Quantifying carbon and amphibian co-benefits from secondary forest regeneration in the Tropical Andes

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Abstract

Tropical land-use change is a key driver of global declines in biodiversity and a major source of anthropogenic carbon emissions, yet there is a substantial shortfall in the funding available to tackle these issues. We urgently need mechanisms that can simultaneously tackle both biodiversity and carbon losses, with carbon-based payments for ecosystem services (e.g. REDD+) of particular interest. A critical question is whether such payments offer strong carbon–biodiversity co-benefits via the regrowth of forests on abandoned farmlands (carbon enhancements) for amphibians, which are the most threatened vertebrate group and reach the greatest richness of threatened and small-ranged species in the montane tropics (>1000 m a.s.l.). Here, we study changes in amphibian communities across a typical Andean habitat transition from cattle pasture through secondary forests (8–35 years) to primary forest. As secondary forests mature, they recovered the abundance, species richness, species composition and Red-listed (near threatened and threatened) species typically found in primary forest. By contrast, cattle pasture contained much lower richness of Red-listed species and a different species composition compared to forest. We then reveal positive relationships between carbon stocks and amphibian species richness and abundance, Red-listed species richness and abundance and the similarity of communities to primary forests, confirming significant carbon–biodiversity co-benefits. Our results underscore the high conservation value of secondary forests and the strong potential for carbon and biodiversity recovery. Using carbon-based funding initiatives to support the regrowth of forests on marginal agricultural land is therefore likely to conserve threatened biodiversity in the Tropical Andes.

Introduction

Earth is currently undergoing a substantial decline in biodiversity (May, 2010; Barnosky *et al.*, 2011), considered by some to be the sixth major extinction of the Phanerozoic Era (May, Lawton & Stork, 1995; Dirzo & Raven, 2003; Ceballos *et al.*, 2015). Tropical land-use change is a major driver of this decline, with over 150 million ha of tropical forest converted into agriculture over the last three decades (Gibbs *et al.*, 2010; Hansen *et al.*, 2013), over 400 million ha of tropical forest in permanent timber concessions that either have been or soon will be selectively logged, and with fragmentation and associated edge effects affecting most areas of the tropics (Haddad *et al.*, 2015).

Deforestation and degradation are also a major source of anthropogenic carbon releases, second only to the burning of fossil fuels (Fearnside & Laurance, 2004; Bonan, 2008; Van der Werf *et al.*, 2009). Emissions of carbon dioxide and other greenhouse gases are subsequently driving climate change, exacerbating the loss of global biodiversity (Thomas *et al.*, 2004). Despite these negative impacts, there is a substantial shortfall in the funding available for stemming the losses of biodiversity and carbon (Stern, 2007; McCarthy *et al.*, 2012; Waldron *et al.*, 2013), suggesting a need for cost-effective and beneficial mechanisms that can simultaneously deal with both problems.

Of particular interest is the potential for carbon-based payments for ecosystem services, for example the United

Nations' Reducing Emissions from Deforestation and Forest Degradation (REDD+) programme, to protect carbon stocks (including above- and below-ground, plus live or dead carbon stocks) and biodiversity. Where REDD+ payments simultaneously protect carbon and high biodiversity, important carbon–biodiversity co-benefits can accrue, although such congruence is lacking in some instances (e.g. Strassburg *et al.*, 2010; Sangermano, Toledano & Eastman, 2012).

An important possibility under REDD+ and the Clean Development Mechanism is for carbon enhancements via regrowth of secondary forest on abandoned farmland to sequester carbon from the atmosphere and also recover important biodiversity. This is especially so in regions where low economic returns from agriculture, such as marginal farmlands that are too dry, steep, high or remote for modern high-intensity farming (Maass *et al.*, 2005; Grau & Aide, 2008; Ferraro, Hanauer & Sims, 2011), mean that carbon prices needed to offset the opportunity costs arising from taking land out of production are likely to be low. In such regions there is already substantial land abandonment (Rudel *et al.*, 2009; Aide *et al.*, 2013) and REDD+ could help to enhance the background rate of this abandonment, to result in a wave of natural regeneration of secondary forest that can potentially combat both biodiversity loss (Barlow *et al.*, 2007; Chazdon, 2008; Queiroz *et al.*, 2014) and human-induced climate change (Asner *et al.*, 2010). Afforestation and reforestation (ARR) regulations stipulate that areas cleared of native vegetation in the 10 years prior to the project start date may be eligible for carbon-based payments, except when clearing occurred due to natural disasters such as floods or hurricanes (VCS, 2013).

The regrowth of secondary forest in tropical landscapes recovers much carbon (Martin, Newton & Bullock, 2013). In turn, biodiversity also recovers to varying degrees, including plants, birds, dung beetles, butterflies and bats (Barlow *et al.*, 2007; Chazdon, 2008; Gilroy *et al.*, 2014b; Hernández-Ordóñez, Urbina-Cardona & Martínez-Ramos, 2015). This suggests strong carbon–biodiversity co-benefits, which have been demonstrated empirically in the cases of carbon–dung beetle and carbon–bird co-benefits in the Tropical Andes (Gilroy *et al.*, 2014b).

Amphibians are the most threatened vertebrate group due to the combined effects of habitat loss and degradation (Vitousek *et al.*, 1997; Alford & Richards, 1999), climate change (Beebee, 1995) and pathogens, such as chytridiomycosis (Whittaker *et al.*, 2013; Jongsma *et al.*, 2014). A key question, therefore, is whether carbon enhancements under REDD+ can offer carbon–amphibian diversity co-benefits. Examination of the literature identified 36 studies on amphibian recovery in tropical secondary forests (Table S1), and while many reported that amphibian diversity in advanced secondary forest reached levels similar to those in primary forest (e.g. Urbina-Cardona & Londoño-Murcia, 2003; Hilje & Aide, 2012; Cortés-Gómez, Castro-Herrera & Urbina-Cardona, 2013), none jointly quantified whether there are strong, positive carbon and amphibian co-benefits resulting from recovery. Furthermore, the potential benefits of secondary forest recovery for amphibians in the montane

tropics (>1000 m a.s.l.), which are global hotspots of threatened and small-ranged amphibians (Jenkins, Pimm & Joppa, 2013), were the focus of just six studies that compared the value of secondary forest for amphibians with primary forest controls. However, of these six studies, just one compared community recovery across the range of secondary forest ages (Mizoram, India; Pawar, Rawat & Choudhury, 2004), and just one also included surveys in farmland or plantation prior to abandonment (Sulawesi, Indonesia; Gillespie *et al.*, 2005), hampering quantification of the true benefits of forest recovery.

In this study, we focus on the critical question of whether secondary forest regrowth offers carbon–amphibian diversity co-benefits. We do so in the Tropical Andes, which are the most species-rich area of the montane tropics globally and a hotspot of extinction risk due to extensive land-use change (Myers *et al.*, 2000), across a full landscape transition from cattle pasture through various ages of secondary forest and primary forest.

Materials and methods

Study location

The study was conducted within the 3295-ha Mesenia-Paramillo reserve located in the department of Antioquia on the Western slope of the "Cordillera Occidental" of the Colombian Andes (−75.8895 lon, 5.4950 lat). The study area spans an altitudinal range 2075–2683 m above sea level, a range typified by submontane cloud forest (Armenteras, Gast & Villareal, 2003). The Mesenia-Paramillo reserve is embedded within contiguous primary forest (>1 000 000 ha) and naturally regenerating secondary forests (age range 8–35 years), embedded with a pasture-dominated agricultural matrix (Fig. S1).

Sampling

We sampled amphibian communities along transects within eighteen 400 m × 400 m quadrat plots located randomly across the landscape in primary forest, secondary forest (8–35 years) and cattle pasture (Fig. S1). Squares were spaced ≥300 m apart between habitats and ≥400 m within habitats. Inside each plot we sampled frogs along three 25 m × 10 m transects sufficiently spaced (200–300 m) to assume community independence (Sinsch, 1990; Duellman & Trueb, 1994; Rödel & Ernst, 2004; Folt & Reider, 2013; Hutter *et al.*, 2016). We thus sampled amphibians at 54 unique transects totalling 19 in primary forest, 20 in secondary forest (spanning 8–35 years) and 15 in cattle pasture. Sampling took place in 2014 between July and August, corresponding to the relatively dry period in the region. We sampled each transect once in the morning from 07:00 to 11:00 and twice at night from 19:00 to 23:00, with each nocturnal session separated by 2–3 weeks. In total, 162 sampling events took place equating to 243 person hours. Diurnal transect data were not analysed due to the lack of frogs found (only 23 individuals) after exhaustive searching. We employed an

active search method along transects (Heyer *et al.*, 1994), which involved two researchers searching for amphibians on all accessible substrates up to 5 m each side of the transect to a maximum of 2 m in height. In forest habitats, it is likely that more individuals and potentially arboreal/canopy specialists will have gone undetected in this study that live above the 2-m height restriction (Herrera-Montes & Brokaw, 2010). Transects had previously been cut and marked with flagging tape 6 months before, thus avoiding any disturbance effects.

All amphibians encountered during transects were captured and held for photos and to measure body size (length of each frog from snout to vent to 1 mm accuracy using a ruler), before release either 200 m away from any sampling transect (including other transects within the same square) or on the same transect if all sessions had already been completed. Some individuals were collected and deposited in amphibian collection (IAvH-Am) at the Instituto Alexander von Humboldt (Villa de Leyva, Boyacá-Colombia) for use as voucher specimens. Photos and specimens were used for subsequent identification, with assistance of experts of the local herpetofauna where necessary.

Carbon and environmental variables

Non-soil carbon stock data were used as our measure of carbon stock biomass (herein carbon stock) from Gilroy *et al.* (2014b), who assessed in 15 m × 5 m plots within our amphibian sampling plots. Diameter at breast height (dbh) was measured for all trees >5 cm dbh, and wood-specific gravity (density) was calculated using tree cores extracted with an increment borer. Root biomass was estimated using the global mean upland forest root:shoot ratio of 0.26 (Cairns *et al.*, 1997; Gibbon *et al.*, 2010). Deadwood was calculated by combining biomass estimates for standing dead wood >5 cm dbh, and all coarse woody debris, utilizing an average wood density for deadwood of 0.31 g cm (Wilcke *et al.*, 2005; Gibbon *et al.*, 2010), and biomass for vines >2 cm diameter was estimated using an equation developed in the Colombian Andes (Sierra *et al.*, 2007). All leaf litter, small plants and grass were collected in smaller sample plots, with a subsample retained for drying and weighing to calculate biomass. Biomasses were summed for each plot and were then multiplied by 0.474, a value derived from a meta-analysis of studies in the tropics (Martin & Thomas, 2011), to give an estimate of total carbon stock (see Gilroy *et al.*, 2014b for full details).

Data analysis

Species richness and abundance

Amphibian species richness was compared between habitats using abundance-based rarefaction curves with 95% confidence intervals, allowing comparison of richness levels while controlling for different sample sizes (Colwell, Mao & Chang, 2004). The completeness of the sampling method used was assessed by calculating the mean of four commonly employed abundance-based estimators of species richness (Abundance-based Coverage Estimator, CHAO1, JACK1 and Bootstrap) using ESTIMATES v. 9.1 (Colwell, 2004). All other analyses were completed using the free-access statistical platform R version 3.1.1 (R Core Team, 2013). Species diversity was determined using the Shannon-Wiener index, and evenness was calculated through Pielou's evenness index (Oksanen *et al.*, 2011). At the transect-level, general linear models were employed to test the relationship between secondary forest age and species richness or abundance. Pairwise comparisons were then utilized to compare abundance, richness, evenness and diversity, among pasture, secondary forest and primary forest transects. We also employed a Morans *I* test in the ape package (R Core Team, 2013) to test whether species richness had been influenced by spatial autocorrelation.

Species composition

To assess differences in species composition between habitats, we used a non-metric multidimensional scaling (NMDS) ordination (Clarke & Warwick, 2001), employing the metaMDS function within the MASS package (R Core Team, 2013) with Bray–Curtis dissimilarity measure and square root transformation. A linear model was used to also test the significance of relationships between secondary forest age and Axis 1 of the NMDS ordination. We tested for differences between habitats using a permutational multivariate analysis of variance with 1000 permutations (ANOSIM function in Vegan; Oksanen *et al.*, 2011; Warton, Wright & Wang, 2012; R Core Team, 2013). These analyses were repeated using raw (non-transformed) and presence–absence data. To test whether the composition of species had been influenced by spatial autocorrelation, we used a Mantel test to compare geographic distance to similarity in species composition between pairs of transects within a habitat and between pairs of transects across all habitats (Edwards *et al.*, 2014). For each habitat (primary forest, secondary forest and cattle pasture), mean transect similarities to the primary forest community were obtained by generating similarity values through the Bray–Curtis dissimilarity measure for every transect against each primary forest transect (18 values in total for each transect, with one primary forest transect excluded as it contained no species; Gilroy *et al.*, 2014b). These values were used to generate habitat-level means, which were compared using a one-way ANOVA pairwise comparison in the Stats package. We compared the species richness between habitats of a subset of species classed as Near-threatened or Threatened by the IUCN (IUCN, 2015), henceforth termed 'priority' species. These analyses were performed using a linear model and one-way ANOVA pairwise comparisons in the Stats package.

Carbon–amphibian biodiversity co-benefits

We employed linear models in the Stats package to test for relationships between carbon (non-soil) stock and community similarity to primary rainforest, and carbon stock and the

richness of priority species. Linear models were also fitted between carbon stock and total abundance, and between carbon stock and the abundance of the subset of priority species.

Results

Recovery of species richness and abundance

Across all habitats, 285 individual frogs of 19 species were found, of which 197 individuals and seven species were IUCN Red-listed and of conservation priority. The four commonly used estimators of species richness suggest that ≥68% of species were sampled in each habitat (Table 1). Overall species richness did not differ between secondary forest and primary forest, but cattle pasture contained significantly lower species richness than both forest habitats (Fig. 1a, b). At the transect level, primary forest had significantly greater species richness (Fig. 1c), abundance (Fig. 1e) and diversity (Table 1) than pasture and secondary forest, which did not differ. Within secondary forests, there was a significant positive relationship between forest age and species richness (Fig. 1d; Regression, $r^2 = 0.366$, y = 0.099x + 0.404, $F_{1,18} = 10.41$, $P < 0.005$), and between age and abundance (Fig. 1f; Regression, $r^2 = 0.5$, y = 0.279x + −0.357, $F_{1,18} = 18$, $P < 0.001$). There was no significant variation in species evenness between habitat types (Table 1). There was spatial autocorrelation of model residuals across habitat types (Moran's I test, $P < 0.001$) but not within habitat types (Moran's I test, three tests, all $P \geq 0.15$), strongly suggesting that differences in species richness among habitat types are caused by land-use change, as opposed to spatial autocorrelation (Edwards *et al.*, 2014).

Table 1 Summary of species metrics across cattle pasture, secondary forest and primary forest

Measure	CP	S	P
Habitat Level			
Abundance	21	71	193
Sobs[c]	4	9	13
Sest[d]	5	12	19
Sobs/Sest[e]	80.00	75.00	68.42
Species diversity[f]	1.14	1.75	2.00
Species evenness[g]	0.82	0.76	0.78
Transect Level			
Species diversity	0.21 ± 0.30[a]	0.53 ± 0.51[a]	1.05 ± 0.58[b]
Species evenness	0.45 ± 0.47[a]	0.63 ± 0.43[a]	0.80 ± 0.24[a]

Means (±1 SE) are at the transect level. P, Primary forest; S, Secondary forest; CP, Cattle Pasture.
[a,b]Represent pairwise differences tested at $P \leq 0.05$.
[c]Observed species richness.
[d]Estimated species richness.
[e]Proportion of species recorded.
[f]Measured using Shannon diversity index.
[g]Measured using Pielou's index.

Recovery of species composition

Species composition differed significantly between habitats (Fig. 2a; ANOSIM: $r^2 = 0.537$, $P < 0.001$), with pairwise comparisons revealing significant differences between all habitat pairs (Table S3; $P < 0.001$). Using presence–absence and non-transformed matrices gave similar results to those of square root transformed matrices (Fig. S2 and Table S3). There was, however, a negative relationship between NMDS Axis 1 and secondary forest age (Fig. 2b; Regression, $r^2 = 0.419$, y = 0.05x + 0.674, $F_{1,13} = 4.94$, $P < 0.01$), with communities in older (25–35 year) secondary forest having similar Axis 1 scores to primary forest communities, suggesting that communities are very similar (see below). The Mantel tests for spatial autocorrelation showed a significant effect of distance on species composition across habitat types ($P < 0.001$) but not within habitat types (three tests, all $P \geq 0.52$). The lack of relationship within habitats between distance and composition strongly suggests that dissimilarities among habitat types are caused by land-use change, as opposed to by spatial autocorrelation and thus that distance effects expected from a non-independent sampling regime could be excluded (Ghazoul, 2002; Edwards *et al.*, 2014).

For mean similarity to the overall primary forest community, pasture transects were least similar, secondary forest transects were more similar and primary forest transects were most similar (Fig. 3a). There was, however, a significant positive relationship between secondary forest age and similarity to primary forest (Fig. 3b; Regression, $r^2 = 0.275$, y = 0.005x + 0.150, $F_{1,13} = 4.94$, $P < 0.05$), such that older (25–35 year) secondary forest had approximately the same mean similarity to overall primary forest community as did primary forest points. Between primary forest and pasture there was complete turnover of species, with none of the 13 species found in primary forest found in cattle pasture, while two of the four species found in cattle pasture (*Pristimantis achatinus* and *Dendropsophus columbianus*) were not found in any forest habitat (Table S4). By contrast, secondary forest shared six species with primary forest (Table S4).

No priority species were found in cattle pasture (Fig. 3c, d; Table S4), whereas primary forest contained all but one (*Pristimantis ruedai*) of the priority species found during this study (Table S4). While secondary forest had not recovered a similar number of priority species to those seen in primary forest (Fig. 3c), secondary forest age did show a significant positive effect on priority species richness (Fig. 3d; Regression, $r^2 = 0.404$, y = 0.089x + 0.111, $F_{1,18} = 12.24$, $P < 0.005$). Priority species richness and abundance followed a similar pattern, with pairwise comparisons between old secondary and primary forest showing no significant differences.

Are there positive carbon–amphibian biodiversity co-benefits?

There was a strong positive co-benefit between carbon and community similarity to the overall primary forest assemblage (Fig. 4a; Regression, $r^2 = 0.342$, y = 0.001x + 0.144,
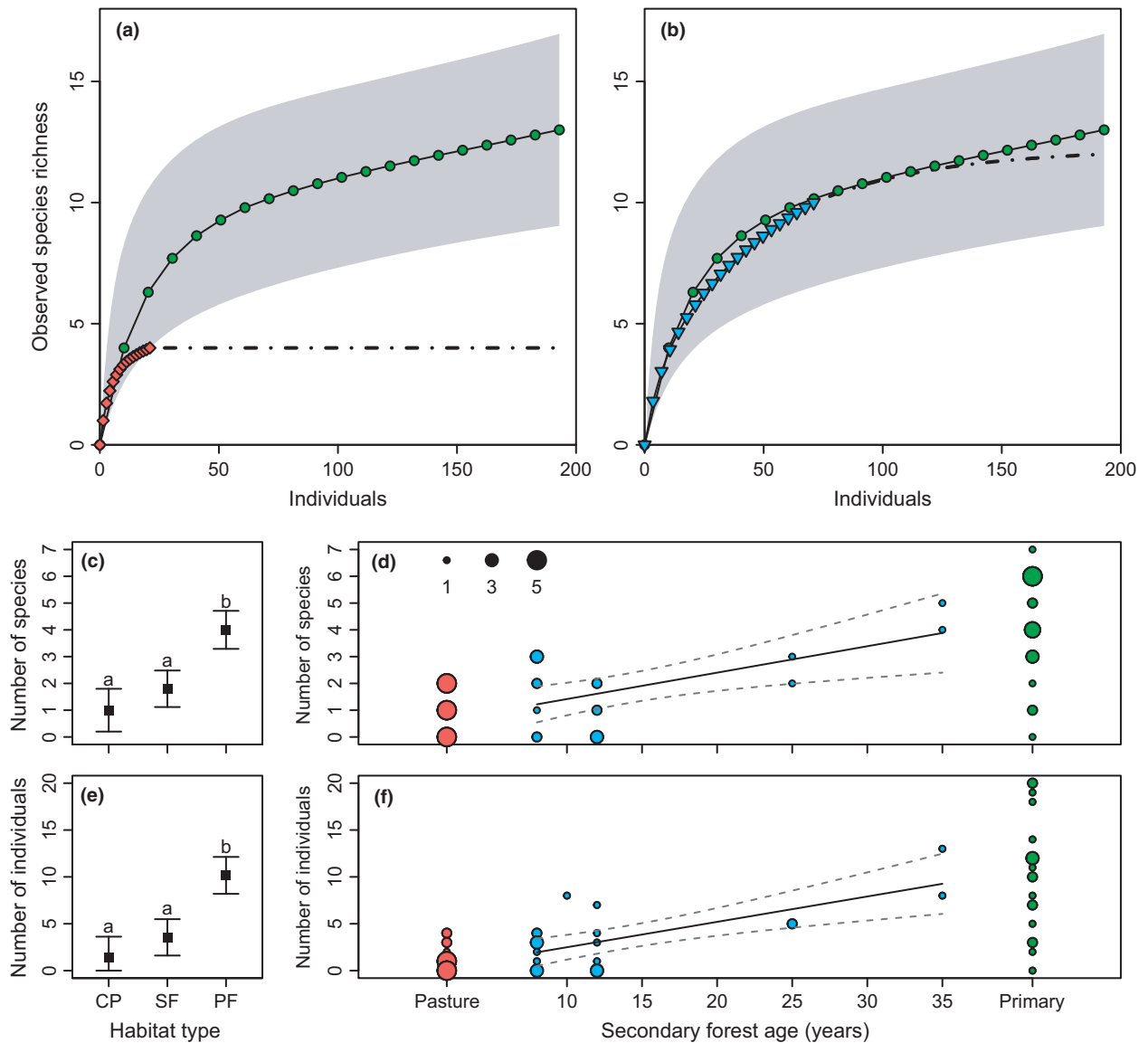
Figure 1 Observed species richness of primary forest (circles) against (a) cattle pasture (diamonds) and (b) secondary forest (triangles), calculated from sample-based rarefaction curves and scaled to show the number of individuals on the *x*-axis. Grey shading represents 95% confidence interval (CI) of primary forest. Dashed lines represent extrapolated results to the maximum number of individuals found in a habitat (193 individuals in primary forest). (c) Pairwise comparison of mean transect-level species richness across habitat types with 95% confidence intervals. (d) Transect-level species richness across habitat types with regression of secondary forest age. (e) Pairwise comparison of mean transect-level abundance across habitat types. (f) Transect-level abundance across habitat types with regression using secondary forest age. (c, e) Different letters indicate significance at $P \leq 0.05$; (d, f) points are proportional to number of transects. Dashed lines and error bars represent 95% confidence intervals.

$F_{1,39} = 20.24$, $P < 0.001$), between carbon and species richness (Fig. 4b; Regression, $r^2 = 0.3096$, y = 0.008217x + 1.4986, $F = 21.98_{1,49}$, $P < 0.001$) and between carbon and priority species richness (Fig. 4c; Regression, $r^2 = 0.275$, y = 0.006x + 0.792, $F_{1,49} = 18.59$, $P < 0.001$). Significant positive co-benefit relationships were also observed between carbon and overall amphibian abundance and between carbon and abundance of priority species (Fig. S3).

Discussion

There is debate as to the importance of secondary forests in the future of conservation in the tropics (Laurance *et al.*, 2012; Martin & Blackburn, 2014). On the one hand, across the tropics, degraded landscapes protect lower levels of biodiversity than primary forest (Brook *et al.*, 2006; Gibson *et al.*, 2011; Laurance *et al.*, 2012). But on the other hand, secondary forests
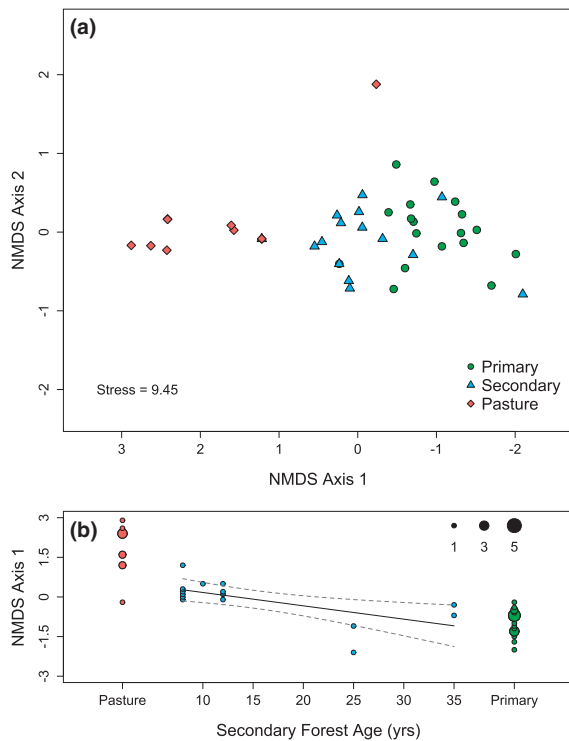
Figure 2 (a) Non-metric multidimensional scaling (NMDS) ordination of community assemblages among primary forest, secondary forest and cattle pasture. (b) NMDS axis 1 scores across habitat types, with a regression against secondary forest age. Dashed lines represent 95% confidence intervals.

retain significant biodiversity, especially in regions where the majority of primary forest cover has already been lost (Chazdon, 2008). Here, we focus on amphibian communities, which are the most threatened group globally, to identify the potential value of secondary forests that are recovering adjacent to primary forests in the Tropical Andes. We show that after three decades of forest recovery, amphibian communities become increasingly similar to those found in primary forest, regaining many threatened species. Furthermore, given that these secondary forests also recover much carbon, there are clear carbon–amphibian diversity co-benefits, suggesting important opportunities to promote the protection and creation of secondary forest to conserve threatened Andean amphibians.

Amphibian species and community recovery

Our analysis shows that secondary forests recover abundance, species richness and composition, and continue to accrue species as forests mature (see also Hernández-Ordóñez *et al.*, 2015). By contrast, cattle pasture contained an entirely different composition of species to primary forest and had much lower species richness. A single juvenile individual of *Gastrotheca nicefori* was found in cattle pasture, despite it being an arboreal species restricted to cloud forest (Trueb & Duellman, 1978), suggesting dispersal between forest patches even across seemingly inhospitable habitat. The

distinct change in species composition across habitats can be attributed to land use rather than distance, as confirmed by Mantel tests, and within secondary forest, time as abandonment is a clear predictor of increasing similarity to the overall primary forest community (Fig. 3a, b). While in some instances even young secondary forests can support communities of amphibians similar to those found in older secondary forests (Hilje & Aide, 2012), after several decades amphibian composition in advanced secondary forests was similar to old growth forests (Fig 2b; but see Hilje & Aide, 2012).

The recovery of forest structure over time, particularly canopy cover, can be a key factor in predicting amphibian species richness, abundance and composition because it serves to increase humidity and regulate temperatures (Herrera-Montes & Brokaw, 2010; Cortés-Gómez *et al.*, 2013; Scheffers *et al.*, 2014), as well as microhabitat availability (Harper *et al.*, 2005). Time is also required for species to spread to recovering forests from colonization nuclei, such as remnant forest patches. The rate of such colonization is dramatically reduced when distance to remnant forest increases (Gardner *et al.*, 2007b; Hilje & Aide, 2012). Because populations of primary forest species survive close by and connected to many of our secondary forest sites, we would expect them to recolonize rapidly provided the habitat met the specific biotic and abiotic requirements of a particular species. How increasing distance and isolation between primary and secondary forest would affect the rate of recovery is a frontier for research and would likely reduce rates of recovery and thus carbon–biodiversity co-benefits.

Recovery of priority species

Many priority amphibian species returned rapidly (25–35 years) in secondary forests (Fig. 3c, d), mirroring patterns for birds in the same study region (Gilroy *et al.*, 2014b). However, two priority amphibian species that we recorded in primary forest had yet to recolonize secondary forest. Many forest-dwelling amphibians only return to a habitat after sufficient recovery of the forest structure and floristic community (Rios-López & Aide, 2007; Urbina & Galeano, 2009), with some priority species likely to be more specialist in their ecological requirements than unthreatened generalists. This balance between priority species and generalists dictates recolonization dynamics over longer timescales (Heinen, 1992; Urbina-Cardona, Olivares-Perez & Reynoso, 2006). While we found that older secondary forest of 25–35 years recovery had similar species composition to that in primary forests (Figs 2b and 3b), the lack of two priority species suggests that to recover the full complement of primary forest species may take several decades to centuries or even that very mature secondary forest may persist as a 'novel community' with similar richness and abundance to an old growth forest, but with some key differences in species composition and structure (Aide *et al.*, 2000; Pascarella *et al.*, 2000; see also Chazdon, 2003; Lugo & Helmer, 2004 for vegetation and trees, respectively). Combined, this suggests that the most important carbon–biodiversity co-benefits
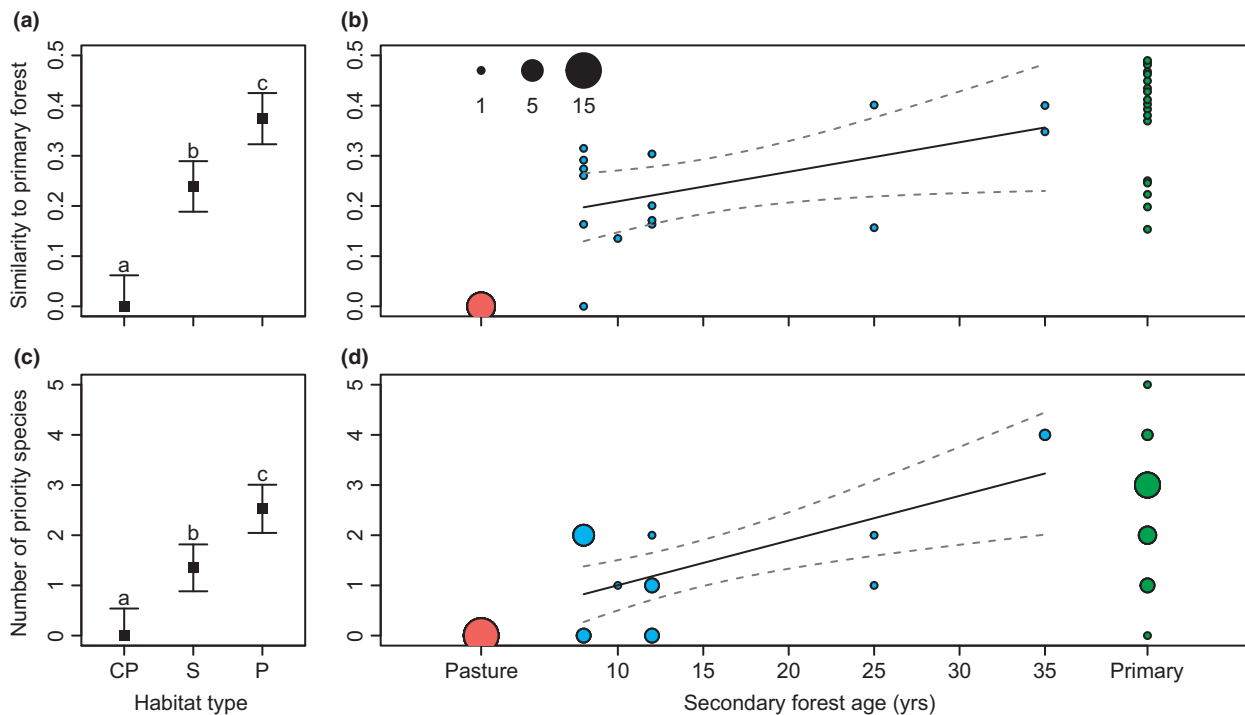
Figure 3 Mean transect-level similarity to primary forest community (a) across habitat types and (b) across habitat types with regression of secondary forest age. Mean transect-level priority species richness (c) across habitat types and (d) across habitat types with regression of secondary forest age. (a, c) Different letters indicate significance at $P \leq 0.05$. (b, d) Points are proportional to number of transects. Dashed lines represent 95% confidence intervals.

accrue only on decadal timescales (see below for further discussion).

Study limitations

All secondary forest sites were adjacent and connected to primary forest, which will have probably enhanced the rate of habitat and species recovery compared to isolated secondary forest patches (Pulliam & Danielson, 1991). Many pastures were also close to primary or secondary forest edges, and there could have been spillover benefits that enhanced their apparent biological value that would degrade with distance from edge (see above; Pineda & Halffter, 2004; Gilroy *et al.*, 2014a). Because we have only sampled in one region, other regions in the Tropical Andes could differ in the strength of biodiversity recovery (elsewhere there are similar rates of carbon recovery; e.g. Gilroy *et al.*, 2014b), and we urgently need similar studies elsewhere to confirm similar biodiversity patterns. In particular, while we found abundant amphibians in our study area, elsewhere in the Tropical Andes the rapid emergence of chytridiomycosis has depopulated many montane forest amphibian communities (Lynch & Grant, 1998; Ruiz & Rueda-Almonacid, 2008). Thus, new secondary forests in such areas may well lack amphibians and primary forests would be unable to act as sources for recolonization, likely reducing co-benefits in such areas.

Carbon and biodiversity co-benefits

Climate change and biodiversity loss are two of the largest challenges facing humanity (Barnett & Adger, 2007; Turner, Oppenheimer & Wilcove, 2009; Cardinale *et al.*, 2012), with an order of magnitude greater funding required to meet 2020 targets set by the Convention on Biological Diversity (CBD, 2011; McCarthy *et al.*, 2012; Waldron *et al.*, 2013). We found that carbon stocks in secondary forest and amphibian richness, composition and priority species are positively related (see also Strassburg *et al.*, 2010). Carbon stocks in secondary forests within this study region are also positively related to bird and dung beetle diversity (Gilroy *et al.*, 2014b), whereas carbon stocks in forest fragments in the Brazilian Atlantic are positively related to the diversity of priority trees (Magnago *et al.*, 2015).

Importantly, the marginal nature of land in our study region means that opportunity costs are low (Gilroy *et al.*, 2014b). This suggests that there are substantial opportunities to use carbon-based payments for ecosystem service schemes, such as ARR and REDD+, to fund the regrowth of tropical forests while additionally protecting important biodiversity. Such funds could be targeted to the most important areas for conservation action, including regions in which the majority of forest has been lost – where promoting secondary forest adjacent or close to remnants would likely offer the best potential to species recovery – to create corridors between protected areas that
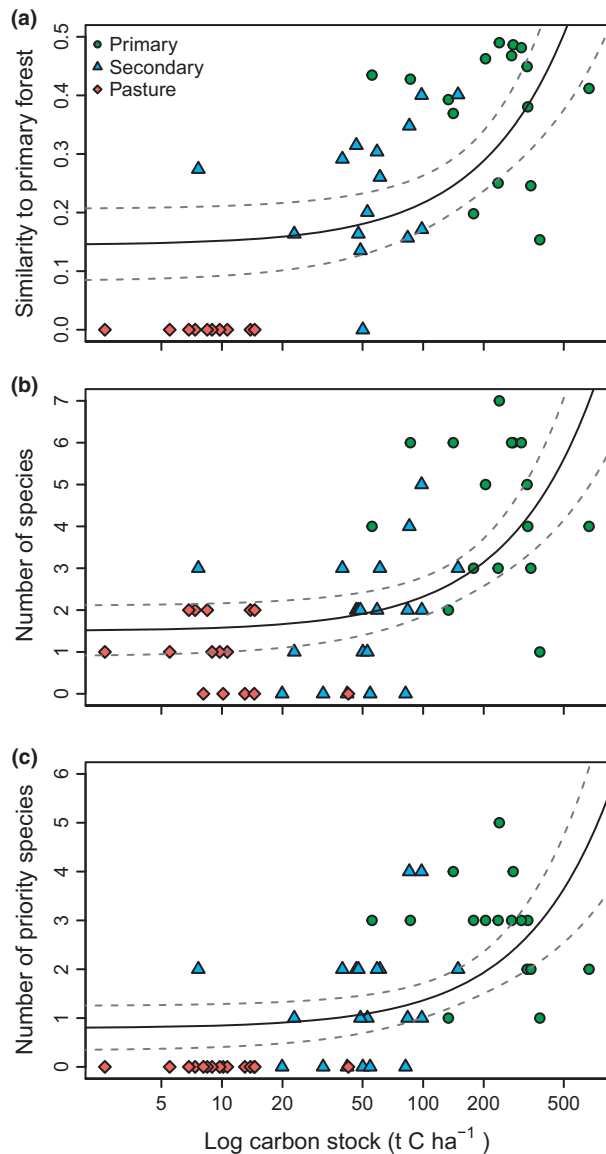
Figure 4 Carbon–amphibian diversity co-benefits across habitat types. Carbon stocks are plotted against (a) similarity to primary forest community, (b) species richness and (c) priority species richness. Black lines show linear regression models, dashed lines represent 95% confidence intervals.

will be particularly important under climate change (Beale *et al.*, 2013; Jantz, Goetz & Laporte, 2014; Lawson *et al.*, 2014; Virkkala *et al.*, 2014), or to buffer forest patches with high conservation importance from edge effects (Lehtinen, Ramanamanjato & Raveloarison, 2003; Cubides & Urbina-Cardona, 2011; Laurance *et al.*, 2011). Although intact forests must remain a conservation priority (Barlow *et al.*, 2007; Gardner, Barlow & Peres, 2007a; Gibson *et al.*, 2011), the massive coverage of selectively logged and secondary forest across the tropics, thought to soon overtake intact forests in area (Wright & Muller-Landau, 2006), exemplifies their impor-

tance for the future of biodiversity conservation and climate change mitigation.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Adapted from Gilroy *et al.* (2014b). Map showing the extent of habitat conversion in the Tropical Andes zone (a) and within our study region (red box, b), with our study site denoted by the white box. Colours 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. (c) The mapped distribution of farmland, contiguous forest and 400×400 m sampling squares in our study site. Colour schemes: green = contiguous forest, orange = farmland, dark green squares = primary forest samples, light blue squares = secondary forest samples, red squares = agriculture samples.

Figure S2. Non-metric multidimensional scaling (NMDS) ordination of community assemblages among primary forest, secondary forest and cattle pasture at the transect scale with (a) non-transformed data and (b) presence/absence transformed data.

Figure S3. Transect-level abundance of (a) all species (Regression, $r^2 = 0.403$, $y = 0.0207x + 2.4697$, $F = 33.14_{1,49}$, $P < 0.001$) and (b) priority species (Regression, $r^2 = 0.344$, $y = 0.020859x + 1.47702$, $F = 25.7_{1,49}$, $P < 0.001$) increases across the transition from cattle pasture through secondary forests (8–35 years) to primary forest, correlating closely with carbon stocks. Black lines show linear regression model, dashed lines represent 95% confidence intervals.

Table S1. Review of literature using WES (Web of Science; search strings; amphibians, frogs, with regenerating forest,

regrowth forest, secondary forest), in addition to existing knowledge from authors and bibliographies of papers found in the search. Studies on single species, outside of the tropics, or utilizing logged or degraded forests were excluded, to focus the review on amphibian community recovery in regenerating tropical forests. Information was then extracted regarding the study taxa, geographical region, altitude, land use, secondary forest age, utilization of a full habitat transition and analysis of carbon stocks.

Table S2. Coordinates of study plots.

Table S3. Analysis of similarity (ANOSIM) statistics between each habitat, using non-transformed, presence/absence and square root transformed data, abbreviations: CP, Cattle Pasture; S, Secondary forest; P, Primary forest.

Table S4. Mean abundance of species with standard error at each habitat type, with IUCN Red-list (conservation priority) status, abbreviations: CP, Cattle Pasture; S, Secondary forest; P, Primary forest.