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Modelling and projecting the response of local assemblage composition to land-use change across Colombia

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Abstract

Aim

Understanding the impact of land-use change within assemblages is fundamental to mitigation policies at local and regional scale. Here, we aim to quantify how site-level terrestrial assemblages are responding to land-use change in Colombia a mega-diverse country and to project future biodiversity under different scenarios of land-use change associated with climate change policies.

Location

Colombia (northern South America).

Methods

We collated original biodiversity data from 17 publications (285 sites) that examined how human impact affects terrestrial biodiversity in Colombia. From each site we estimated compositional intactness (i.e., compositional similarity to undisturbed sites). We fitted generalized linear mixed effects models to estimate how these measures of local biodiversity vary across land-use habitats. Using space-for-time substitution, we applied our estimates to hindcast biodiversity changes since 1500 and project future changes under climate change policies of the four Representative Concentration Pathways (RCPs).

Results

Assemblages in urban, cropland and pasture sites were compositionally very different from those in primary vegetation. We infer that average compositional intactness has been reduced by 18% across Colombia to date, with strong regional variation. The best RCP scenario for future biodiversity is GCAM-RCP4.5, a path that favor the expansion of secondary forests under a strong carbon market; while the worst is MESSAGE-RCP8.5, “the business as usual” scenario.

Main conclusions

Land-use change has driven an increasing change in the composition of ecological assemblages in Colombia. By 2095, the implementation of carbon markets policy of climate change from GCAM-RCP4.5 could mitigate these changes in community composition. In contrast, the business-as-usual scenario MESSAGE-RCP8.5 predicts a steep community change placing the quality of ecosystems at risk.

Keywords: community composition, GLMM, hindcast, land-use impact, Neotropics, PREDICTS project, RCP.

A. Introduction

The socio-economic benefits of exploiting natural resources have resulted in pressures that pose a serious threat to ecosystems (Chapin III et al., 2000; Foley et al., 2005; Green et al., 2005; Millennium Ecosystem Assessment, 2005; Sala et al., 2000). Landscape transformation, disruption of biogeochemical cycles, invasive species and climate change are among the main consequences of a human-modified world (Chapin III et al., 2000; Foley et al., 2005). Land-use activities are currently the most important global driver of change in terrestrial biodiversity (Alkemade et al., 2009; Jetz, Wilcove & Dobson, 2007; Pereira et al., 2010; Sala et al., 2000; van Vuuren et al., 2006). Pressures that alter the composition and diversity of species assemblages are likely to also alter many ecological processes and services (Cardinale et al., 2012; Díaz et al., 2013; Hooper et al., 2012; Srivastava & Vellend, 2005). Given the ongoing growth of human populations and the rising demand for food and fresh water, it is important to understand how assemblage-level (i.e., local) community composition and richness are affected by human activities and how they would be affected under different future socio-economic assumptions. Understanding biotic effects of human impacts is a particularly urgent priority in tropical forests, because of their combination of high biodiversity and rapid land-use change (Dirzo & Raven, 2003; Hansen et al., 2013; Sala et al., 2000).

Colombia, in the northwestern part of South America, is among the most biodiverse and vulnerable countries on Earth (Brooks et al., 2002; Mittermeier et al., 2003; Myers et al., 2000; Olson & Dinerstein, 2002). The variation in altitude, geological substrates and rainfall among its regions make Colombia a land of climatic and ecological contrasts: such distinct ecosystems as deserts, rainforest and páramos can all be found within a small area. As a result of the biophysical, socioeconomic and political variety across its main five regions Andean, Caribbean, Pacific, Orinoco and Amazonian Colombia shows regional patterns of landscape transformation and human impact (Etter et al., 2011; Etter & van Wyngaarden, 2000). Colombia's environmental and socioeconomic gradients make it a valuable case study on how biodiversity responds to human impact in the tropics.

The exploitation of natural resources is an important asset in Colombia's economy more than 6% of GDP in 2015 came from agriculture: forestry, fishing, cultivation of crops and livestock production (Dinero, 2015; The World Bank, 2015) so unplanned land-use change may be a major cause of biodiversity decline in the country. Previous studies have identified the expansion of cattle industry, agriculture and deforestation (mainly due to illicit crop production) as main reasons for land-use change in Colombia, with additional influences of soil fertility, proximity to roads, rural population density and forced migration (Armenteras et al., 2011; Etter et al., 2006a,b). Quantifying the average impacts of land-use change on local ecological assemblages is important because conservation and land-management decisions are typically implemented at national or lower levels; such understanding can also be combined with approaches such as the planetary boundaries framework (Steffen et al., 2015) to mitigate societal impacts of land-use change.

Several studies have quantified the impact of land-use change on diversity, but they have usually (though not always: Gilroy et al., 2015, 2014) been restricted geographically and taxonomically, which is problematic given that responses can vary among regions and taxa (Gibson et al., 2011; Newbold et al., 2014). Additionally, studies so far have focused mostly on species-richness which can mask large changes in community composition if losses of species are balanced by colonisation of new species or spread of disturbed-tolerant native species (McCune & Vellend, 2013; Thomas, 2013). We have therefore collated data from many Colombian field studies that have assessed land-use effects on biodiversity, and which between them cover a wide range of taxonomic groups and represent four of Colombia’s five main regions. Assuming spatial comparisons can be used in lieu of time-series data, we model responses of community composition to land-use change and two related pressures (human population density and proximity to roads).

Because Colombia’s land-use history is relatively well known (Etter, McAlpine & Possingham, 2008; Etter & van Wyngaarden, 2000), we are able to couple our models with historical land-use maps to explore regional variation in the biotic impact of human activities to date. Likewise, we use scenario-based estimates of future land use in Colombia (Hurtt et al., 2011) to project changes in biodiversity through this century under a range of possible climate policies (Jantz et al., 2015; Newbold et al., 2015).

A. Methods

B. Diversity data

C. Search criteria

We collated field data from reports and scientific literature in English and Spanish of Colombian studies that aimed to quantify how human pressures affect site-level biodiversity. Nearly all such studies have used space-for-time substitution, comparing biodiversity at otherwise-matched sites facing different land use or use intensity under the assumption that differences in community composition are caused by difference in pressure. Although this approach has limitations (Luck, 2007; Wearn, Reuman & Ewers, 2012), it is the only approach currently feasible to obtain a large evidence base to support dose-response models of land-use change (Alkemade et al., 2009; Newbold et al., 2015, 2014). An initial pool of 120 promising papers was identified in January 2013 from a Web of Knowledge search that used the following terms:

((habitat* OR forest* OR land*) AND (impact OR effect OR influence OR role) AND (species abundance OR species diversity OR biodiversity) AND (natural* OR semi-natural* OR primary OR manag* OR unmanag* OR virgin OR old-growth OR remnant* OR ancient* OR silviculture OR cut* OR clear-cut* OR felling OR clear-fell* OR clearfell* OR select* cut* OR thinning* OR coppic* OR logging OR unlogging OR logged OR unlogged OR regeneration OR plantation* OR planting OR drainage OR ditching OR intensification OR old OR abandonment OR drug OR unrest) AND (Colombia* OR equator* OR neotrop*))

As well as examining these 120 papers, we also searched Colombian journals and university library catalogues for relevant papers and dissertations (see Appendix S1 in Supporting Information).

We retained all studies that:

1. Sampled, in a comparable way, multiple terrestrial sites or landscapes having different land-use or intensity impact; and
2. Considered the impact of a human pressure on a set of taxa; and
3. Reported any metric of species' occurrence or abundance, or of site-level diversity (e.g., species richness or diversity indices).

Subsequently, S. E. -L. contacted the corresponding authors (73 in total) from 61 retained sources (papers and dissertations) to request the following information, if it was not presented:

1. Locations of the sampling points, as precisely as possible;
2. An indication of the predominant land use at each site (e.g., primary forest, secondary forest, intensely-farmed crop, hedgerow between two fields);
3. Data on occurrence or ideally the abundance of each species at each site (many papers included only summaries).

We obtained the raw biodiversity data and matching land-use information relating to 17 sources, 26 studies and 285 within-study sites (Figure 1 and Table S1). Some sources provided multiple sets of data, collected using different sampling methods. We treated each such data set as a different study, because diversity cannot be compared directly between samples collected in different ways, while recognising this risks a degree of pseudoreplication. The available data are strongly biased geographically (Figure 1): 73% of studies are from the Andean region, while one of the five regions (the Pacific region) is not represented. Taxonomic bias is also present but less pronounced: arthropods are the main taxon sampled (71% of studies), followed by vertebrates (18%), plants (7%) and fungi (4%). A total of 2582 species were sampled.

C. Site-level variables

Each site was allocated to one of eight land-use classes (primary vegetation, mature secondary vegetation, intermediate secondary vegetation, young secondary vegetation, plantation forest, croplands, pastures, and urban) by applying the criteria in Table S1 in Hudson et al., 2014, to descriptions in the source papers or directly from the authors. These decisions were all made by one person (S. E. -L., a native Spanish speaker) after training and with discussion where necessary, to maximise consistency in the use of categories (intensity classes were assigned to all sites, but the design was too unbalanced and sample sizes too small to permit use in modelling, see Table S2). Only primary forests were reported in our studies as primary vegetation type (i.e., no other primary vegetation types such as natural grasslands were used in our studies). Each site was also characterised by its human population density and distance from the nearest road, two pressures shown to predict site-level diversity in a global analysis (Newbold et al., 2015); these variables were logarithmically transformed log (x + 1) prior to analysis to reduce skew.

We use compositional intactness as a proxy of site-level biodiversity, which has shown to respond more sensitively to disturbance than other species diversity metrics (Dornelas et al., 2014; Magurran & Henderson, 2010). Compositional intactness is a more sensitive indicator of biodiversity change than species richness, because it captures gains and losses of species, rather than only the difference between them (Dornelas et al., 2014; Thomas, 2013). We estimated compositional intactness as the mean Sørensen similarity index (Magurran, 2004) between primary vegetation sites and sites within each other land use within each study (or within each block, where present), scaled by the mean Sørensen index between primary vegetation sites within the same study (Newbold et al., 2015). This scaling avoids conflating natural spatial turnover with human impact, but means values can exceed 1. Compositional intactness was estimated for studies that include primary vegetation sites as reference (15 out of 26). The independence of explanatory variables was assessed using generalized variance inflation factors (GVIFs, Zuur et al., 2009), which never breached the threshold of 10 (see Table S3).

B. Statistical analysis

C. Estimating biodiversity response to human pressures

The studies use in this analysis sampled biodiversity in different ways: sampling effort, sampling method, area sampled, temporal duration of sampling and taxonomic focus all differed among studies. Because such differences will affect site-level diversity, we used generalized linear mixed-effects models (Bolker et al., 2009), to control for among-study (and, for studies with blocked designs, among-block) differences. All the models were fitted using the lmer function from the LME4 package version 1.1-6 (Bates, Maechler & Bolker, 2012) in the software environment R 3.0.0 (R Core Team, 2013). Given the small sample size and unbalanced distribution of stages in secondary vegetation, mature and intermediate secondary vegetation were merged as “I-MSV” (see Figure 2). Because our response variable can exceed 1, we did not apply transformations prior to analysis; model diagnostics suggested our treatment was reasonable. The optimal structure of random effects was first found using stepwise selection among (i) random slopes and intercepts, (ii) random intercepts only, or (iii) no random effects (Bolker et al., 2009; Zuur et al., 2009). The minimal adequate model (optimal fixed structure) was then chosen using stepwise selection from the candidate models ranking under the second order Akaike

Information Criterion (AICc), which increases the penalty for model complexity when sample size is small in comparison to the number of estimated parameters. We used a threshold of 4 AICc units to adopt a simpler model or to drop a term (Burnham & Anderson, 2002).

B. Hindcasting and projecting

Spatiotemporal estimates of land use are needed in order to estimate how average compositional similarity to primary vegetation have changed through history, and how they may change throughout this century. We used gridded (0.5° x 0.5° resolution) historical estimates of how the area under each land-use class changed from 1500-2005, from the History Database of the Global Environment HYDE 3.1 (Klein Goldewijk et al., 2011). HYDE's historical land-use maps of Colombia are based on Etter & van Wyngaarden (2000) and Etter, McAlpine & Possingham (2008) statistics for historical landscape change in each region, which were derived from contemporary and historical maps, statistical data (socio-economical, demographic and geographic variables) and historical writings (books and chronicles). Projecting compositional intactness from 2005-2100 used the gridded land-use change data associated with the four Representative Concentration pathways (RCPs): IMAGE-RCP2.6, GCAM-RCP4.5, AIM-RCP6.0 and MESSAGE-RCP8.5 (Hurtt et al., 2011). The Intergovernmental Panel on Climate Change (IPCC) developed the RCPs as a reference group of climate-change projections having different rates and magnitudes of land-use changes and greenhouse gas emissions (Moss et al., 2010; Van Vuuren et al., 2011). Each RCP aims to meet its specified level of radiative forcing (denoted by the number in its name, in W/m^2) using a different combination of socio-economic, demographic, technological and policy assumptions (Harfoot et al., 2014; Moss et al., 2010).

We applied the coefficients from the minimal adequate model for compositional intactness with the historical and future land-use estimates to produce maps of compositional intactness, i.e., similarity to primary vegetation every 15 years from 2005-2095 for all the RCPs except MESSAGE-RCP8.5 (2005 and then every 20 years 2010-2090). We then aggregated the map for each date to give time series of the estimated average change within each region and across Colombia as a whole. When aggregating in this way, we weighted grid cells by their land area and current vertebrate species richness (Newbold et al., 2015), to reflect that changes in more diverse regions might be of more concern (though vertebrate richness is at best an imperfect surrogate for invertebrate richness). We used the uncertainty in the model coefficients and model structure to place 95% confidence intervals around the biodiversity estimates for past and future dates, rescaling uncertainty to be zero in 2005 to separately show uncertainty in hindcasts and projections. However, we were unable to integrate uncertainty in the pressure data, because no uncertainty estimates are available for them (Newbold et al., 2015).

A. Results

B. Biodiversity response to land use change

Compositional intactness varied significantly among land uses (x^2 = 51.98; d.f = 5; P < 0.001). While species composition in secondary vegetation, especially older secondary vegetation was similar to that in primary vegetation, the composition in all human-dominated land uses was markedly different (Figure 2). Human population density and distance to roads did not explain significant additional deviance (Table 1).

Maps for the year 2005 of compositional intactness (Figure 3) show markedly lower values outside the Amazonian region, especially in the Andean region. Across Colombia as a whole, we estimate that average compositional intactness was 82% in 2005 (see Figure S1)

B. Historical and future projections of diversity

Our hindcasts suggest that the extent and timing of declines in compositional intactness have varied markedly among regions (Figure 4). Although all regions show a tendency for accelerating decline through the 20th century, this acceleration is most pronounced in the Pacific and especially in the Caribbean region. While the Amazonian region was still 92% compositionally intact in 2005, the estimates for the other regions are between 75% and 79%. Projections of compositional intactness differ strongly among RCP scenarios (Figure 4). It is projected to increase under GCAM-RCP4.5, because of a projected expansion of secondary forest outside Amazonia. In all regions compositional intactness is projected to decrease under MESSAGE-RCP8.5 scenario.

A. Discussion

B. Time course of compositional change in Colombia

During the history of Colombia, the complexity of primary vegetation has increasingly been replaced with relatively simple croplands, plantations, urban environments and especially pastures (Etter, McAlpine & Possingham, 2008; Etter & van Wyngaarden, 2000). We have shown (Figure 2), using Colombian data from a wide range of taxonomic groups, that these land uses support assemblages whose composition differs markedly from those in primary vegetation. The consequence of ongoing habitat conversion has been to drive down the average compositional intactness of assemblages across Colombia to 82% (Figure S1), with the greatest reductions being in regions where conversion has been widespread (Figure 3). Only the Amazonian region is inferred to have largely intact assemblages (>90% intact: Figure 3 and 4).

In this analysis, three land uses in particular are associated with low compositional intactness: pasture, cropland and urban. Of these, pasture is most important in reducing overall compositional intactness: historically cattle grazing have expanded at expense of forests and croplands dominating over the 90% of cleared areas Colombia in 2000 (Etter, McAlpine & Possingham, 2008; Etter & van Wyngaarden, 2000).

Anthropogenic effects on assemblage composition are likely to involve biotic homogenisation (McKinney & Lockwood, 1999), as the simplification of habitats favours ecological generalists over specialists (Gámez-Virués et al., 2015), reducing assemblage-level functional diversity (Olden et al., 2004). The average decline in compositional intactness shown in Figure 4 is therefore potentially of concern from the perspective of ecosystem function as well as conservation.

Our projections of how compositional intactness may change in the future within each region (Figure 4) should not be viewed as exact predictions; rather they provide a practical way to explore the possible effects of different climate-change policies on ecological assemblages. Each representative concentration pathway (RCP) makes different socio-economic assumptions (summarised in Table 2) to achieve its target level of radiative forcing. Among the scenarios, MESSAGE-RCP8.5 (business-as-usual) projects the fastest decline, with compositional intactness falling to an average of 79% (77%-81%) by 2090. Under this RCP, despite yield improvements, forested areas will be replaced by croplands and pastures to meet rising demands for food, energy and fibre from a rapidly-growing human population (Brooks et al., 2002; Harfoot et al., 2014; Hurtt et al., 2011). In contrast, GCAM-RCP4.5 is projected to offer the best outcome for biodiversity in Colombia — intactness rising to an average of 86% (82%-90%) by 2095 — agreeing with conclusions of a global study (Newbold et al., 2015). This RCP is based on a fairly low stabilization scenario of greenhouse-gas (GHG) emissions through an expansion of forested areas by means of effective carbon pricing. Under this scenario, croplands and pastures will be replaced by forested areas, with yield improvement, dietary shifts and international trade able to satisfy food demand from a human population that is smaller than under MESSAGE-RCP8.5 (Harfoot et al., 2014; Hurtt et al., 2011). The expansion of secondary forest, which is permitted to mature in GCAM-RCP4.5, is projected to improve average compositional intactness in Colombia (Figure 4). However, these results focus only on land use change, ignoring the effects of climate change on biodiversity. The combination of land-use change and climate could increase the impact of the GCAM-RPC4.5 scenario on biodiversity compared with the most ambitious climate-change mitigation target IMAGE-RCP2.6. Therefore, future analyses should study the effects of climate change, land-use change and their interaction to evaluate in more detail the potential impact of future climate policies on biodiversity.

B. Secondary vegetation

Assemblages in maturing (but not young) secondary vegetation had similar composition to those in primary vegetation (Figure 2). Such assemblages are also often comparable to those in primary vegetation in terms of species richness (Barlow et al., 2007; Gilroy et al., 2014; Martin, Newton & Bullock, 2013; Newbold et al., 2015; Wright & Muller-Landau, 2006) and plant biomass (Gilroy et al., 2014; Martin, Newton & Bullock, 2013; Poorter et al., 2016), suggesting that natural forest regeneration may provide important conservation and ecosystem services to buffer human disturbances. However the conservation value of secondary vegetation is likely to depend on the configuration of the landscape (Gardner et al., 2009), which we were unable to incorporate in our analyses. Patches of recovering forest that are near to mature forest are likely to recover more quickly and more completely than are isolated patches, given many forest specialists are dispersal-limited (Hermy & Verheyen, 2007). Edge effects can mask the real contribution of regenerated habitats since generalist species can move through secondary vegetation from nearby pristine habitats (Brook et al., 2006; Chazdon et al., 2009; Norden et al., 2009;

Pulliam & Danielson, 1991). Because the surveys in our analyses mostly considered sets of sites that were close together (the median separation between the most distant pair of sites within each study was 1.6km), the inferred high compositional intactness of maturing secondary vegetation should be viewed as being contingent on there being nearby primary forest.

Assemblages in plantations and young secondary vegetation were less compositionally intact than those in primary or older secondary vegetation, but more so than those in cropland or pasture. This finding is consistent with Gilroy et al.'s (2015) multi-taxon assessment of community composition in natural forest, oil palm plantations and improved pasture in the Colombian Llanos in the Orinoco region. They found the amount of forest cover was an important determinant of diversity in birds, but not of dung beetles, ants or herpetofauna. They also reported depauperate diversity and reduction of compositional intactness in pastures compared with plantations. Once again the proximity of remnant forest could play an important role in maintaining compositional intactness in plantations and secondary vegetation. Other variables such as forest cover could also have a positive effect on the probability of occurrence of certain species (Newbold et al., 2014). Further research regarding the role of indirect factors such as edge effects, habitat fragmentation and forest cover would help to improve estimates of the impacts of these land uses on diversity.

B. Biases and limitations

Although our models and projections infer a marked decline in compositional intactness in four of Colombia's five regions (Figure 4), there are several reasons why the decline may have been more severe than we estimate. First, published biodiversity surveys that set out to compare different habitat types may tend to underestimate the true diversity difference between habitats. Natural habitats tend to be more structurally complex than converted ones, often greatly so. Surveys comparing habitats of differing structural complexity are likely to use only those sampling methods that can easily be used in the simpler habitat. The sampling methods most commonly used in our data sets are baited/pitfall traps (six studies); fixed plots/quadrats (three studies) and visual encounter survey (three studies), all of which can be used in agricultural fields as well as in primary forest. A suite of methods widely used in mature forest (e.g., canopy fogging), and which sample different species pools (Longino, Coddington & Colwell, 2002), are unlikely to be applied to structurally simpler sites. Therefore, even though our models indicate assemblages in pasture to be very distinct from those in primary vegetation, we may be underestimating how distinct they are. A related possible bias is that researchers may tend to make comparisons in which the result is not obvious. For example, intensively managed monoculture plantation forests obviously have fewer tree species than natural forest, but few surveys comparing the two habitats consider tree diversity (one exception being Phalan et al., 2011). These biases apply not only to our study, but also to any synthetic comparisons that attempt to estimate overall effects of land-use change on species richness (e.g., Alkemade et al., 2009; Gibson et al., 2011; Newbold et al., 2015) or composition (e.g., Martin, Newton & Bullock, 2013; Newbold et al., 2016).

There are further grounds for caution in interpreting our statistical models and projections from them. First, different taxonomic groups may respond differently to human impacts (Gilroy et al., 2014; Lawton et al., 1998; Newbold et al., 2014). Even the similarity between assemblages in primary and secondary vegetation can vary among taxa and functional groups: Barlow et al. (2007) multi-taxon comparison in Brazil showed that the proportion of primary-forest species also found in secondary forest ranged from below 40% (for trees, lianas, birds and grasshoppers) to over 80% (scavenger flies, large mammals and orchid bees). Martin, Newton & Bullock (2013) meta-analysis of mostly Neotropical (but not Colombian) studies reported that local species richness in secondary forest recovered much more quickly for trees than for epiphytes. Furthermore, in amphibians and reptiles assemblages in secondary forests in southeastern Mexico, Hernández-Ordóñez, Urbina-Cardona & Martínez-Ramos (2015) showed that the recovery of local species richness is faster than abundance or composition. Our data set was not large enough or balanced enough to allow models to be fitted that explicitly test for and accommodate among-taxon variation. Whereas a multi-continent analysis of responses of tropical forest vertebrates showed marked differences among classes (Newbold et al., 2014), a still-broader global analysis found responses of vertebrates, invertebrates and plants did not differ significantly (Newbold et al., 2015). Differences in site size – especially within studies – could affect our model estimates; however, we did not find a significant relationship between maximum linear extent (MLE, our site size measure) and compositional intactness ($\chi^2_{1,84} = 0.016, p = 0.90$) (see Figure S2). Only three studies reported differences in maximum linear extent among sites; removing these studies did not alter significantly our model estimates (see Figure S3).

A second reason for caution is the uneven geographic coverage of our data.

Within Colombia, biodiversity sampling appears to be biased towards the Andean region, from which around three quarters of our studies come (Figure 1). This bias is not surprising since this area harbours the main cities and therefore the main academic institutions in Colombia (Arbeláez-Cortés, 2013); proximity to research institutions has been identified as a strong biasing factor in the state of global biodiversity knowledge (Meyer et al., 2015). Lacking enough data to test for regional differences, we have assumed that the compositional similarity between sites in different land uses is consistent among regions; the differences in the trajectories shown in Figure 4 arise because of different land-use histories rather than because the regional biotas differ in their intrinsic sensitivity to land-use change. Such differences have been suggested previously (e.g., Gibson et al., 2011, argued that Asia's biota is more sensitive than that of other regions). A priority is therefore to increase sampling effort in areas having limited information, perhaps focusing on identified hotspots of land-use change in the country (Armenteras et al., 2013; Etter et al., 2006a). Moreover, additional studies would improve the confidence in all parameter estimates and would allow more complex model structures (e.g., random slopes and intercepts models), as well as allowing investigation of variation among taxa and regions, and robust modeling of a wider range of biodiversity measures (e.g., species richness). Unfortunately, few data sets are available from regions with recent and ongoing transformation, places where the knowledge of species composition is scarce, and where there is a strong demand for natural resources such as the Orinoco and the Pacific regions. However, since the Andean region has a long history of transformation since the pre-Spanish colonization, further sampling is also needed in view of possible extinction debts (Tilman et al., 1994), high levels of endemism (Orme et al., 2005), unique evolutionary history (Madriñán, Cortés & Richardson, 2013) and high risk of extinction (Brooks et al., 2002).

Publication bias can cause negative (i.e., non-significant) results to be under-represented in the literature, especially in high-impact journals (Murtaugh, 2002); this potential bias is mitigated somewhat here as our literature search includes unpublished dissertations and articles published in Spanish in local journals as well as English-language papers in international journals. Eleven of the 17 sources had been published in local journals, and seven were written in Spanish, showing that there is still a language barrier to accessing biodiversity studies in highly diverse and vulnerable countries like Colombia. Since most of the biodiversity data are still hidden in unpublished information (Corlett, 2011), more effort should be invested in translation and migration of local field-data studies especially in the tropics where most of the diversity and recent land-use change is concentrated.

A final caveat is that the uncertainty in hindcasts and projections of compositional uncertainty through time (Figure 4) incorporates only the uncertainty of parameter estimates, meaning that the true uncertainty is greater than we have been able to accommodate. This reflects the lack of any uncertainty estimates associated with the historical and future land-use data we used (Hurtt et al., 2011).

A. Conclusions

This study represents the first attempt to hindcast and project land-use impacts on local biodiversity in Colombia, and highlights the irreplaceability of natural forest. We estimate that land-use change has already reduced average compositional intactness by 18% across this megadiverse country, though we caution that the decline may have been even larger. Our projections suggest that future trends depend on the socioeconomic path that is chosen: expansion of secondary forests under a strong carbon market (GCAM-RCP4.5) can reverse the decline, whereas “business as usual” (MESSAGE-RCP8.5) will exacerbate it. Given the rate of land-use change in the country, particularly in those areas considered vulnerable, additional field-based studies are urgently needed to improve the robustness of models such as ours and to account for differences among regions, taxa and studies making them better able to inform mitigation policies of land-use change.

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A. Biosketch

Susy Echeverría-Londoño conducted this work as part of her MRes in Biodiversity Informatics and Genomics and PhD at Imperial College London and the Natural History Museum. Her research now focuses on macroecology and macroevolution of the megadiverse plant genus *Solanum* L (Solanaceae).

Author contributions: S.E-L. and A.P. conceived the ideas. E.A-C, I.A., T.B., J.C-G., Y.D-H., G.N-P., D.L.G-L., D.H., P.J.I-C., C.A.L-Q., E.M., D.R.M-E., L.E.N-I., J.A.N., S.E.O., A.P-H., K.P., M.P. R-P., J.C.R-V., L.R., A.S-P., J.N.U-C provided the data. L.N.H., S.C., S.L.L.H., and I.L., curated the data. S.E-L. and T.N. analysed the data. A.P. and S.E-L. led the writing with inputs from all co-authors.

A. Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1{Journals and University library catalogues used to explore studies with field data in Colombia}

Appendix S2{Statistical Model Structure}

Table S1{Data sources descriptions}

Table S2{Number of sites per land-use and intensity class}

Table S3{Variance inflation factors (VIF) for the exploratory variables used to model site-level compositional intactness}

Figure S1{Projected global net change in compositional intactness from 1500 to 2095 in Colombia}

Figure S2{Relationship between maximum linear extent (MLE) and study-level difference in compositional intactness }

Figure S3{Influence of studies with differences in site size on Community intactness }

Tables

Model	d.f.	ΔAIC	Rank
LU	9	0.00	1
LU + logdistRd	10	6.32	2
LU + ogHPD	10	8.01	3
Null	4	17.46	4
logdistRd	5	21.18	5
logHPD	5	24.44	6
LU + logHPD × logdistRd	12	25.58	7
LU × logdistRd + logHPD	15	38.55	8
LU × logHPD + logdistRd	15	42.13	9
LU × logHPD × logdistRd	24	100.27	10

Table 1: Change in Akaike’s information criterion (Δ AIC) and model rank for all models fitted in the community similarity analysis. LU, Land use; logHPD, log(human population density + 1); logdistRd, log(distance to roads + 1). See Figure 2 as a reference for land use classes used in the analysis. N = 115 sites in 15 studies

Scenario	**IMAGE-RECP2.6**	**GCAM-RCP4.6**	**AIM-RCP6.0**	**MESSAGE-RCP8.5**
Climate change policy	Very-low greenhouse concentration pathway. Mitigation of air pollutants through energy efficient policies based on renewable energy and bio-fuels.	Medium-low greenhouse concentration pathway. Mitigation based on carbon storage pricing, diet shift, decrease of energy consumption, crop yield improvement.	Medium baseline greenhouse concentration pathway. Mitigation based on technology development. Growing economy and population density.	High baseline greenhouse concentration pathway. No mitigation policies. High population growth and lower rate of technology development
Primary	Decrease	Decrease	Decrease	Decrease
Secondary	Medium increase	Significant increase	Significant increase	Medium increase
Cropland	Significant increase	Decrease	Medium increase	Medium increase
Pasture	Constant	Medium decrease	Decrease	Medium increase
Urban	Constant	Constant	Increase	Increase

Table 2: Main feature of RCP scenarios. Information based on Harfoot et al. (2014); Van Vuuren et al. (2011)

A. Figures captions

Figure 1. Map of Colombia displaying the distribution of sources collected in this study. The main polygons correspond to the main regions in Colombia and blue dots represent the 285 within-study sites.

Figure 2. Community similarity for each land-use classes compared to primary vegetation as measured by the Sørensen similarity index. Error bars show coefficients estimates ± 95% CI. Black points correspond to the estimates from the minimal adequate model (optimal fixed structure). The studies in cropland and plantations (grey points) were merged as “planted” in this model to keep a balanced distribution of studies among land use classes. Numbers within the left parenthesis represent the number of studies used per land-use level. I-MSV = Intermediate and mature secondary vegetation combined, YSV= Young secondary vegetation, Planted= Cropland and plantation.

Figure 3. Net change in community composition in Colombia caused by land use by 2005 using 0.5° x 0.5° resolution map.

Figure 4. Projected net change in compositional intactness from 1500 to 2095 by region in Colombia. Grey shading (historical) and error bars (future) show ± 95% confidence intervals. Future projections are based on the four RCP scenarios (Table 2). We used the uncertainty in the model coefficients and model structure to place 95% confidence intervals around the biodiversity estimates for past and future dates, rescaling uncertainty to be zero in 2005 to separately show uncertainty in hindcasts and projections. We were unable to integrate uncertainty in the pressure data, because no uncertainty estimates are available for them (Newbold et al., 2015).