung beetle sampling points:			
Primary forest	33	13	23
Advanced secondary forest	7	5	2
Young secondary forest	19	13	5
Lower-intensity pastoral matrix	9	6	11
Higher-intensity pastoral matrix	13	9	14
Carbon sampling points:			
Primary forest	39	13	28
Advanced secondary forest	8	5	2
Young secondary forest	26	12	5
Lower-intensity pastoral matrix	12	6	14
Higher-intensity pastoral matrix	15	9	21

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Supplementary Table S2. Carbon stock estimates measured across habitat types in the Tropical Andes. We estimated carbon stocks per hectare using allometric equations to estimate living tree biomass. For primary forest trees, we used three sets of equations based on pantropical datasets (Chave 'Type II wet forest' from ref. 1; Feldpauch Western Amazonia[a], Feldpauch pantropical[b], both from ref. 3) and two based on datasets from Colombia (Alvarez 'Lower montane wet forest model I.3', ref. 4, Sierra 'primary forest', ref. 5). For secondary forest trees, we one set of equations based on data from Colombia (Sierra 'secondary forest', ref. 5), one from Panama (van Breugel 'model 2', ref. 6) and one from Indonesia (Ketterings 'secondary forest', ref. 7). We applied each to our data using measurements of tree diameter at breast height (d.b.h; we excluded trees <5cm d.b.h.) and wood density measured from core samples. Carbon estimates also include three other carbon pools: dead wood, leaf litter and living vines.

	Primary forest	Advanced secondary forest (>15 yrs)	Young secondary forest (<15 yrs)
Chave	170.5 ± 13.4	-	-
Feldpauch [a]	193.1 ± 14.7	-	-
Feldpauch [b]	193.2 ± 15.5	-	-
Alvarez	274.3 ± 22.4	-	-
Sierra primary	176.4 ± 16.4	-	-
van Breugel	-	84.1 ± 13.7	40.8 ± 4.0
Sierra secondary	-	112.0 ± 19.7	48.4 ± 4.7
Ketterings	-	90.1 ± 15.7	40.2 ± 4.4
Mean	202.7 ± 20.2	95.4 ± 16.7	43.3 ± 4.4

513 **Supplementary Table S3. Patterns of land use in the Colombian Andes**. Primary land uses

514 are listed by area ($\times$ 1,000 km^2), and as a percentage of total area, for the principal departments

515 spanning the Colombian Andes (ranked by size, including low elevation inter-Andean valleys).

516 Note that areas of sugar cane, coffee and maize are included in the values for category "all

517 crops", and are shown separately only for interest. Departmental data are from the Colombian

518 Sistema de Información Geográfica para la Planeacion y el Ordenamiento Territorial (SIGOT),

519 http://sigotn.igac.gov.co/sigotn/, for the years 2006-2008. Also shown are national trends

520 showing the % change in area under each land use in Colombia from 2001-2011, using data from

521 http://faostat.fao.org/.

Department	Total area ($\times$ 1,000 km^2)	Area ($\times$ 1,000 km^2) of:											
		Cattle pasture		All crops		Sugar cane		Coffee		Maize		Forest	
		Area	(%)	Area	(%)	Area	(%)	Area	(%)	Area	(%)	Area	(%)
Antioquia	63.6	28.4	(44.7)	10.3	(16.1)	0.4	(0.6)	1.1	(1.8)	0.4	(0.7)	22.4	(35.3)
Santander	30.5	17.4	(57.1)	3.1	(10.3)	0.3	(0.9)	0.3	(1.1)	0.3	(0.8)	8.7	(28.5)
Cauca	29.2	9	(30.7)	8.2	(28.1)	0.4	(1.5)	0.6	(2.0)	0.1	(0.3)	11.3	(38.7)
Bolivar	25.3	11.2	(44.1)	3.9	(15.3)	0	(0.2)	0	(0.0)	0.8	(3.3)	6.1	(24.0)
Tolima	23.5	13	(55.1)	3.9	(16.5)	0.2	(0.7)	0.9	(3.9)	0.2	(1.1)	5.5	(23.3)
Boyaca	23.1	12.8	(55.3)	1.7	(7.4)	0.2	(0.7)	0.1	(0.5)	0.2	(0.8)	7.4	(32.0)
Magdalena	23.1	14	(60.6)	2.5	(10.6)	0	(0.1)	0.2	(0.8)	0.3	(1.3)	3.1	(13.3)
Cundinamarca	22.6	14.3	(63.1)	2.1	(9.2)	0.5	(2.4)	0.3	(1.3)	0.3	(1.5)	4.9	(21.8)
Vallede Cauca	22.1	7.3	(33.1)	6.6	(29.7)	1.4	(6.2)	0.8	(3.5)	0.3	(1.3)	7	(31.7)
Huila	19.8	10.4	(52.1)	3.4	(17.3)	0.1	(0.6)	0.9	(4.5)	0.3	(1.4)	5.2	(26.3)
Caldas	7.8	4.6	(58.4)	1.4	(18.2)	0.2	(2.4)	0.8	(9.5)	0.1	(0.7)	1.6	(20.7)
Risaralda	4.1	1.1	(27.3)	1.4	(32.8)	0.1	(1.2)	0.5	(11.5)	0	(0.6)	1.6	(37.5)
Quindio	1.8	0.6	(33.4)	0.6	(31.4)	0	(0.1)	0.4	(21.3)	0	(0.7)	0.6	(31.3)
All	**297.2**	**144.1**	**(48.5)**	**49.1**	**(16.5)**	**3.8**	**(1.3)**	**6.9**	**(2.3)**	**3.3**	**(1.1)**	**85.4**	**(28.7)**
Change in area 2001-11	**-**	**+2.8%**		**+7.5%**		**-59.3%**		**+4.9%**		**-16.7%**		**-1.6%**	

522

523

524 **Supplementary Table S4. Comparison of break-even carbon prices for tropical PES schemes reported in the literature.** For

525 each study, we indicate the type of action involved (avoided deforestation, natural forest regeneration, plantation forestry) and the

526 primary competing land use for which opportunity costs are calculated. We also show market trends for competing land uses,

527 calculated from global mean annual producer price indices for each primary use over the last 10 years (data from http://faostat.fao.org,

528 2004-2006 = 100). We indicate the timeframe and discount rates used, and whether or not costs of leakage and

529 management/implementation were considered in break-even carbon price calculations. All prices are inflation-adjusted to 2013 US$;

530 reported price values were adjusted from $ t^{-1} C to $ t^{-1} CO_2 where necessary. The final column shows a direct comparison with the

531 median break-even price estimate from our study. Comparisons are given relative to our lCER price (US$ 1.99 t-1 CO2) for studies

532 reporting permanent or lCER credit types (or our leakage-inclusive lCER price US$ 4.34 if the study also estimated leakage), and

533 relative to our tCER price (US$ 0.80 t-1 CO2) for studies reporting tCER credits (or US$ 1.78 if the study also estimated leakage).".

534 Studies were found by searching Web of Science and Google Scholar search engines using the term (Carbon OR CO_2)+(cost OR

535 price)+(deforestation OR REDD*).

Study	Region	Action	Competing land use	Market trend	Years	Discount rate	Leakage?	Management costs?	Credit type	Price US$ t^{-1} CO_2	Comparison
Bellassen et al. (2008)[1]	Cameroon	Deforestation	Shifting cultivation	n/a	50	5	No	No	Permanent	3.11	+1.12
Busch (2013)[2]	Bolivia	Deforestation	All agriculture	n/a	30	10	No	No	Permanent	2.71	+0.72
Busch (2013)[2]	Bolivia	Deforestation	All agriculture	n/a	30	10	No	No	Permanent	3.22	+1.23
Busch (2013)[2]	Bolivia	Deforestation	All agriculture	n/a	30	10	No	No	Permanent	3.79	+1.80
Busch (2013)[2]	Indonesia	Deforestation	All agriculture	n/a	30	10	No	No	Permanent	0.46	-1.53
Busch (2013)[2]	Indonesia	Deforestation	All agriculture	n/a	30	10	No	No	Permanent	0.56	-1.43
Busch (2013)[2]	Indonesia	Deforestation	All agriculture	n/a	30	10	No	No	Permanent	0.73	-1.26

Busch (2013) [2]	Madagascar	Deforestation	All agriculture	n/a	30	10	No	No	Permanent	0.76	-1.23
Busch (2013) [2]	Madagascar	Deforestation	All agriculture	n/a	30	10	No	No	Permanent	1.26	-0.73
Busch (2013) [2]	Madagascar	Deforestation	All agriculture	n/a	30	10	No	No	Permanent	1.72	-0.27
Coomes et al. (2008) [3]	Panama	Regeneration	Cattle	105.8	25	n/a	No	Yes	Unstated	3.73	+1.74
Coomes et al. (2008) [3]	Panama	Regeneration	Cattle	105.8	25	n/a	No	Yes	Unstated	2.62	+0.63
Fisher et al. (2011a) [4]	Malaysia	Deforestation	Oil palm	117.6	25	10	No	No	Permanent	51.23	+49.24
Fisher et al. (2011a) [4]	Malaysia	Deforestation	Timber	n/a	25	10	No	No	Permanent	27.25	+25.26
Fisher et al. (2011b) [5]	Tanzania	Deforestation	All agriculture	n/a	30	10	No	Yes	Permanent	6.96	+4.97
Fisher et al. (2011b) [5]	Tanzania	Deforestation	All agriculture	n/a	30	10	Yes	Yes	Permanent	13.16	+8.82
Koning et al. (2005) [6]	Ecuador	Regeneration	Cattle	105.8	30	7	No	Yes	tCER	0.74	-0.06
Koning et al. (2005) [6]	Ecuador	Plantation	Cattle	105.8	30	7	No	Yes	tCER	1.24	+0.44
Nepstad et al. (2007) [7]	Brazil	Deforestation	Cattle	105.8	30	5	No	Yes	Permanent	0.54	-1.45
Nepstad et al. (2007) [7]	Brazil	Deforestation	Cattle	105.8	30	5	No	Yes	Permanent	1.97	-0.02
Olschewski & Benitez [8] (2005)	Ecuador	Regeneration	Cattle	105.8	30	7	No	Yes	tCER	1.24	+0.44
Olschewski & Benitez [8] (2005)	Ecuador	Regeneration	Cattle	105.8	30	7	No	Yes	lCER	3.24	+1.25
Olschewski & Benitez [8] (2005)	Ecuador	Plantation	Cattle	105.8	30	7	No	Yes	tCER	1.72	+0.92
Olschewski & Benitez [8] (2005)	Ecuador	Plantation	Cattle	105.8	30	7	No	Yes	lCER	2.64	+0.65
Osafo. (2005) [9]	Ghana	Deforestation	Maize	116.1	30	n/a	No	No	Permanent	8.47	+6.48
Silva-Chávez (2005) [10]	Bolivia	Deforestation	Soybean	113.8	30	n/a	No	No	Permanent	2.72	+0.73
Sist et al. (2014) [11]	Brazil	Deforestation	Logging	n/a	n/a	n/a	No	No	Permanent	6.5	+4.51
Tomich et al. (2002) [12]	Indonesia	Deforestation	Rubber	113.4	25	15	No	No	Permanent	2.61	+0.62
Tomich et al. (2002) [12]	Indonesia	Deforestation	Oil palm	117.6	25	15	No	No	Permanent	3.64	+1.65
Venter et al. (2009) [13]	Indonesia	Deforestation	Oil palm	117.6	30	8	No	Yes	Permanent	1.84	-0.15
Venter et al. (2009) [13]	Indonesia	Deforestation	Oil palm	117.6	30	8	No	Yes	Permanent	2.68	+0.69
Venter et al. (2009) [13]	Indonesia	Deforestation	Oil palm	117.6	30	8	No	Yes	Permanent	3.57	+1.58
Venter et al. (2009) [13]	Indonesia	Deforestation	Oil palm	117.6	30	8	No	Yes	Permanent	5.27	+3.28
Venter et al. (2009) [13]	Indonesia	Deforestation	Oil palm	117.6	30	8	No	Yes	Permanent	11.13	+9.14
Venter et al. (2009) [13]	Indonesia	Deforestation	Oil palm	117.6	30	8	No	Yes	Permanent	18.95	+16.96
Venter et al. (2009) [13]	Indonesia	Deforestation	Oil palm	117.6	30	8	No	Yes	Permanent	22.17	+20.18
Venter et al. (2009) [13]	Indonesia	Deforestation	Oil palm	117.6	30	8	No	Yes	Permanent	37.79	+35.8

| Yamamoto & Takeuchi (2012)[14] | Indonesia | Deforestation | Rice | 118.1 | 30 | 10 | No | No | Permanent | 4.5 | +2.51 |
| Warr & Yusuf (2011)[15] | Indonesia | Plantation | All agriculture | n/a | 30 | n/a | Yes | No | Unstated | 1.15 | -3.19 |

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Supplementary Table S5. Threatened bird species detected during surveys in Tropical

567 **Andes.** Species are listed according to threat severity (IUCN categories, data from

568 www.birdlife.org/datazone). The probability of occurrence at a single sampling point in each

569 habitat is given for each species (controlling for detection probability and altitude).

Species	Status*	Point-level occurrence probability by habitat[†]				
		Primary	Pasture (high)	Pasture (low)	Secondary(<15)	Secondary(>15)
Coeligena orina	CR	p	-	-	-	-
Henicorhina negretti	CR	0.14	-	-	-	-
Bangsia aureocincta	EN	0.43	-	-	0.3	-
Diglossa gloriosissima	EN	0.08	0.04	-	-	-
Ognorhynchus icterotis	EN	0.24	-	-	0.15	0.25
Vireo masteri	EN	0.52	-	-	0.41	0.54
Bangsia melanochlamys	VU	0.56	-	p	0.4	0.47
Chlorochrysa nitidissima	VU	P	-	-	-	p
Chlorospingus flavovirens	VU	-	-	-	-	p
Dysithamnus occidentalis	VU	0.35	-	-	0.23	-
Herpsilochmus axillaris	VU	0.21	-	-	-	0.15
Hypopyrrhus pyrohypogaster	VU	0.16	0.37	0.5	0.28	0.17
Oreothraupis arremonops	VU	0.22	-	-	-	-
Patagioenas subvinacea	VU	0.28	0.21	0.11	0.33	0.27
Sericossypha albocristata	VU	0.12	-	-	0.09	0.03
Spizaetus isidori	VU	-	-	-	-	p
Aburria aburri	NT	-	-	-	-	p
Arremon castaneiceps	NT	0.17	-	-	0.14	0.16
Cyanolyca pulchra	NT	0.39	-	-	0.3	0.05
Drymotoxeres pucherani	NT	0.05	-	-	-	-
Grallaricula flavirostris	NT	0.32	-	-	0.36	-
Harpyhaliaetus solitarius	NT	-	-	p	-	p
Iridosornis porphyrocephalus	NT	0.89	0.47	0.32	0.51	0.89
Margarornis stellatus	NT	0.6	-	-	-	-
Odontophorus hyperythrus	NT	0.76	-	-	0.83	0.66
Semnornis ramphastinus	NT	0.39	-	-	0.3	0.34
Synallaxis moesta	NT	-	0.09	0.06	0.09	-
Xenopipo flavicapilla	NT	-	-	-	p	p
Aglaiocercus coelestis	RR	0.88	0.4	0.23	0.7	0.8
Boissonneaua jardini	RR	0.52	-	-	0.26	0.46
Chamaeza turdina	RR	0.05	-	-	-	0.02
Chlorochrysa phoenicotis	RR	0.71	-	-	0.33	0.68
Chlorophonia flavirostris	RR	0.19	-	-	0.19	-
Chlorospingus semifuscus	RR	0.62	-	p	0.28	0.48
Chrysothlypis salmon	RR	P	-	-	-	0.12
Coeligena wilsoni	RR	0.67	-	-	0.4	0.55
Diglossa indigotica	RR	0.52	-	-	0.16	0.35
Entomodestes coracinus	RR	0.41	-	-	0.23	0.28
Grallaria flavotincta	RR	0.62	-	0.02	0.34	0.62
Habia cristata	RR	0.34	-	-	0.29	0.37
Heliodoxa imperatrix	RR	0.52	-	-	-	0.39
Machaeropterus deliciosus	RR	P	-	-	-	0.15
Pipreola jucunda	RR	0.22	-	-	-	-
Scytalopus vicinior	RR	0.46	0.18	0.09	0.39	0.39
Thripadectes ignobilis	RR	0.56	0.08	0.06	-	0.47
Urosticte benjamini	RR	0.62	0.1	-	0.44	0.56

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570 *CR= critically endangered, EN = endangered, VU = vulnerable, NT = near-threatened, RR =
571 range-restricted.

572 †Pastures were classed as lower-intensity if non-pasture habitats (e.g. forest fragments) covered

573 more than 30% of the area within a 100m radius surrounding the sampling point. Secondary

574 forests were classed as advanced at 15 years and older. Species never detected in a given habitat

575 type are denoted "-", whilst species detected only anecdotally in a given habitat type (i.e. outside

576 point count sessions) are denoted "p".

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Supplementary Table S6. Values used to estimate net present value of cattle farming within

the study region, **and a comparison with local interviews**. We derived economic values from

governmental data compiled at the local (municipality) and regional (department) level

surrounding our three field sites. Data on costs of cattle production were derived from a national

level survey[1], adjusted for mean stock densities to generate cost estimates at the municipality and

department level. Means calculated across municipalities and departments are weighted by land

area. We also conducted informal interviews with farmers (n=14) within each study area, who

exclusively raised beef cattle for local markets. These farmers reported their costs to be higher

than national estimates, and also reported their stock densities to be considerably higher. The

NPV estimate derived from interview data was US $183.50. However, most farmers interviewed

were uncertain as to the exact size of their holdings, undermining our confidence in the accuracy

of this interview-derived value.

	Local interviews (± s.d)	Municipality				Department			
		Jardin	Pueblo Rico	El Carmen	Mean	Antioquia	Risaralda	Chocó	Mean
Mean cattle stock density (head ha^{-1})[a]	3.20 ±0.35	0.79	1.53	0.25	0.48	0.88	1.01	0.65	0.87
Mean weight at market (kg)[b]	295 ± 16.5	-	-	-	215	215	212	218	215
Mean meat production (kg ha^{-1} yr^{-1})	-	-	-	-	26.34	47.29	34.29	54.99	46.75
Market price	1.44 ±0.04	-	-	-	1.41	1.41	1.42	1.41	1.41

(US$ kg^{-1})[b]									
Labour costs (US$ ha^{-1} year^{-1})[c]	64.6 ±11.3	-	-	-	11.2	-	-	-	20.1
Materials costs (US$ ha^{-1} year^{-1})[c]	58.9 ±17.5	-	-	-	3.2	-	-	-	5.8
Transport costs (US$ ha^{-1} year^{-1})[c]	10.2 ±3.2	-	-	-	1.5	-	-	-	2.7
Other costs (US$ ha^{-1} year^{-1})[c]	91.0 ±11.5	-	-	-	12.1	-	-	-	21.5

592 [a]Municipality and departmental data from SIGOT 2006 dataset http://sigotn.igac.gov.co/

593 [b]Municipality and departmental data from FEDEGAN 2011 dataset http://www.fedegan.org.co/

594 [c] Municipality and departmental data from 2012 national survey[1] adjusted for appropriate stock

595 densities.

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597 **Reference**

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