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Research Article

How much potential biodiversity and conservation value can a regenerating rainforest provide? A 'best-case scenario' approach from the Peruvian Amazon.

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Abstract

The structure and underlying functions of the majority of the world's tropical forests have been disrupted by human impacts, but the potential biodiversity and conservation value of regenerating forests is still debated. One review suggests that on average, regenerating tropical forests hold 57% (±2.6%) of primary forest species richness, raising doubt about a viable second chance to conserve biodiversity through rainforest regeneration. Average values, however, likely underestimate the potential benefit to biodiversity and conservation because they are drawn from many studies of short-term regeneration and studies confounded by on-going human disturbance. We suggest that the true potential biodiversity and conservation value of regenerating rainforest could be better assessed in the absence of such factors and present a multi-taxa case study of faunal biodiversity in regenerating tropical forest in lowland Amazonia. We found that biodiversity of this regenerating site was higher than might have been expected, reaching 87% (±3.5%) of primary forest alpha diversity and an average of 83% (±6.7) of species estimated to have occurred in the region before disturbance. Further, the regenerating forest held 37 species of special conservation concern, representing 88% of species of highest conservation importance predicted to exist in primary forest from the region. We conclude that this specific regenerating rainforest has high biodiversity and conservation value, and that whilst preserving primary forest is essential, our results suggest that under a best-case scenario of effective conservation management, high levels of biodiversity can return to heavily disturbed tropical forest ecosystems.

Keywords: Habitat modification, multi-taxonomic, tropics, threatened species, secondary forest

Resumen

Las estructuras y funciones subyacentes de la mayoría de los bosques tropicales del mundo han sido afectadas por impactos humanos, pero el valor potencial para la biodiversidad y la conservación de estos bosques en regeneración sigue siendo un tema de debate. Un estudio sugiere que los bosques tropicales en regeneración conservan de media el 57% (±2.6%) de la riqueza de especies de los bosques primarios; lo que genera dudas sobre si existe una segunda oportunidad viable para conservar la biodiversidad a través de la regeneración de las selvas tropicales. Aquí destacamos que estos valores medios probablemente subestiman el beneficio potencial para la biodiversidad y la conservación porque contienen muchos estudios de regeneración a corto plazo y estudios donde los efectos de la regeneración se confunden con perturbaciones humanas en curso. Sugerimos que el verdadero potencial del valor para la biodiversidad y la conservación de las selvas en regeneración se podría evaluar mejor en ausencia de dichos factores y presentamos un estudio de caso multi-taxa sobre la biodiversidad faunística en un bosque tropical en regeneración en las tierras bajas amazónicas. Nuestros resultados muestran que la biodiversidad de este sitio en regeneración era significativamente más alta que la que se podría haber predicho, alcanzado una media del 87% (±3.5%) de la diversidad alfa de los bosques primarios y una media del 83% (±6.7) de las especies que se infirieron estar presentes en la región previas a la alteración. Además, el bosque en regeneración albergó 37 especies de especial importancia para la conservación, que representan el 88% de las especies de mayor importancia para la conservación predichas para bosque primario en la región. Concluimos que esta selva en regeneración en concreto tiene altos valores de biodiversidad y de conservación, y sugerimos que mientras preservar los bosques primarios es esencial, nuestros resultados apoyan la idea de que bajo el mejor escenario posible de gestión efectiva de la conservación podemos tener como objetivo volver a tener altos niveles de biodiversidad en ecosistemas de bosque tropical fuertemente alterados.

Palabras clave: modificación del hábitat, multitaxonómico, tropicos, especies amenazadas, bosque secundario

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Introduction

Human impacts have disrupted the structure and underlying functions of many of the world's tropical forests [1]. The Global Forest Resources Assessment [2] classifies only 36% of global forest cover as primary and shows that despite forest regeneration helping to reverse the overall trend of global forest loss in recent years, most forest loss still occurs in tropical regions, with a net loss of 12.3 million hectares per year [3]. According to Wright [4] this includes approximately 64,000 km^2 of tropical forest per year being deforested, and approximately 21,500 km^2 per year of natural forests regenerating on abandoned land. There is therefore a pressing need to determine the future biodiversity and conservation value of areas following tropical rainforest regeneration [5-7].

In this study the term regenerating rainforest refers to once-pristine or primary tropical forests that have undergone significant human impacts (including clear-cutting, heavy logging resulting in partial clearance, or substantial levels of selective logging) and subsequently regenerated to a state where a closed canopy has been re-established [8]. Regenerating forests can represent a number of types of original land use and modification with different potential values for biodiversity conservation; such as logged regenerating forests, secondary regenerating areas, once-cleared regenerating forest, and abandoned agricultural regenerating lands [8-11]. Although such human-modified ecosystems represent the majority of remaining tropical forest, their potential to provide important habitat for the conservation of rainforest biodiversity is contentious. Whilst some authors argue that the key conservation priority is to protect primary forest [11-13], others suggest that regenerating and secondary forests will become increasingly important as human populations in tropical countries increase and primary forest is converted to agricultural land and then abandoned to regenerate [14-20].

Chazdon et al. [15] reviewed 51 studies evaluating the potential of tropical secondary forests for biodiversity conservation and found that the average proportion of primary forest animal species richness detected in regenerating forest in the tropics was 57% (±2.6). Considering only the 12 studies with at least 20 years of regeneration, the average value of primary forest species found was 66% (±5.4). Barlow et al. [21] found similar levels and showed that regenerating secondary forests (14-19 years old) within Brazilian Atlantic forest areas, held on average, 59% of primary forest species richness (including data from vertebrates, invertebrates and plant groups). Individual studies have shown that regenerating forest can hold higher levels of biodiversity; Edwards et al. [22], for example, found that twice-logged forests in Asia sustained 75% of primary forest species of birds and dung beetles. Despite the notable biodiversity losses indicated by the average values reported above, regenerating forests could still possess the potential to sustain future levels of biodiversity comparable to that of primary forest habitats [18], particularly given the premise that biodiversity will continue to increase over time as forests continue to regenerate [4,15].

Gardner et al. [23] suggest that the current lack of agreement on the conservation and biodiversity value of regenerating forests arises largely because information on how well tropical forest biodiversity can recover from devastating environmental change is often difficult to determine and interpret. We agree, and highlight four key reasons for the controversy and therefore on where conservation efforts should be focused [24]. First, because many of the regenerating tropical forests studied continue to experience human impacts, studies have measured both the impact of the original disturbance and the impacts of any ongoing disturbance (for example hunting or extraction of timber) that limit recovery [9]. Second, many studies are conducted too soon after disturbance: the types of forest evaluated in the majority of reviews [11-15,17-20] are relatively young areas of regenerating forest (< 15 years), too young for detecting species that take far longer to recolonize an area [15]. Third, a key point raised by some critics is that there is a bias towards examining changes in overall species richness patterns, and that overall richness alone may not be the best measure of biodiversity value from a conservation perspective (*e.g.* [7]). Anand et al. [14] suggest the potential dominance of species of low conservation concern in species richness measures and show that two communities can have altered community structures but display similar richness values. One possible way to tackle this issue is to look specifically at species of key conservation concern or groups that have been highlighted as key indicators, instead of simply analysing estimated overall richness values of communities [25,26], which provide little indication which conservation targets are present and which absent. Fourth, many studies only investigate the response of a single taxon to regeneration [27], providing limited insight into the general patterns in a wider biodiversity context.

In this study we assess the potential conservation value of a regenerating tropical rainforest in one of the world's most biodiverse and important conservation areas, while controlling for the above difficulties. Our case study focuses on a regenerating study site within the Manu Biosphere Reserve, a UNESCO World Heritage Site designated to protect the globally important Amazon rainforest in and around Manu National Park, SE Peru. Within this area we specifically chose a site that had been effectively protected from confounding on-going human disturbances and that had a long regeneration time since the initial disturbance (>30 years). We focused on species richness values to compare with the majority of studies that had measured biodiversity value in this way, but we also assessed specific groups of indicator species and species of conservation concern in order to place these species richness values in the context of conservation value. Finally, we looked at multiple taxa to test the generality of any observed patterns. Our goal was not only to assess the actual value of such regenerating forest for conservation in Manu, but also propose this as a case study to assess the potential value of regenerating forest as a conservation tool more generally.

We believe this is the first multi-taxa study to assess the potential conservation value of a regenerating rainforest in the Amazon without the key potentially confounding factors of young regenerating forest age and on-going human disturbance. In this case study we address three key questions about the potential biodiversity and conservation value of regenerating tropical rainforest : 1. How does the observed species richness of the regenerating rainforest study site (alpha diversity) compare with measured alpha diversity of nearby primary forest locations? 2. How does the observed species richness (alpha diversity) of the regenerating rainforest study site compare with estimated richness of the habitat prior to disturbance? and 3. How do the numbers of key indicator species and species of special conservation concern (globally threatened and near-threatened species) compare between the regenerating rainforest study site and those predicted to have existed before human disturbance?

Methods

Choice of study site

We chose the regenerating rainforest area for this study because it had a known human disturbance history and was located in a well-understood geographic context, in close proximity to a large protected area network. The study was carried out at the Manu Learning Centre (MLC) research station, owned and operated by conservation NGO the Crees Foundation, in the Peruvian Amazon (71°23'28"W 12°47'21"S; Fig. 1). The study site lies within the cultural buffer zone of the Manu biosphere reserve and consisted of ~800 ha of regenerating lowland tropical forest accessed by a 20 km trail system and covering an altitude range of 450-740 m asl. The forest had historically experienced various types of major human disturbance, such as selective logging (ceased mid 1980s; ~332 ha), partial clearance for small scale (largely subsistence) agriculture (ceased ~1980; ~183 ha) and complete clearance by felling and conversion to large scale agriculture (ceased ~1970; ~293 ha). This history was determined by two of the authors visiting the site to visually inspect it and by consulting local guides with expert local knowledge of historic land-use of the study site. Both approaches identified consistent points that were marked as the boundaries of the different disturbance histories, in order to calculate the respective areas of disturbance.

The study site was directly bordered to the north by areas of small-scale agricultural land and areas of current logging activities, but had been strictly protected from hunting and other negative human impacts since 2002. Beyond the study site to the west (~9.5 km) lies the core area of the Manu National Park, over 1.5 million ha of protected tropical forest. To the east (~1.8 km) of the reserve lies the second largest protected area in the biosphere reserve, the Amarakaeri Communal Reserve (a 402,335 ha forest reserve, created in 2002). By the end of this study, the site had been regenerating for 30-50 years, so that the whole area was once again covered by closed canopy tropical forest and had been strictly protected from ongoing human disturbance for 11 years. Ferraz et al. [28] have recently proposed an ecosystem condition scoring system for tropical forests that provides an objective way to categorise sites based upon the following features of past landscape dynamics and present landscape structure: forest age (used as a surrogate for forest integrity); proximity to nearby forest (a surrogate of local habitat connectivity); the proportion of surrounding area covered by forest (to represent interior-edge); and the size of the forest patch (forest contiguity). Using this system our study site would fall within the highest category (a score of 12, with >30 yrs of regeneration time, in close proximity to large swathes of primary protected areas, and with an area over 800 ha in size). It therefore is an ideal site to investigate the potential biodiversity and conservation value of what we will term a “best-case scenario” for regenerating rainforest, without the confounding effects of on-going human disturbance. This allows us to examine the true value that a regenerating rainforest can have under successful conservation management, designed to take advantage of and create the best of circumstances.

Choice of study groups

We measured the biodiversity of four key taxonomic groups (amphibians, birds, medium-large mammals and reptiles), chosen because they are of well-known conservation importance, have been identified in some cases as key indicators, and most importantly, have been well-studied locally at both the regenerating forest study site and primary forest sites in the Manu region. Specifically, more than 70% of the world's amphibian species are thought to be in decline [29], and because habitat destruction and fragmentation are among the leading causes of this global decline [30-32], it is important to understand how amphibians respond to regenerating landscapes. Birds, in particular understorey guilds, are sensitive to environmental changes and habitat fragmentation within neotropical rainforests [33], and are likely another useful group for discovering how biodiversity responds to rainforest regeneration. Medium–large mammals are relatively understudied within tropical forests [34] and play a key role in forest ecosystems, directly through seed dispersal [35] and prey population control or indirectly by helping to maintain assemblages of other faunal groups [36, 37]. Reptiles are a vastly understudied group both globally and within Amazonia, despite acting as important meso-predators within many ecosystems [38].

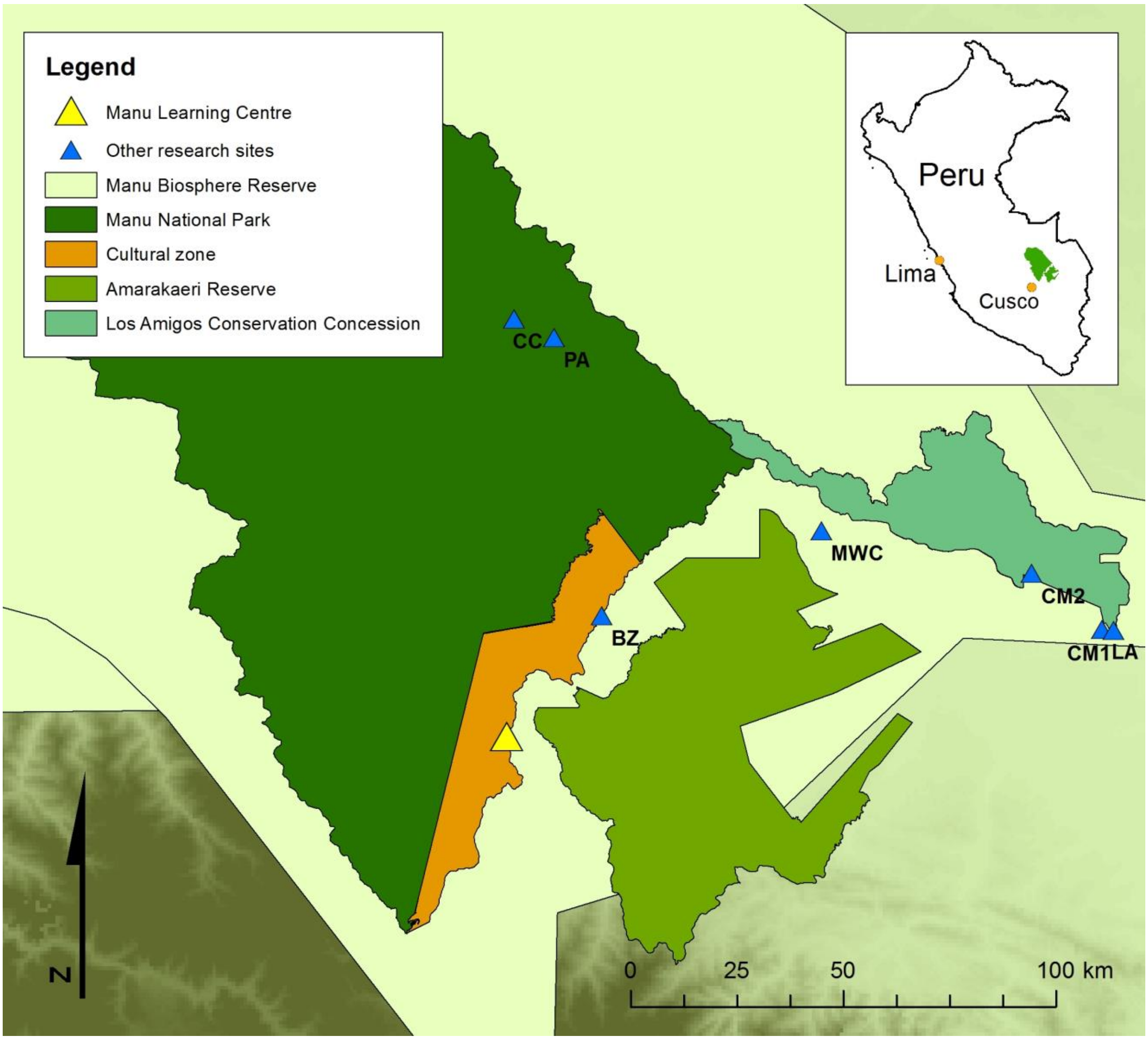

Fig. 1. Protected areas in SE Peru, the relative location of field sites mentioned within the study area, and context map within Peru. Site acronyms: LA = Los Amigos, CM1 = Centro de Monitoreo 1, CM2 = Centro de Monitoreo 2, CC = Cocha Cashu, PA = Pakitza, MWC = Manu Wildlife Centre, BZ = Bonanaza and MLC = Manu Learning Centre. Shape files gathered from The World Database on Protected Areas.

Comparing observed richness (alpha diversity) in the regenerating forest and primary forest

Many studies comparing biodiversity rely on calculations of estimated species richness based on relatively short periods (a few months) of intensive, standardised surveys at individual sites [39, 40]. Biodiversity estimators have many advantages, but they can only produce estimates of the number of species present and cannot provide information on which individual species of conservation importance are likely to make up the overall species richness. To compare the conservation value of regenerating forest to primary forest, we needed to compare actual biodiversity in terms of the alpha diversity recorded in regenerating forest to that of primary forest. Species richness estimators also require at least some standardised information on the frequency at which each individual species has been observed (*e.g*., whether a species has been seen once, twice or more etc). The available data for potential primary forest comparison sites in the Manu area showed that although many sites have richness data in the form of overall lists of species observed, there was little standardisation of available abundance data among different primary forest sites, making the calculation of comparable species richness estimates impractical. We therefore selected observed species richness as the most appropriate measure for comparing the biodiversity of regenerating and primary rainforest. Because the majority of previous studies assessing the importance of regenerating forest for biodiversity have based comparisons on species richness, it was desirable to do the same to make the results of our study comparable to such previous work. Using observed values will provide a conservative estimate, as they will likely underestimate the true value of such a biodiverse region, despite intensive survey efforts over a number of years.

To assess the alpha diversity of the regenerating forest study site, we used a combination of intensive field work surveys and long-term data that had been recorded at the site since its creation as a protected area in 2002. The long-term data consisted of relatively comprehensive lists of birds and medium to large mammals, but depauperate lists of amphibians and reptiles, partly due to the bias and interests of previous researchers and visitors towards birds and mammals, but also due to the fact that visitors often walk diurnally instead of nocturnally, when many amphibians and reptiles are active. More intensive survey data were collected between August 2011 and February 2013 in order to maximise the data coverage and detect as many species as possible within the regenerating forest study site. Birds and mammals were surveyed through early morning line transects (*e.g.* [34, 41]), and for birds mist nets were also used (*e.g.* [42]). Camera traps were used for medium to large mammals and game birds (*e.g.* [43]), and amphibians and reptiles were surveyed using nocturnal visual encounter transects (*e.g.* [44, 45]), pitfall traps (*e.g.* [44]), and leaf litter plots (*e.g.* [45, 46]).

Survey efforts during the intensive phase were: for mist netting 3,180 net hours (10m long x 3m high), providing 1,143 captures; 227 early morning bird/mammal transect hours by teams of two observers (covering 213.72 km along 19.8 3km of trail – 11 transects comprising 118 transect surveys); 4,860 camera trap days from 10 survey sites; 754 observer hours of nocturnal herpetological transects; 2,060 pitfall array days, and 30 leaf litter plots (5m^2). Uncertain or doubtful records (from the less intensive long-term data collection phase) were excluded from the overall site species lists unless species presence could be confirmed during the intensive data collection phase. Incidental records outside of systematic survey times were added to each of the overall species lists. The result was a species list for each taxonomic group that recorded all species detected in the regenerating tropical forest study site over a 10-year period. This provided the data for assessing observed species richness in regenerating tropical forest.

For data on primary forest biodiversity to which we could compare the data from our regenerating forest site, we reviewed published inventories and identified all tropical forest survey sites within 100 km of the regenerating forest study site that had detailed species lists and significant amounts of research conducted at them in the past 10 years. As with the regenerating forest site, the data from each comparison site were generated from a similar combination of long-term biodiversity records supplemented by intensive survey efforts during more focused studies. In general, because the primary forest sites had longer spans of data collection by more scientists, their species lists were presumably at least as comprehensive as the regenerating forest sites (see Appendix A for a detailed description of comparative sites and respective survey efforts). Use of observed species richness (rather than estimated species richness, which was not possible due to insufficient published data on the frequency of species records at the comparison primary sites) should therefore provide a conservative test of the relative biodiversity and conservation value of this regenerating forest compared to nearby primary forest sites.

Estimating overall richness of the study sites regional area prior to disturbance

Although the primary forest comparison sites are the best studied sites available in Manu, we considered the possibility that the species lists available for the primary forest comparison sites might not be exactly comparable to those of the regenerating site, due to local variations in elevation, habitat types, and the likelihood that some species remain undetected at each site despite comprehensive monitoring efforts. We therefore also used existing ecological and distributional information on each individual species to assess whether species known from the general Manu area were likely to have existed in the regenerating forest area prior to any human impact (*i.e.,* we estimated species lists of primary forest habitats with conditions similar to the regenerating forest study site). We started with the conservative assumption that current records of observed species from the regenerating forest indicated that the species was likely present in the area before any anthropogenic effects occurred. This assumption seemed reasonable as most generalists found after human disturbance were likely there prior to the disturbance, because natural disturbances (such as large tree fall events induced by extreme weather) often creates opportunities similar to those created by humans, and species that had re-colonized the regenerating site from nearby source populations were likely to have existed there before disturbance. These assumptions allowed our results to act as conservative estimates of original biodiversity at the regenerating site.

To the list of the regenerating forest records we added all species that were known from the general Manu area (the sources of these lists are described in Appendix B). We then edited the primary forest lists to omit species that occurred outside of the altitudinal range of the regenerating study site and bird species strictly associated with large water bodies (*e.g.* oxbow lakes), as there were no such water bodies in the regenerating site. This kept the focus specifically upon forest-associated species within an expected altitudinal range. The result was a primary forest species list for each taxonomic group that included all species estimated to have occurred in the regenerating forest area before human disturbance.

To produce the primary forest comparison lists, we obtained information from the International Union for Conservation of Nature (IUCN) Red List for each species with known distributions in the Manu area, to provide distributional data on all species (including species of least conservation concern) in the target taxonomic groups [47]. Altitudinal ranges were noted along with information available from the range maps provided by IUCN. These range maps were used to assess whether the species distributions (a) were included directly within the range of the regenerating forest site and therefore automatically included, or (b) were within 50 km of the site or within 100 km of the site depending on taxonomic group. If an amphibian species was within 50 km of range then we assumed that it could have been present if there were no significant physical barriers (such as major rivers or mountain ranges) between the known distribution and regenerating site. For mammals and birds the cut off figure was 100 km due to their ability to move over greater distances, but again special physical features such as rivers were considered for each case.

Other resources, outlined below, were then used to aid decisions in any cases that were difficult to determine from this initial information. The predicted bird lists were confirmed with the aid of information in

Schulenberg et al. [48], which is the most authoritative and up to date source on bird distributions in Peru. The amphibians were confirmed by information from AmphibiaWeb [49], one of the most up to date resources for amphibians globally, and the reptiles from The Reptile Database [50], another updated global online database. This part of the analysis estimated the historic presence of individual species in the regenerating rainforest study area prior to disturbance. The method generally produced clear outcomes for species in the majority of study groups. However, due to lack of available information on the reptiles, we felt that species presence in the generated list was fairly arbitrary and more dependent on the quality (or lack) of data available for each species, rather than reflecting whether the true distribution included the regenerating study site. We therefore chose not to use this approach for reptiles.

Choice of species of special conservation concern / indicator groups

In order to look beyond overall species richness levels to assess the conservation value of the regenerating forest study site, we assessed in more detail the occurrence of specific, well-known indicator groups for good habitat quality and species of special conservation concern (defined for this study as globally threatened or near-threatened species, according to the IUCN Red List of threatened species, [47]). This avoided the potential problem of regenerating forest species richness values that might be elevated by including generalist or common species. Since previous research has found that at-risk species can perform well as indicators themselves [25], and as no more specific list of indicator species was available, we focused on this group for mammals. For birds we used the indicators of good quality habitat for Southern Amazonian lowland tropical forest, as described by Stotz [51] (see Appendix C). Amphibian indicators of good quality habitat were assessed by focussing on the family Craugastoridae, containing the genus *Pristimantis* (previously *Eleutherodactylus*), a key indicator group identified by Pearman [26]. Leaf-litter and understorey dwelling herpetofauna lend themselves well to biological conservation studies, as they are abundant in neotropical forests and are relatively easy to sample [26, 52, 53] (see Appendix D). Because no suitable list of indicator species of good habitat quality for reptiles has yet been proposed, reptiles were excluded from this section of the analysis.

Results

Observed richness in the regenerating forest and comparable primary forest sites (alpha diversity)

We recorded high levels of biodiversity in the regenerating rainforest study site, with a total of 570 species detected in the four target groups. These observed totals included 60 amphibian species, 406 bird species (species associated with forest habitat, excluding those associated with open water bodies), 38 medium-large mammal species (excluding bats and small ground mammals) and 66 reptile species (see Appendices E-H for full species lists). Compared with alpha diversity of nearby primary forest sites, we found that alpha diversity of the regenerating forest site was 81% for amphibians, 84% for birds, 80% for medium-large mammals, and 100% for reptiles (an average of 87% ±3.5; Table 1).

Three sites, Cocha Cashu, Los Amigos and Pakitza, had more developed amphibian and reptile lists compared to the 60 and 66 species, respectively, of the regenerating site (Fig. 2). The most detailed medium–to-large mammal inventories from primary sites close to the regenerating rainforest site, Cocha Cashu-Pakitza and Los Amigos, contain 47 and 48 species respectively, compared to the 38 found in the regenerating forest. The forest-associated bird inventories from primary sites close to the regenerating site were: Cocha Cashu (454 species), Manu Wildlife Centre (501 species) and Los Amigos (499 species), compared to the 406 species of the regenerating site.

Table 1. Species richness in the regenerating tropical forest (alpha diversity) site compared to primary forest sites. Primary forest site abbreviations; CC = Cocha Cashu, LA = Los Amigos, MWC = Manu Wildlife Centre, PA = Pakitza. Values in brackets represent the percentage of the species present at the regenerating forest site (MLC).

Taxa	Primary forest sites used to determine average alpha diversity from primary forest					*Alpha diversity at the MLC*
	CC	*CC-PA*	*LA*	*MWC*	*PA*	
Amphibians	78 (77)	-	82 (73)	-	63 (95)	60
Birds	454 (89)	-	499 (81)	501 (81)	-	406
Mammals	-	47 (81)	48 (79)	-	-	38
Reptiles	64 (103)	-	75 (88)	-	60 (110)	66

Comparing alpha diversity of regenerating forest to inferred species lists of the region

When inferred species lists were estimated for the regenerating forest area, 74 amphibian, 563 bird and 40 mammal species were estimated to have existed prior to human disturbance (Table 2). There were insufficient distribution data available for reptiles to make a reliable presumption for this group. If the three taxa had been sampled to complete saturation (which is almost impossible in most tropical forests) at the MLC, this would suggest the regenerating forest site contains 81% of amphibians, 72% of birds and 95% of medium-large mammals that may have existed in primary forest before human disturbance (Table 2). Overall, this represents an average value of 83% (±6.7) of species from inferred species lists from the region detected within the regenerating forest site.

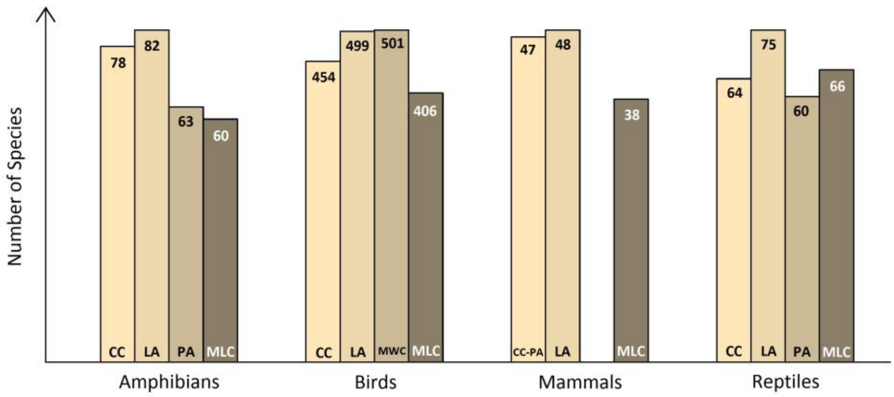

Fig. 2. Species richness in the regenerating tropical forest site (MLC) compared to primary forest sites. Primary forest site abbreviations; CC = Cocha Cashu, LA = Los Amigos, MWC = Manu Wildlife Centre, PA = Pakitza.

Table 2. Number of species in the regenerating forest of the MLC compared to inferred species lists for the region and observed primary forest sites. Primary forest site abbreviations; LA = Los Amigos, CC = Cocha Cashu, PA = Pakitza, MWC = Manu Wildlife Centre.

Taxa	Alpha diversity at the MLC (as % of inferred regional species lists)			Inferred regional species lists			Average species richness from primary forest sites	Species richness of MLC as a % of species richness at primary forest sites	Primary forest sites used to determine average primary forest species richness
	Total	*Indicators*	*Conservation concern*	*Total*	*Indicators*	*Conservation concern*			
Amphibians	60 (81)	13 (72)	-	74	18	-	74	81	LA, CC, PA
Birds	406 (72)	30 (86)	27 (87)	563	35	31	485	84	LA, MWC, CC
Mammals	38 (95)	-	10 (91)	40	-	11	48	80	LA, CC-PA
Reptiles	66	-	-	-	-	-	66	100	LA, CC, PA

Comparing key species of conservation concern / indicator groups from the regenerating forest with those of primary forest

Overall, an average of 84% (±4.1) of indicator species and species of conservation concern for the region were detected within the regenerating forest site. Thirteen medium-large mammal species of special conservation concern (threatened and near-threatened species) are known from the Manu region (Appendix I). Range data and ecology suggested that 11 of these species could have existed before human disturbance at the regenerating forest study site (Table 2) and of these, we recorded 10 species (91%) in the regenerating forest. The only species not recorded was the pacarana (*Dinomys branickii*). Therefore, we found that the regenerating forest held almost all mammal species of high conservation concern that could have existed prior to disturbance in the study area. Of the 36 bird species of special conservation concern in the Manu region, range data and ecological information suggested that 31 species could have existed in the regenerating forest prior to disturbance. Of these, 27 species (87%) were recorded within the regenerating forest site (Appendix J). The scarlet-shouldered parrotlet (*Touit huetii*), the green-thighed parrot (*Pionites leucogaster*), the cerulean warbler (*Dendroica cerulea*) and the black-and-white tanager (*Conothraupis speculigera*) were the four threatened/near-threatened species not recorded. In total, we found 37 bird and mammal species of special conservation concern (threatened and near-threatened species) in the regenerating forest, representing 88% of the 42 species estimated to be present before human disturbance.

Of 40 lowland tropical forest indicator bird species (for high quality habitat) known from the region, 35 were estimated based on range data and ecological information to have existed before human disturbance at the regenerating forest site (Appendix C). Of these 35 species, 30 (86%) were recorded at the regenerating forest site. The Amazonian barred woodcreeper (*Dendrocolaptes certhia*), the ruddy spinetail (*Synallaxis rutilans*), the banded ant bird (*Dichrozona cincta*), the striated ant thrush (*Chamaeza nobilis*) and the red-crowned ant-tanager (*Habia rubica*) were the five indicator birds not yet recorded.

Of the 23 species of Craugastoridae (indicator amphibians) found within the lower Manu region, we presume that 18 could have existed before human disturbance at the regenerating forest site (Appendix D). Thirteen

(72%) of these species were recorded at the regenerating study site. *Oreobates cruralis, Pristimantis diadematus, P. mendax, P. ventrimarmoratus* and *Strabomantis sulcatus* were the five species not recorded at the regenerating site (Table 2.).

Discussion

We report what we believe is the first multi-taxa case study to assess specifically the potential conservation value of a regenerating rainforest study in the Amazon, in the absence of the key potentially confounding factors of young regenerating forest age and on-going human disturbance [9]. We detected an average species richness value of 87% (±3.5) of alpha diversity found in primary forest areas and an average value of 83% (±6.7) of the inferred species lists from the region. This included 88% (37 out of 42) of the species of highest conservation concern. Our assessment of the actual biodiversity and conservation value of this regenerating tropical forest therefore suggests that high levels of vertebrate species richness could be found in areas of regenerating forest, particularly forests that score highly on the ecosystem condition scoring system proposed by Ferraz et al. [28]. Our results also show that the high levels of biodiversity found within a regenerating forest study site need not be dominated by generalist species, but can contain high levels of key indicator species and species of conservation concern.

We suggest our results are likely to be conservative estimates of the biodiversity value of regenerating forest. Because it would be unlikely within such a diverse and species-rich landscape to have detected the presence of all species, our comparisons identify only the minimum biodiversity value of the regenerating forest. For example, five of the mammals not found at the regenerating site but found at comparison primary sites are primates, at least one of which (the pygmy marmoset, *Cebuella pygmaea*), is restricted to lower elevations and likely absent due to physical geographic barriers *(e.g.* the Manu river) rather than the site's regenerating status. The giant river otter (*Pteronura brasiliensis*) is a species restricted to low-lying areas with oxbow lakes, a feature not found along the Alto Madre de Dios river (location of the regenerating forest site) but a common feature along the Manu and Madre de Dios rivers (primary forest comparison site locations). Also, the two mammals presumed to have once existed that remain undetected so far are particularly cryptic species: the silky pygmy anteater *(Cyclopes didactylus)* and the pacarana *(Dinomys branickii).* Both are secretive and inconspicuous species that are easily overlooked and evade detection. It is quite plausible that they do exist at the MLC but have thus far not been recorded. Similarly, considering our indicator amphibian group, three species found at the regenerating site could not be identified (*Pristimantis* sp1, sp2 and sp3). It is quite possible that they are variations of *P. diadematus*, *P. ockendeni* and *P. ventrimarmoratus*, or even species new to science, which would again suggest that our results are conservative. Finally, because two of the four threatened/near-threatened bird species not recorded at the regenerating site are migratory species and are only potentially present at the site for part of the year, they may have been overlooked. The cerulean warbler is a patchily distributed species absent from many primary forest areas, and since the regenerating study site is at the lower edge of its altitudinal range it may be absent for reasons not linked to the area's status as regenerating forest. As a result the 87% occurrence rate of bird species of conservation concern is also likely a conservative estimate of species of conservation interest.

Our results from this best-case scenario are higher and more promising for future biodiversity conservation than average-value approaches of assessing regenerating rainforest biodiversity (Fig. 3). Therefore, suggesting that a large proportion of the original, primary forest vertebrate species richness might be well conserved in regenerating rainforests that score highly under the ecosystem condition scoring system [28], especially considering that the study site location is situated between two large protected areas of largely primary tropical forest, one of the most important factors related to high levels of biodiversity [54, 55]. Recent reviews have shown average values of regenerating rainforest species richness to be 59% [21], 57% [15] and 68% [15] of primary forest biodiversity, but most of these studies have confounding effects of on-going disturbances and a short regeneration period, which may have depressed average biodiversity levels.

We suggest that the type of best-case scenario adopted here should be a focus for further research using a replicated study design, to determine the potential of regenerating study sites that score highly under the ecosystem condition scoring system [28], in the absence of on-going human impacts.

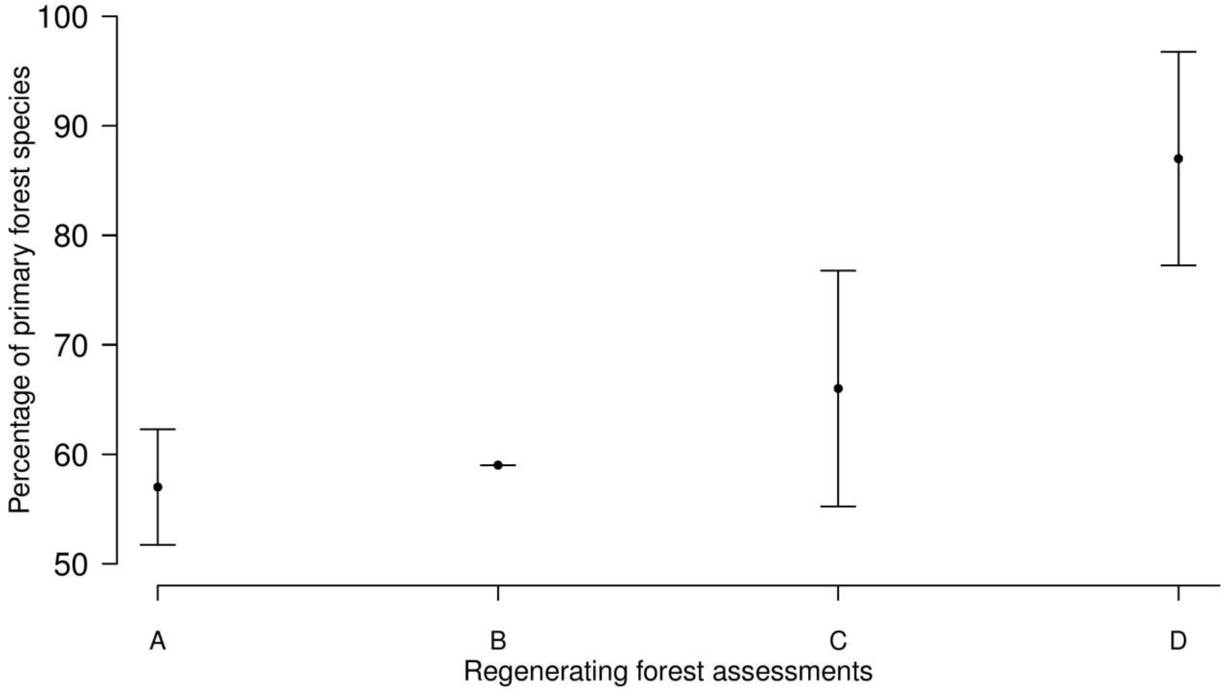

Fig. 3. The overall percentage of primary forest species detected within regenerating forests from two previous papers (A-C), compared to the values presented within this study (D). Where appropriate data are available, 95% confidence intervals are included. The assessments included are: A = Chazdon et al. [15], containing data from invertebrates and vertebrates from regenerating forests aged 1-100 years; B = Barlow et al. [21], containing data from invertebrates, vertebrates and plants from regenerating forests aged 14-19 years; C = Chazdon et al. [15], containing data from invertebrates and vertebrates from regenerating forests aged 21-100 years; and D = data on amphibians, birds, mammals and reptiles from regenerating forest aged 30-50 years, the field site sampled within this study.

More generally, our findings are consistent with the work of Dunn [56] who found that richness for ants and birds could be predicted to resemble that of primary forest after roughly 20-40 years of regeneration following abandonment. We also found this pattern for birds, and show that similar high levels may be true for other taxa, including amphibians, medium–to-large mammals, and reptiles. Our results are also consistent with the patterns observed by Dent and Wright [5] who reviewed 65 studies that compared the level of similarity between primary and regenerating areas, and found that similarity was higher with increasing age of the regenerating areas and when they were contiguous to primary forest. The location of the study site and the types of surrounding forest are vital to the pace of recovery and the composition of regenerating areas [57]; along with other important factors including fragment size, the distance to contiguous primary forest patches, and the scale of past disturbance [58-60]. However, on-going habitat disruption, such as hunting and forest exploitation, have been shown as the strongest predictors of declining reserve health, and a failure to halt further degradation could increase the likelihood of serious biodiversity loss [61].

The use of inferred species lists is only feasible for relatively well-studied groups and at the very least, basic distributional and altitudinal information is needed. For birds and mammals this was relatively straightforward and for amphibians slightly more complex, but for the reptiles this proved unfeasible. Böhm et al. [38] emphasise the need to discover more about the status, distribution and ecology of reptiles, particularly within tropical forest regions. This method of estimating species presence, however, did allow comparison of regenerating site richness values with inferred species lists for primary forest, and has potential as a useful and cost effective way of assessing biodiversity value of regenerating forest for sites when information from nearby primary forest sites is unavailable. As is common in previous efforts at assessing conservation value of regenerating forest, we used species richness levels for comparative analysis. It would have been desirable to use detailed information on abundance and community structure, but this level of detail was not available from many of the primary control study sites. Dunn [56] found that community composition can take longer than species richness to resemble the original state found within primary areas. Nevertheless, we were still able to show that regenerating forest holds high levels of key conservation species and species recognised as indicators of good quality habitat. Richness levels in our study are therefore not dominated by generalist species or species associated with disturbed habitats, as has often been suggested [5, 7, 14, 57].

It should be noted that although biodiversity assessments are often based upon estimates of species richness, such estimates often use one or a small number of survey techniques that only target specific subsets of a community over a relatively short timeframe. This is certainly useful where rapid assessments are necessary and survey effort can be controlled for in detail [62,63], but it does not allow for a detailed representation of the overall biodiversity at the sites, as provided by well-developed species inventories from intensively surveyed field sites over a number of years. Not only do these provide a more complete and detailed representation of biodiversity, but they can also be a very cost effective form of assessing sites that have already been well-surveyed by conservation researchers [62,63].

Implications for conservation

In conclusion, we suggest that case studies like ours, which focus on best-case scenarios for regenerating rainforest, and avoid confounding effects of on-going disturbance and short regeneration times, could be a clearer way to assess the potential biodiversity and conservation value of regenerating tropical forests in the best of cases. Such an approach would avoid the problems of relying on average values from a number of studies. Which, if the aim is to assess long term conservation value of well-protected regenerating rainforest, are likely to be confounded by on-going disturbance, isolated from contiguous primary forest, and have shorter regeneration periods. Although our results highlight a high potential of "best-case scenario" regenerating areas to conserve biodiversity, they also show that primary rainforest still holds higher levels of biodiversity and is of the utmost importance in safeguarding the future persistence of species potentially not found within regenerating forests. Nonetheless, we suggest that effective protection and management of regenerating rainforest could offer a second chance to conserve and support species biodiversity and wildlife of high conservation value. With the majority of the world's remaining tropical forests in various states of regeneration following human disturbance or destruction, our results are encouraging, in particular for those areas scoring highly under the ecosystem condition scoring system [28], and emphasise the potential value of regenerating rainforest areas to buffer the pressure of deforestation and habitat alteration on remaining primary tropical forests.

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We confirm that this work has no financial or non-financial conflicts of interests. This study has adhered to strict ethical guidelines, as set out by the permit issued by the Ministerio de Agricultura of Peru; Permit Number 'Codigo de Tramite': 25397; Authorisation Number 'Autorización No.' 2904-2012-AG-DGFFS-DGEFFS. When handling animals in the field codes of good practice were strictly adhered to and the systematic cleaning of tools and equipment was carried out.

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Appendix A. Comparative study sites (with references)

The existing primary forest field sites used as a comparison to herpetofaunal levels found at the Manu Learning Centre (MLC) were from Cocha Cashu, Pakitza and Los Amigos. Herpetological work at Cocha Cashu consisted of 395 person days [1-3], Pakitza, 286 person days [3], through eight field visits between 1987 and 1993 for project BIOLAT [4] and the Los Amigos list was developed from 711 person days between 2001 and 2007, with seven sampling periods and a variety of nocturnal survey methods, including visual encounter surveys, leaf litter plots and pitfall traps. Just like the herpetological research at the MLC (consisting of ~300 person days) all of these studies were conducted in both wet and dry seasons. Cocha Cashu is one of the richest and most well studied sites in the Amazon basin, in which bird and mammal research began in 1973 [5-7]; and the mist netting data for example, has gathered over 5000 captures representing over 260 species. Los Amigos is one of the most active research stations in the Amazon [8], established in 2000 with over five years of intensive mammal studies; including camera trapping, censuses, incidentals, trapping and interviews [9, 10] and has a particularly well-developed bird list [11, 12]. Mammal field work has also been conducted at a tourist lodge known as Bonanza, consisting of diurnal line transects, making up 310 records from 12 three km transects. This resulted in a total of 62 standardised surveys and 186km of trails walked and a further 84km walked from non-standardised surveys. Medium-large mammal lists therefore included combined field data from Bonanza, Cocha Cashu and Los Amigos, and bird lists from Cocha Cashu and Los Amigos.

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Appendix B. sources for generating the primary forest predicted diversity lists (with references)

The sources for generating the primary forest base lists and distributional data were as follows: the baseline primary forest comparison site list for the amphibians was taken from von May et al. [1] and amended to include species unique to the regenerating forest site, as some species found in the regenerating site were potential undescribed species but closely related to those found in nearby primary forest sites. The reptile site lists were developed by the authors by combining inventories from literature to date [2-4] and the first publication of reptile lists from four field sites within the Madre de Dios region (see Appendix H). These new site lists include the Los Amigos Research Centre (CICRA is the Spanish acronym), 12°34′07″S 70°05′57″W, 270 m elevation; Centro de Monitoreo 1 (CM1), 12°34′17″S 70°04′29″W, ca. 250 m elevation; and Centro de Monitoreo 2 (CM2), 12°26′57″S 70°15′06″W, 260 m elevation and finally the MLC regenerating forest area. The baseline primary forest comparison site lists for the birds were taken from the Manu National Park list [5] and lists from other well-known sites in the region [6-9]. The base mammal list was taken from Salvador et al. [10].

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