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Mapping tree species vulnerability to multiple threats as a guide to restoration and conservation of tropical dry forests

Running title: multi-threat vulnerability mapping

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ABSTRACT

Understanding the vulnerability of tree species to anthropogenic threats is important for the efficient planning of restoration and conservation efforts. We quantified and compared the effects of future climate change and four current threats (fire, habitat conversion, overgrazing, and overexploitation) on the 50 most common tree species of the tropical dry forests of northwestern Peru and southern Ecuador. We used an ensemble modelling approach to predict species distribution ranges, employed freely accessible spatial datasets to map threat exposures, and developed a trait-based scoring approach to estimate species-specific sensitivities, using differentiated trait weights in accordance with their expected importance in determining species sensitivities to specific threats. Species-specific vulnerability maps were constructed from the product of the exposure maps and the sensitivity estimates. We found that all 50 species face considerable threats, with an average of 46% of species' distribution ranges displaying high or very high vulnerability to at least one of the five threats. Our results suggest that current levels of habitat conversion, overexploitation, and overgrazing pose larger threats to most of the studied species than climate change. We present a spatially explicit planning strategy for species-specific restoration and conservation actions, proposing management interventions to focus on (i) *in-situ* conservation of tree populations and seed collection for tree planting activities in areas with low vulnerability to climate change and current threats, (ii) *ex-situ* conservation or translocation of populations in areas with high climate change vulnerability, and (iii) active planting or assisted regeneration in areas under high current threat vulnerability but low climate change vulnerability, provided that interventions are in place to lower threat pressure. We provide an online, user-friendly tool to visualize both the vulnerability maps and the maps indicating priority restoration and conservation actions.

1 INTRODUCTION

Anthropogenic threats such as climate change, habitat conversion, and overexploitation are among the main drivers fuelling the global biodiversity crisis (Bradshaw, Sodhi, & Brook, 2009; Ceballos et al., 2015). Assessing the vulnerability of ecosystems and species populations to these threats is critical for the planning of cost-effective restoration and conservation actions (Auerbach, Tulloch, & Possingham, 2014; Carwardine et al., 2012), which has led to a surge of vulnerability assessments over the last decade. Most studies have focused on climate change (e.g., Foden et al., 2013; Thomas et al., 2011), or the combined effects of climate change and land use change (e.g., Elías-Velazco, Villalobos, Galvão, & De Marco Júnior, 2019; Reece, Noss, Oetting, Hctor, & Volk, 2013). Less commonly, vulnerability assessments have also addressed other threats such as fire, overexploitation, and overgrazing (e.g., Gaisberger et al., 2017; Jarvis, Touval, Schmitz, Sotomayor, & Hyman, 2010).

Species vulnerability assessments often estimate three dimensions of vulnerability: exposure, sensitivity and adaptability (Pacifci et al., 2015; Wheatley et al., 2017). Exposure is defined as the magnitude and rate of a threat to which species populations are likely to be exposed. Sensitivity usually refers to the degree to which survival and reproduction are affected by the threat, whereas adaptability concerns the capacity of species populations to either respond to a threat through phenotypic plasticity and genetic adaptation, or to avoid its negative impacts through dispersal and colonization (Dawson, Jackson, House, Prentice, & Mace, 2011; Ofori, Stow, Baumgartner, & Beaumont, 2017). As the distinction between sensitivity and adaptability is not always clear-cut, adaptability has often been considered as an integral component of sensitivity (e.g., Williams, Shoo, Isaac, Hoffmann, & Langham, 2008; Young et al., 2012).

Species vulnerability assessments have employed a variety of methodologies, which can be grouped into correlative, trait-based and mechanistic approaches (Foden et al., 2018; Pacifci et al., 2015). Correlative approaches use correlative species distribution models to assess species vulnerability, for example by projecting these models to future climate conditions (e.g., Mancheogo et al., 2017; Rogers, Jantz, & Goetz, 2017). Trait-based assessments use species traits to estimate species-specific sensitivities, usually combined with information on threat exposure (e.g., Foden et al., 2013; Spencer, Hollowed, Sigler, Hermann, & Nelson, 2019). Mechanistic approaches explicitly incorporate the biological processes underlying species vulnerability by parametrizing mechanistic models (e.g., Mantyka-Pringle, Martin, Moffatt, Linke, & Rhodes, 2014; Morin,

Viner, & Chuine, 2008). There is a growing consensus that a combination of different approaches (e.g., Aubin et al., 2018; Maggini et al., 2014) may yield the most useful results, depending on the study objectives and data availability (Foden & Young, 2016; Willis et al., 2015).

Because of the spatially explicit nature of anthropogenic threats and the fact that species are likely to respond differently to these threats, the assessment of the vulnerability of multiple species to multiple threats is a complex exercise. Multi-threat vulnerability assessments have therefore often assumed that threats are homogenous across species ranges or that different species are equally sensitive to threats. Only a few studies have assessed the impacts of multiple threats on multiple species in a species-specific and spatially explicit way (e.g., Gaisberger et al., 2017; Maggini et al., 2014; Reece et al., 2013).

Tropical dry forests (TDFs) are among the most threatened ecosystems worldwide (Hoekstra, Boucher, Ricketts, & Roberts, 2005; Janzen, 1988). In the Americas, around two-thirds of the original TDF cover has been converted to other land uses (Portillo-Quintero & Sánchez-Azofeifa, 2010). In spite of this, TDFs have long been largely neglected in scientific literature, receiving much less attention than tropical humid forests (Pennington, Lehmann, & Rowland, 2018). While research efforts have been increasing in recent years (e.g., Banda et al., 2016; Derroire et al., 2016), a pressing need remains to step up science-based restoration and conservation efforts in TDF ecosystems (Pennington et al., 2018).

The TDFs of northwestern Peru and southern Ecuador are known for their high degree of endemism (Linares-Palomino, Kvist, Aguirre-Mendoza, & Gonzales-Inca, 2009; Marcelo-Peña, Huamantupa, Särkinen, & Tomazello, 2016), but they are under great pressure from anthropogenic threats. Some 40% of the TDFs in northwestern Peru and southern Ecuador have been converted to agriculture (annual crops and fruit tree plantations) by both smallholders and agribusiness companies, the latter of which are usually linked to large-scale irrigation projects (MAE, 2012; MINAM, 2018). Many of the non-converted forests are severely impacted by overexploitation, overgrazing, and forest fires (Aguirre-Mendoza & Geada-Lopez, 2017; Linares-Palomino, 2006; Marcelo-Peña et al., 2016). Overexploitation occurs both for local (timber for rural constructions, firewood) and commercial (charcoal, timber) purposes. Overgrazing is caused by free-roaming cattle, goats, and donkeys owned by smallholders, and occurs in almost all TDFs of the region. Most fires are caused by human activities, including fires deliberately initiated by land traffickers to ease land titling (Muñoz, 2018).

In addition to the current threats mentioned above, TDFs are expected to be sensitive to climate change, owing to their dependence on often erratic seasonal rainfall (Allen et al., 2017). Most general circulation models (GCMs) predict an increase in annual precipitation in northwestern Peru and southern Ecuador, but a decrease in dry season precipitation, especially in the lowland forests. Previous studies suggest that marked drought events can engender strong negative impacts on the recruitment, survival, and growth rates of TDF tree species (Castro, Sanchez-Azofeifa, & Sato, 2018; Maza-Villalobos, Poorter, & Martínez-Ramos, 2013; Spann et al., 2016).

Here we quantified and compared the effects of five key threats (climate change, habitat conversion, overexploitation, fire, overgrazing) on 50 common tree species of the TDFs of northwestern Peru and southern Ecuador. We used an ensemble modelling approach to predict species distribution ranges, employed freely accessible spatial datasets to estimate threat exposures, and developed a trait-based scoring approach to estimate species-specific sensitivities to each of the five threats. Our approach is similar to other vulnerability assessments combining correlative species distribution models and trait-based methods (e.g., Aubin et al., 2018; Garcia et al., 2014; Maggini et al., 2014), but to the best of our knowledge, it is the first spatially explicit multi-threat vulnerability assessment using species traits to estimate the sensitivity of a large number of tree species. We further show how the results of this study can be used to guide species-specific restoration and conservation actions.

2 MATERIALS AND METHODS

2.1 Study region

The study region comprises the TDFs of southern Ecuador and northwestern Peru between 9°30' S and 3°15' S, roughly covering an area extending from the Marañón valley in Peru in the south to the Jubones river in Ecuador in the north, the latter of which can be considered the northwestern limit of the Amotape-Huancabamba biogeographic region (Weigend, 2004). These TDFs can be subdivided in lowland, montane and interandean forests (Linares-Palomino, 2006). The lowland TDFs, located into the coastal plains on the western side of the Andes, are characterized by relatively low stem densities and canopy heights. With increasing altitudes along the western flanks of the Andes, the lowland TDFs transition into montane TDFs, reaching an altitude of ca. 1600 masl, with higher stem densities and canopy heights (Linares-Palomino, 2006). The interandean TDFs are situated in the Marañón river valley and its tributaries, flanked on both sides

by Andean mountain ranges. Their biogeographical isolation has resulted in one of the highest endemism rates in the world, with 33% of the woody species present in these forests being restricted to this valley (Marcelo-Peña et al., 2016).

2.2 Tree species occurrence records

Tree species occurrence records were compiled from a variety of sources (Supporting Information 2). While the compilation focused on TDF records, we also included the georeferenced records of all tree and shrub species from national checklists of Peru (Brako & Zarucchi, 1993), Ecuador (Jørgensen & León-Yáñez, 1999) and Colombia (Bernal, Gradstein, & Celis, 2015) available on the GBIF (Global Biodiversity Information Facility; www.gbif.org) and BIEN (Botanical Information and Ecology Network; <http://biendata.org/>) platforms, which were used as an input in the distribution modelling (section 2.5).

2.3 Modelling the potential distribution of tropical dry forest

Given the limited quality of existing maps depicting the potential distribution of TDFs (Särkinen, Iganci, Linares-Palomino, Simon, & Prado, 2011), we first modelled the potential distribution of TDFs in the study region, using a combination of presence locations of TDF habitat specialist species and TDF presence points randomly sampled from existing land cover maps (MAE, 2012; MINAM, 2018). The use of habitat specialist species is based on the assumption that their presence or absence is a good proxy of the distribution of TDF (Särkinen et al., 2011). The selection procedure of TDF habitat specialist species, the modelling methodology and the corresponding results are detailed in Supporting Information 3.

2.4 Selection of tree species

We selected the 50 most frequent tree species (i.e. with most occurrence records) in our study region for in-depth analysis (Supporting Information 1 Table S3). Species frequency was determined as the number of records within the modelled TDF distribution. We determined the frequency of species after spatially thinning the occurrence records with a 4 km thinning distance, using the spThin package for R (Aiello-Lammens, Boria, Radosavljevic, Vilela, & Anderson, 2015), in order to reduce the effects of spatial bias.

2.5 Species distribution modelling

We estimated the distribution of the selected tree species through an ensemble modelling approach (i.e. combining different modelling algorithms), implemented in the BiodiversityR package for R (Kindt, 2018). The following twelve algorithms commonly used in distribution modelling were included. The corresponding package is given between parentheses: MaxEnt (dismo), random forests (randomForest), support vector machines (kernlab), flexible discriminant analysis (mda), multivariate adaptive regression splines (earth), DOMAIN (dismo), stepwise and non-stepwise implementations of boosted regression trees (dismo and gbm), generalized linear models (stats), and generalized additive models (gam). We selected these algorithms out of a total of 23 (see Kindt 2018) based on their superior performance during preliminary runs for the selected species, based on cross-validated AUC (area under the receiver operating characteristic curve) values. Maxent is a presence-background method, DOMAIN a presence-only method, whereas the remaining algorithms are presence-absence algorithms.

Presence locations used for estimating the distribution ranges of the selected tree species were sourced from the compiled occurrence data (section 2.2). Presence locations were filtered to a resolution of 30 arcsec (ca. 0.9 km at the equator) prior to modelling. After filtering, all 50 selected tree species had more than 30 occurrence records, which is generally considered sufficient to build accurate distribution models (van Proosdij, Sosef, Wieringa, & Raes, 2016; Wisz et al., 2008).

Background points used for calibrating the Maxent models were selected using the target group approach, proposed by Phillips et al. (2009) as a method to reduce the effects of spatially biased occurrence records on model calibration. This involves the selection of background records from grid cells with presence coordinates of species belonging to a similar group as the target species, under the assumption that these locations reflect a bias similar to the sampling bias of the target species (Phillips et al., 2009). We constructed the target group grid using the occurrence records of all tree and shrub species of the national checklists of Peru, Ecuador and Colombia (section 2.2).

For the presence-absence algorithms, absence locations were selected using an approach similar to the target group method, by selecting grid cells that did not contain records of the modelled species, but that had been sufficiently covered by botanical sampling activities to provide some confidence of species absence. The minimum sampling intensity of each grid cell was set at a minimum of two forest inventory plots, ≥ 20 observed tree or shrub species from non-plot-based

data, or the combination of at least one inventory plot and ≥ 10 observed tree or shrub species from non-plot-based data. Given that the median site-level woody species richness in the TDFs of the study region and the interandean TDFs of Ecuador and Colombia is below twenty (Banda et al., 2016), these ‘target group absences’ (Mateo, Croat, Felicísimo, & Muñoz, 2010) were expected to be close to real absence records.

We selected 34 climatic, edaphic and topographic variables as possible predictors for modelling (Supporting Information 1 Table S1), consisting of 19 bioclimatic variables (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), annual aridity, 10 continuous soil variables (Hengl et al., 2017), and 4 topographic variables. This set of variables was reduced to 14 variables (Supporting Information 1 Table S1) using a stepwise procedure. First, the importance of each of the variables was estimated by fitting random forest distribution models for the selected tree species. Next, the variance inflation factors (VIFs) of the predictor variables were calculated with the *usdm* package (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014), using extracted values of the predictor variables at all the locations of the compiled occurrence records within the modelling extent (see below). Of the three variables with the highest VIF, the one variable with the lowest average variable importance was discarded. This was repeated until all predictor variables had a VIF lower than 5.

To reduce the possible confounding effects of regional niche variation due to local adaptation (Dorado-Liñán et al., 2019; Hällfors et al., 2016) and to ensure the capacity of the models to accurately distinguish between presence and absence within the TDF biome (rather than between different biomes), we restricted our modelling extent to the areas within Peru, Ecuador and Colombia falling within the broad environmental space occupied by TDFs, slightly extended to include neighbouring ecosystems. TDFs can be defined as (a) having an annual aridity lower than 1 (Murphy & Lugo, 1986), (b) a mean annual temperature higher than 17°C (Murphy & Lugo, 1986), and (c) at least 5 months with less than 100 mm rainfall (Pennington, Pradot, & Pendry, 2000). Accordingly, presence, absence and background points were drawn from areas with (a) an annual aridity lower than 1.25, (b) a mean annual temperature higher than 14°C, and (c) at least 3 months with less than 100 mm rainfall. In addition, at least half of the occurrence records were always taken from the study region, randomly subsampling the occurrence records outside the study region if necessary. The modelling extent was further restricted to the convex hull around

the presence locations of the modelled species, extended with a buffer corresponding to 10% of the longest axis between presence points.

The accuracy of the distribution models was estimated using the AUC statistic. The AUC measure has been criticized, mainly because AUC values are easily inflated by increasing the environmental extent in which absence points are selected (Lobo, Jiménez-Valverde, & Real, 2008). However, AUC values remain valid to compare modelling results of the same species in the same area (Kindt, 2018), and inflated AUC values were avoided by restricting the modelling extent as outlined above. Overly optimistic AUC values can also result from randomly partitioning spatially auto-correlated occurrence records in testing and training points (Bahn & McGill, 2013). The distribution models were therefore cross-validated using spatial blocks, using the `blockCV` package for R (Valavi, Elith, Lahoz-Monfort, & Guillera-Arroita, 2019). This approach, which partitions the presence and absence locations in training and testing locations using a set of spatial blocks, has the additional advantage that the obtained AUC values provide a better measure of model transferability, which is crucial when projecting species distributions to future climates (Muscarella et al., 2014; Wenger & Olden, 2012). Presence and absence points were partitioned using 10 folds, each fold consisting of one or more 100 km-wide squared blocks. For species for which the distribution range was not large enough for 10 blocks (the minimum number of presence and absence records per block was set at 4), fewer folds were used.

In each of the cross-validation folds, the weights of the different algorithms in the ensemble model were optimized using the `ensemble.tune` function of the BiodiversityR package, which maximizes the AUC value of each ensemble model by optimizing the weights of the different algorithms through a factorial procedure (Kindt, 2018). The suitability predictions of the final ensemble model were made with the average of these optimized weights.

The suitability maps were converted to presence-absence maps by using the suitability threshold at which model sensitivity and specificity are equal, which is one of the two threshold selection methods recommended by Jiménez-Valverde & Lobo (2007). The presence-absence maps were masked by the aforementioned extended convex hull to exclude areas without any occurrence records, and masked by the modelled potential distribution of TDF to focus our analysis on the TDFs of our study region.

2.6 Threat exposure

For each of the five selected threats (climate change, fire, habitat conversion, overgrazing, and overexploitation), threat exposure estimates were constructed using freely accessible spatial datasets (Table 1), based on a set of assumptions derived from literature and expert knowledge (see below). The exposure estimates were created as grid layers with values ranging from 0 (zero exposure) to 1 (maximum exposure). They reflect current exposure levels, except for climate change, in which case they reflect expected future exposure. All the grid layers used to construct the exposure maps have a resolution of 30 arcsec (ca. 0.9 km at the equator). To assess the impact of the aforementioned assumptions on our results, we carried out a sensitivity analysis (section 2.9). For this purpose, the ‘reference’ exposure maps were complemented with best-case and worst-case threat exposure maps, the details of which are given below.

Climate change

The calibrated distribution models of the studied species were projected to downscaled future climate conditions for the 2040 – 2059 period, as predicted by general circulation models (GCMs) under different representative concentration pathways (RPCs). The reference exposure map was created using RCP4.5, whereas RCP2.6 and RCP8.5 were used for the best-case and worst-case exposure maps, respectively. To select a number of GCMs, we first selected all GCMs that perform better than the median GCM performance (against observed temperature and precipitation values) following Knutti et al. (2013) and are available at the CCAFS Climate Data Portal (<http://www.ccafs-climate.org/>). Next, we maximized the dissimilarity between GCMs by selecting the GCM with the best performance in each node of the GCM family tree of Knutti et al. (2013), determined after cutting the tree at level 16 (Schlaepfer et al., 2017). This procedure resulted in the selection of 5 GCMs: CESM1(CAM5), GFDL-CM3, HADGEM2-ES, MIROC5, and MPI-ESM-LR.

For each of the GCMs, we created exposure maps for each of the studied species. Grid cells that were predicted to remain suitable (based on current suitability) were given an exposure value of 0, whereas those expected to lose suitability were given an exposure value of 1. In the reference exposure maps, grid cells predicted to remain suitable under novel climate conditions were given an exposure value of 0.5. Novel climate conditions were determined as those conditions outside

the range between the 5% and 95% percentile of the conditions used to calibrate the distribution models, using the *ensemble.novel* function of the BiodiversityR package. In the best-case exposure maps, novel climate conditions were given an exposure value of 0, whereas in the worst-case exposure maps, they were given an exposure value of 1. The overall exposure maps for each species were obtained by averaging the exposure maps corresponding to the five GCMs.

As many tree species are unlikely to be able to keep track of the fast-changing climate conditions through migration (Corlett & Westcott, 2013; Zhu, Woodall, & Clark, 2012), we aimed at obtaining conservative estimates of climate change vulnerability by only considering suitable habitat losses and no suitable habitat gains. Nevertheless, areas expected to become suitable were also identified as currently unsuitable areas for which at least four out of five GCMs predict presence under future climate conditions.

Fire

The current exposure to fire was derived from the MODIS Active Fire Detection data between 2013 and 2017 (NASA EOSDIS, 2018). Under the assumption that grid cells bordering cells where fires have taken place are equally under threat, the exposure to fire of each cell was calculated as the sum of the number of fires in a 3x3 grid cell window. The resulting fire frequency grid was rescaled between 0 and 1, with the maximum exposure set at a frequency of 5 or more (i.e. an average of one fire per year in the grid cell in question or its neighbouring grid cells). For the worst-case and best-case exposure maps, the maximum exposure was set at a fire frequency of 3 and 10, respectively.

Habitat conversion

The current exposure to habitat conversion was estimated using the most recent land use maps of Peru and Ecuador, freely available in vector format (MAE, 2012; MINAM, 2018). As a proxy for habitat loss resulting from habitat conversion, we constructed a grid layer reflecting the proportion of each grid cell within the potential distribution of TDF (section 2.5) that is currently converted to other land uses. This proportion was obtained by dividing each 30 arcsec grid cell in sixteen subcells, which were considered to be converted if their centre is currently covered by an anthropogenic land use. A second grid layer was constructed to estimate the impact of forest fragmentation resulting from habitat conversion, which may negatively affect tree species through increased edge effects and isolation (Lôbo, Leão, Melo, Santos, & Tabarelli, 2011; Vranckx,

Jacquemyn, Muys, & Honnay, 2012). We constructed this grid layer using a similar approach as Riitters, Wickham, O'Neill, Jones, & Smith (2000): The fragmentation value of each grid cell was set as equal to the proportion of a 3 x 3 grid cell window converted to land uses other than TDF. However, contrary to Riitters et al. (2000), the central grid cell of the window was not considered, so that grid cells entirely surrounded by converted grid cells are always assigned the maximum exposure value (i.e. a value of 1) for forest fragmentation. The reference estimate of the overall habitat conversion exposure was obtained as the average of the two aforementioned layers, except for entirely converted grid cells, which were always given the maximum exposure value. In the best-case estimate, the layer estimating the impact of fragmentation was not included, whereas in the worst-case estimate, this layer was constructed using a 5x5 grid cell window, thus assuming that edge effects may act on a distance larger than the size of one grid cell (ca. 0.9 km).

Overexploitation

Human population density (Lloyd et al., 2017) and distance to the nearest road were used as proxies for the current exposure to overexploitation for local and commercial purposes respectively. As rural communities in dry forests usually collect wood up to only a few kilometres from where they live (Dons, Bhattarai, Meilby, Smith-Hall, & Panduro, 2016; Ektvedt, 2011), the population density map was smoothed with a moving weighted average window of 9x9 grid cells, roughly corresponding to a distance of ca. 4 km, with the weight decreasing linearly from the central grid cell of the window towards the outer grid cells. The resulting grid was rescaled between 0 and 1, with the maximum exposure corresponding to a population density of 95 people per grid cell or more. This threshold corresponds to the 90th percentile of the population density values of the rural areas in our study region; it is based on the assumption that only the upper 10% of the most populated rural areas are maximally exposed to overexploitation. For the best-case and worst-case exposure maps, the maximum exposure was set at population density values of 147 and 51, corresponding to the 95th and 80th percentiles of the rural population density values, respectively. The exposure to overexploitation for commercial uses was assumed to decrease linearly with the distance to the nearest road, with the minimum exposure corresponding to distances beyond 10 km. This threshold was based on the findings of Asner et al. (2006), who found that more than 90% of the selective logging in the Brazilian Amazon occurs within a 10 km distance from roads. The thresholds of the worst and best-case exposure maps were set at 15 km and 5 km, respectively. The overall exposure maps were obtained by averaging the exposure maps

for local and commercial uses. As wood extraction in protected areas is regulated, exposure values within protected areas were multiplied with 0.25, 0.50 and 0.75 in the best-case, reference and worst-case scenarios, respectively.

Overgrazing

The current exposure to overgrazing was estimated as the number of tropical livestock units (TLUs) per grid cell, using the Gridded Livestock of the World v2.0 dataset (Robinson et al., 2014). One TLU is equal to a ruminant animal of 250 kg live weight; with conversion factors of 0.7 for cattle and 0.1 for goats and sheep (Chilonda & Otte, 2006). As most livestock in the study region is free-roaming, the TLU density grid was smoothed using a moving weighted average window of 9 x 9 grid cells, under the assumption that the area grazed by animals extends ca. 4 km from their stables or corrals (Perevolotsky, 1991).

Optimal livestock densities in dryland ecosystems strongly depend on precipitation levels (Pallas, 1986). For the lowland TDFs of our study region, most of which are characterized by an annual precipitation less than 250 mm, optimal stocking rates have been estimated as ca. 20 to 25 TLU per 30 arcsec grid cell (Parodi & Zambrano 1967; Solano-Zamora 1977, as cited by Perevolotsky 1991). To the best of our knowledge, no estimates of optimal stocking rates exist for the montane TDFs of our study region, but estimates in ecosystems with similar climates range between ca. 40 and 70 TLU per 30 arcsec grid cell (Isabirye, Magunda, Poesen, Maertens, & Deckers, 2013; Kihui & Amuakwa-Mensah, 2015; Mulindwa, Galukande, Wurzinge, Okeyo Mwai, & Sölkner, 2009). Optimal stocking rates are often based on the “take half, leave half” rule of thumb, implying that the forage consumption rate should be half of the forage production rate. Stocking rates 2.5 times higher than the optimal stocking rates (i.e. forage consumption rate exceeding biomass production rate) were therefore assumed to correspond to a maximum overgrazing exposure. Using the lower ends of the aforementioned ranges of optimal stocking rates, the maximum reference exposure was set at 50 TLU in grid cells with less than 250 mm annual precipitation, increasing linearly up to 100 TLU in areas with 1000 mm annual precipitation or more. For the worst-case and best-case exposure maps, TLU densities corresponding to a maximum overgrazing exposure were obtained by multiplying the optimal stocking rates by 2 and 3, respectively. In this way, the maximum overgrazing exposure of the worst-case exposure map was set to vary between 40 TLU to 80 TLU, and between 60 and 120 TLU for the best-case estimate. As livestock access to protected areas is usually strictly regulated, the exposure inside

protected areas was capped at a maximum of 0, 0.25 and 0.50 for the best-case, reference and worst-case exposure map, respectively.

2.7 Sensitivity and vulnerability

The sensitivity of the studied species to each of the five threats was estimated using a set of 18 species traits (Figure 1). In line with the framework proposed by Williams et al. (2008), traits providing information on species' adaptive potential were included in the estimation of the sensitivity values. Most of the traits are biological traits, but species cultivation status (i.e. if a species is cultivated or not), timber provision, and fuelwood provision were also included.

The relation between each of the traits and the sensitivity of tree species to each of the five threats were established through a literature study and expert judgement. The rationale is documented in Table S2 (Supporting Information 1). In order to obtain sensitivity scores, we assigned each trait a weight in accordance with the expected magnitude of its influence on species sensitivity, ranging from 1 to 5, i.e. very low to very high influence (Figure 1). In turn, each trait level was linked with a partial sensitivity score in accordance with the expected nature of its influence on species sensitivity, varying between zero (i.e. maximally decreasing species sensitivity) and one (i.e. maximally increasing species sensitivity). For example, bark thickness was given a 'very high' trait weight for estimating species sensitivity to fire, because it has been identified as the most important trait in determining tree sensitivity to fire (Brando et al., 2012; Pinard & Huffman, 1997; VanderWeide & Hartnett, 2011). Species with thick (> 1 cm), intermediate (0.5 – 1 cm) and thin bark (< 1 cm) were given partial fire sensitivity scores of 0.5, 0.75, and 1, respectively. The compiled trait data are available in Supporting Information 4 and a spreadsheet with the trait-based sensitivity scoring approach is available in Supporting Information 5.

The overall sensitivity of species to each of the five threats was calculated as the weighted mean of the partial sensitivity scores (Figure 1), using the trait weights mentioned above. In some cases, specific trait levels were considered to play a decisive role in determining species sensitivity, in which case a fixed sensitivity score was used. More specifically, an overgrazing sensitivity score of 0.25 was given to all species with unpalatable leaves, and an overexploitation sensitivity of 0.25 was given to species that are not used for timber nor firewood. A value of 0.25 was chosen because these trait levels do not necessarily render species entirely insensitive (e.g., a species with unpalatable leaves may still experience negative effects of overgrazing such as soil compaction and trampling).

Species-specific vulnerability maps were obtained by multiplying the threat exposure maps with the species-specific sensitivity values (Figure 2). The grid cells of these vulnerability maps were categorized into five categories (zero, low, medium, high and very high vulnerability), using thresholds of 0.01, 0.25, 0.50 and 0.75 respectively. In order to identify the most vulnerable species, we calculated two different statistics: (1) the proportion of grid cells within species distribution ranges with a high to very high vulnerability to at least one of the five threats, and (2) the average vulnerability towards all five threats of the grid cells within species distribution ranges.

2.8 Priority maps for restoration and conservation

The vulnerability maps were used to create species-specific maps with priority restoration and conservation actions. For this purpose, we considered climate change vulnerability and vulnerability to current threats separately, the latter of which was calculated as the highest among the vulnerabilities to fire, habitat conversion, overexploitation, and overgrazing. However, as different threat factors are likely to have additive or even synergistic effects on species' vulnerability (Côté, Darling, & Brown, 2016), the vulnerability of a grid cell towards current threats was adjusted to 'very high' where its vulnerability to at least three current threats was 'high', and adjusted to 'high' if the vulnerability to at least three current threats was 'medium'.

Based on the vulnerability to climate change and current threats, we present a spatially explicit and species-specific planning strategy. First, the *in-situ* conservation of seed sources and seed collection for tree planting activities is prioritized in areas with low vulnerability to current threats and climate change. In areas with low vulnerability to current threats, the likelihood that human disturbance has led to increased inbreeding and reduced genetic variability is reduced (Lowe, Boshier, Ward, Bacles, & Navarro, 2005), whereas low climate change vulnerability enhances the likelihood of continued seed production under future climate conditions. To maximize the probability of species presence in these areas, the modelled distribution was reduced to only include grid cells with centres within 5 km of known occurrence localities. Second, *ex-situ* conservation or translocation of populations is prioritized in areas with high climate change vulnerability, in order to safeguard the genetic resources that might disappear due to climate change. Third, active planting or assisted regeneration is recommended in areas under high to very high current threat vulnerability but low climate change vulnerability, provided measures are in place to lower threat pressure. Areas with a high or very high vulnerability to current threats were

assumed to be the most in need of restoration intervention, whereas the low climate change vulnerability increases the probability of survival of the planted or regenerating trees under future climate conditions. The maps also indicate the areas that are expected to become suitable under future climate conditions (section 2.6). In addition to the species-specific maps, we also constructed general maps depicting priority areas for restoration and *in-situ* conservation of seed sources, based on the proportion of species per grid cell for which the grid cell in question is recommended for conservation or restoration. To avoid the confounding effects of species richness gradients, these proportions were calculated based on the number of species for which the grid cell in question is predicted to be suitable under current climate conditions.

2.9 Sensitivity analysis

In light of the fact that several of the assumptions on threat exposure and sensitivity are based on literature and expert judgement, and that trait data was incomplete for some species, we assessed the robustness of our results with a one-at-a-time sensitivity analysis, analysing the impact of single parameters separately (Saltelli et al., 2008). The sensitivity analysis included three different aspects: (a) methodological decisions made when constructing threat exposure layers, (b) trait weighting schemes used to estimate sensitivity values, and (c) missing traits. For each aspect, two ‘treatments’ of the vulnerability assessment were applied, the results of which were compared with those of the ‘reference’ treatment (i.e. the original results). The first aspect was evaluated by creating a best-case and worst-case version of each exposure map (treatment 1 and 2), as described in section 2.6. For the second aspect, two alternative trait weighting schemes (treatment 3 and 4) were used. In the ‘converging weights’ scheme, the reference weights, ranging between 1 and 5, were converted to weights between 2 and 4 (i.e. a value of 1 was summed to the weights below 3 and subtracted from the weights above 3). Similarly, in the ‘diverging weights’ scheme, the reference weights were converted to weights between 0 and 6. Third, the sensitivity to missing trait values was assessed by replacing all missing trait values with trait levels that confer a minimum sensitivity and a maximum sensitivity to each of the five threats (treatment 5 and 6). The sensitivity analysis was carried out on the maps with priority restoration and conservation actions. For each species, six alternative versions of this map were made, corresponding to the six sensitivity treatments described above. The sensitivity of our results towards the treatments mentioned above was calculated as the percentage of grid cells within species distribution ranges that changes from one category to another (e.g., from ‘recommended for *in-situ* conservation of

seed sources' to 'recommended for assisted regeneration and active planting') as compared to the reference map.

3 RESULTS

3.1 Selected tree species

The selected tree species (Supporting Information 1 Table S3), all native to our study region, belong to 24 families, the most speciose family being Fabaceae (16 species), followed by Malvaceae (6 species) and Boraginaceae (3 species). 18 out of 50 species are endemic to Peru and Ecuador, 2 of which occur only in our study region (*Schrebera americana* and *Tetrasida chachapoyensis*).

The selected tree species comprise the most important species of our study region, both in frequency and abundance. They account for 68% of the total frequency and 83% of the total abundance of 330 DRYFLOR plots in northwestern Peru (Banda et al., 2016), 58% of the total frequency and 64% of the total abundance of 48 transects in southern Ecuador (Espinosa & Cabrera, 2011), and 59 % of the total frequency and 58% of the total abundance of 92 plots of the Marañón valley TDFs (Marcelo-Peña et al., 2016).

3.2 Species distribution modelling

Mean AUC values of the species distribution models ranged from 0.71 to 0.96, with an average value of 0.86 (Supporting Information 1 Table S3), indicating good to excellent accuracy. Considering the measures taken to avoid inflated AUC values (section 2.5), we considered these values satisfactory for using the distribution maps in the vulnerability assessment. The average AUC value of the individual modelling algorithms ranged from 0.77 (DOMAIN) to 0.85 (boosted regression trees). The ensemble model was the most accurate for 20 of 50 species, followed by boosted regression trees (10 species), stepwise boosted regression trees (4 species) and MaxEnt (4 species).

3.3 Vulnerability

The relative frequency of the different vulnerability levels to the five threats within the current distribution range of each of the 50 tree species is presented in Figure 3. All species showed high to very high vulnerability to most of the threats in a considerable part of their distribution range, with an average value of 21% (± 7 SD) for habitat conversion, 20% (± 8 SD) for overexploitation,

11% (± 9 SD) for overgrazing, 8% (± 4 SD) for fire, and 4% (± 9 SD) for climate change, respectively. When considering medium to very high vulnerability levels, these average values increase to 68% (± 26 SD) for overexploitation, 45% (± 30 SD) for overgrazing, 37% (± 10 SD) for habitat conversion, 18% (± 6 SD) for fire, and 13% (± 10 SD) for climate change. On average, 46% (± 10 SD) of the grid cells within species distribution ranges had a high to very high vulnerability for at least one of the five threats. When medium to very high vulnerability levels are considered, this number increases to 87% (± 9 SD).

The average vulnerabilities of the 50 tree species are shown in Figure S1 (Supporting Information 1), with the highest reference vulnerability values observed for overexploitation (0.35 ± 0.10 SD), followed by overgrazing (0.26 ± 0.12 SD), habitat conversion (0.24 ± 0.06 SD), climate change (0.13 ± 0.10 SD), and fire (0.11 ± 0.04 SD).

The species with the largest proportion of their distribution ranges classified as highly to very highly vulnerable to at least one of the five threats are *Triplaris cumingiana*, *Schrebera americana*, *Maclura tinctoria*, *Loxopterygium huasango*, and *Handroanthus chrysanthus* (Figure 3). In terms of average vulnerability to all five threats, the most affected species are *Terminalia valverdeae*, *Coccoloba ruiziana*, *Schrebera americana*, *Cordia macrantha*, and *Caesalpinia paipai* (Supporting Information 1 Figure S1).

3.4 Priority maps for restoration and conservation

Maps highlighting priority areas for restoration and conservation actions were made for all the selected species, distinguishing between areas that are prioritized for (i) in-situ conservation of seed sources and seed collection for tree planting activities, (ii) assisted regeneration or active planting, and (iii) ex-situ conservation of seed sources. Figure 4 shows such a map for *Leucaena trichodes* as an example. The vulnerability maps and maps highlighting restoration and conservation priorities are available in an online tool (section 4.4). All maps are available in a reference, best-case and worst-case version, based on the corresponding assumptions made when creating the exposure maps.

Figure 5 shows the proportion of species per grid cell for which in-situ conservation of seed sources and restoration are prioritized. Only a relatively small part of our study region is prioritized for the in-situ conservation of seed sources (panel a), whereas large parts are indicated

as priority areas for the assisted regeneration and active planting of the studied tree species (panel b).

3.5 Sensitivity analysis

The results of the sensitivity analysis (Supporting Information 1 Table S4) reveal that the maps with priority areas for restoration and conservation are relatively robust against the chosen trait weighting schemes and missing traits, but relatively sensitive to the methodological decisions made when creating the threat exposure layers. In the best-case priority maps, an average of 18% (± 6 SD) of the grid cells within species' distribution ranges changed from one category to another as compared to the reference maps, whereas an average of 25% (± 8 SD) of grid cells changed from one category to another when considering the worst-case exposure estimates.

4 DISCUSSION

4.1 Guiding restoration and conservation interventions

We quantified the effects of five threats (climate change, habitat conversion, fire, overgrazing and overexploitation) on the vulnerability of 50 common tree species of the TDFs of northwestern Peru and southern Ecuador. Our results reveal that anthropogenic threats are pervasive in these TDFs, with tree species facing medium to very high vulnerability levels to at least one of the five threats in an average of 87% of their distribution range (Figure 3), underscoring the need to increase restoration and conservation efforts in this highly threatened ecosystem.

Our results suggest that current levels of habitat conversion, overexploitation, and overgrazing pose higher threats to the persistence of populations of most of the selected species than climate change (Figure 3). This is in line with Manchego et al. (2017), who found current habitat conversion rates to result in higher annual area losses than future climate change for tree species in the TDFs of southern Ecuador. Our models also predicted suitability gains at lower altitudes for many species, a consequence of the predicted increases in annual precipitation levels (Manchego et al., 2017). TDFs often harbour relatively high human population densities (Miles et al., 2006; Murphy & Lugo, 1986), which are commonly associated not only with habitat conversion but also high levels of overexploitation and overgrazing. The negative effects of such anthropogenic pressure on the remaining TDFs in our study region is confirmed by the results of a survey of natural regeneration of tree species throughout the TDFs of the Lambayeque region (Peru), in

which only one-third of the studied tree species presented healthy regeneration levels (Fremout et al., unpublished data). In order to better inform management decisions for ecosystems under pressure from resource extraction, which often affects species and ecosystem vulnerability in developing countries disproportionately (Schulze et al., 2018; Yiming & Wilcove, 2005), vulnerability assessments should categorically include threat factors other than climate change and habitat conversion. Similarly, restoration and conservation efforts should not overlook the importance of protecting TDFs from overexploitation and overgrazing.

Using two different statistics to identify the most vulnerable species (section 3.3), we found that only *Schrebera americana* occurs in the top-5 of both statistics. Its high vulnerability ranking is mainly a consequence of its high climate change vulnerability, which is likely related to its endemic status and narrow ecological niche, which tends to increase the vulnerability of species populations to climate change (Pearson et al., 2014; Thuiller, Lavorel, & Araújo, 2005). Several other species occurring in the top-5 of either one of both statistics are endemic to Peru and Ecuador (*Cordia macrantha*, *Loxopterygium huasango*, *Terminalia valverdeae*, *Caesalpinia paipai* and *Coccoloba ruiziana*). Among these endemics, only *C. paipai* has been assessed in the IUCN Red List. While it was given the “least concern” status (LC), only its presence inside protected areas is given as justification (Groom, 2012). While the global conservation status of these endemic species will largely depend on the restoration and conservation efforts in our study region, only *L. huasango* and *C. paipai* have thus far been included in restoration plantings or protected seed sources in the TDFs of northern Peru (Cerrón, Fremout, Atkinson, Thomas, & Cornelius, 2019). Future restoration and seed conservation efforts should urgently be extended to include a wider variety of species.

Considering the limited resources available for restoration and conservation interventions, there is a need to identify priority areas (Birch et al., 2010; Brooks et al., 2006; Molin, Chazdon, Frosini de Barros Ferraz, & Brancalion, 2018). Contributing to this need, we present a user-friendly online tool with species-specific and general maps highlighting recommended restoration and conservation actions. The conservation of seed sources is predominantly prioritized in protected areas (Figure 5a), underlining the pervasiveness of anthropogenic threats outside of protected areas. It is therefore no surprise that large parts of the distribution of most species are highlighted as priority areas for restoration (Figure 5b). We distinguish between converted and non-converted areas, as they may require different types of restoration interventions. For example, due to high

pressure on arable land in our study region, it is unlikely that agricultural lands will be used to implement large-scale restoration projects with biodiversity conservation purposes; other forest landscape restoration strategies such as agroforestry may be more appropriate.

4.2 Improving tree species vulnerability assessments

The results of the sensitivity analysis indicate that our approach is sensitive to the methodological decisions made during the construction of threat exposure maps. While it is relatively straightforward to create threat exposure maps with freely available proxy data (e.g., Gaisberger et al., 2017; van Zonneveld et al., 2018), standardizing exposure values (for example between 0 and 1) is not trivial, as it often requires decisions on thresholds of exposure proxies (e.g., livestock densities). Quantitative studies on the relationship between such proxies and tree species vulnerability are largely lacking, making it difficult to make these decisions in a well-informed way. Vulnerability assessments should recognize this source of uncertainty, for example by considering different versions of exposure maps. More research is needed on the thresholds and tipping points of exposure levels which, once crossed, significantly impact the persistence of tree populations, for example on the livestock densities that can be sustainably supported by TDFs.

In areas with high anthropogenic disturbance, trait-based filtering is expected to drive plant community composition towards a higher abundance of species with traits that make them less sensitive to these disturbances (Bernhardt-Römermann et al., 2011; Mouillot, Graham, Villéger, Mason, & Bellwood, 2013). While there is anecdotal evidence for such trait-based community filtering in our study region (e.g., overgrazed forests dominated by grazing-resistant species in the understorey), formal studies on this subject are lacking. Recently, Cueva-Ortiz et al. (2019) found that anthropogenic disturbances affect forest structure and diversity in the TDFs of southern Ecuador, but species traits were not part of their study. Future research on trait-based filtering in response to anthropogenic threats would contribute to a better understanding of the importance of different traits in determining species' sensitivities to these threats.

4.3 Study limitations

The reliability of our results depends on the quality of the exposure maps. While the proxies for fire, habitat conversion, overgrazing, and climate change are closely linked to the exposure to these threats, this is less the case for the exposure to overexploitation, for which human population density and distance to the nearest road were used as proxies. It is clear that these two variables

can only partly describe the exposure to this threat, which is also influenced by other socio-economic characteristics (e.g., poverty status, law enforcement). In regions where spatially explicit data on such characteristics are available, they could be incorporated in vulnerability assessments.

The use of species traits allowed us to obtain sensitivity estimates in a transparent and scalable way, while also avoiding two other issues of expert appraisal of species sensitivity: Different experts may have different understandings of the concept of sensitivity (Gaisberger et al., 2017) and some species may be well-known by very few experts. The latter is especially relevant in our study region, which is vastly understudied and characterized by high endemism. Nevertheless, the trait-based approach also has limitations; the most important being the availability of data. In order to minimize the number of missing trait data, we focused on a set of well-known 'soft' functional traits, which are easy-to-measure and serve as proxies for functional mechanisms (Lavorel & Garnier, 2002), complemented by a few non-biological traits (e.g. firewood provision). However, more accurate sensitivity estimates could be obtained by using 'hard' traits more directly linked to these functional mechanisms (Lavorel & Garnier, 2002). For example, leaf flammability or observed fire mortality rates would be highly relevant to estimate species sensitivity to fire. It is clear that more trait-based research is needed to improve vulnerability assessments, especially in tropical ecosystems, where 'hard' trait data are usually scarce.

While we included the five most important threats to tree species in our study region, the list is not complete, nor does it consider the indirect consequences of the threats studied. For example, populations of the keystone species *Prosopis pallida* have experienced mortality levels exceeding 75% in some regions (SENASA, 2016). Current research suggests that the causal agent could be the citrus tristeza virus (Mialhe, 2019), whose fast dispersal and disastrous impact is possibly related to ongoing climate change, which may have resulted in more favourable conditions for its yet-to-be-determined vector. Such indirect climate change effects are impossible to predict with our approach, underlining the need to interpret our climate change vulnerability estimates with care. Other indirect impacts of climate change include an increase in annual precipitation levels which is likely to lower the altitude threshold above which rainfed agriculture is possible, which will presumably lead to increased habitat conversion rates in the future. Additionally, higher annual precipitation combined with increasing dry season aridity will likely lead to an increase in fires fuelled by the biomass of annuals (Bravo, Kunst, Grau, & Aráoz, 2010; Staal et al., 2018), and may even cause an increase in livestock pressure during the dry season.

4.4 Final considerations

Our study provides the first tree species vulnerability assessment spanning the TDFs of northwestern Peru and southern Ecuador, using a methodology that can easily be adapted to other countries and ecosystems. The results are available in a tool (https://bioversityinternational.shinyapps.io/vulnerability_assessment/) that is easily interpretable by practitioners and policy makers. We hope that uptake of the tool will contribute to a science-based restoration and conservation planning in the region, and that national and local research institutions will become integral players in improving the vulnerability assessment by collection of more field data.

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6 CONFLICT OF INTEREST

The authors declare no conflict of interest.

7 DATA SHARING AND ACCESSIBILITY

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.11794365>, including the trait data used to estimate species sensitivities (Supporting Information 4), the trait-based sensitivity scoring method (Supporting Information 5), the R script used for the species distribution modelling (Supporting Information 6), the necessary data to run the distribution modelling script (Supporting Information 7), and the

calibrated ensemble distribution models (Supporting Information 8). The species occurrence records in Supporting Information 7 do not include occurrence records that were directly provided by researchers. Supporting Information 4 to 6 are also available in the supplementary material of this article.

8 TABLES

Table 1: Summary of the expected impacts of the five key threats and the spatial layers used to estimate the exposure to these threats.

Key threat	Impact at population level	Indicators	Spatial layers
Climate change	Negatively or positively affects the survival and reproduction of individuals	Loss of modelled suitability	Suitability maps projected to future climate conditions using 5 Global Climate Models (GCMs) and three representative concentration pathways (RCP2.6, RCP4.5 and RCP8.5)
Fire	Causes tree mortality, reducing abundance; inhibits or promotes natural regeneration; fragments populations	Fire frequency per unit area	NASA Fire Information for Resource Management System (FIRMS). MODIS Active Fire Detections 2012 – 2017 (NASA EOSDIS, 2018)
Habitat conversion	Eliminates and fragments natural populations; promotes species that are cultivated or tolerated by farmers	Percentage of a grid cell converted to land use types other than tropical dry forest Proportion of neighbouring grid cells converted to land use types other than tropical dry forest	National land cover maps of Peru and Ecuador in vector format (MAE, 2012; MINAM, 2018)
Overexploitation	Reduces tree density and genetic diversity; fragments populations	Human population density Distance to the nearest road Presence/absence of a protected area	Global human population density (Lloyd, Sorichetta, & Tatem, 2017) National road network datasets of Peru and Ecuador in vector format (IGM, 2017; MTC, 2018) Protected areas (SERNANP, 2018; SNPD, 2018)

Overgrazing	Inhibits natural regeneration; can promote seed dispersal of tolerant species	Number of tropical livestock units per unit area Presence/absence of a protected area	Gridded Livestock of the World v2.0 (Robinson et al., 2014) Protected areas (SERNANP, 2018; SNPD, 2018)
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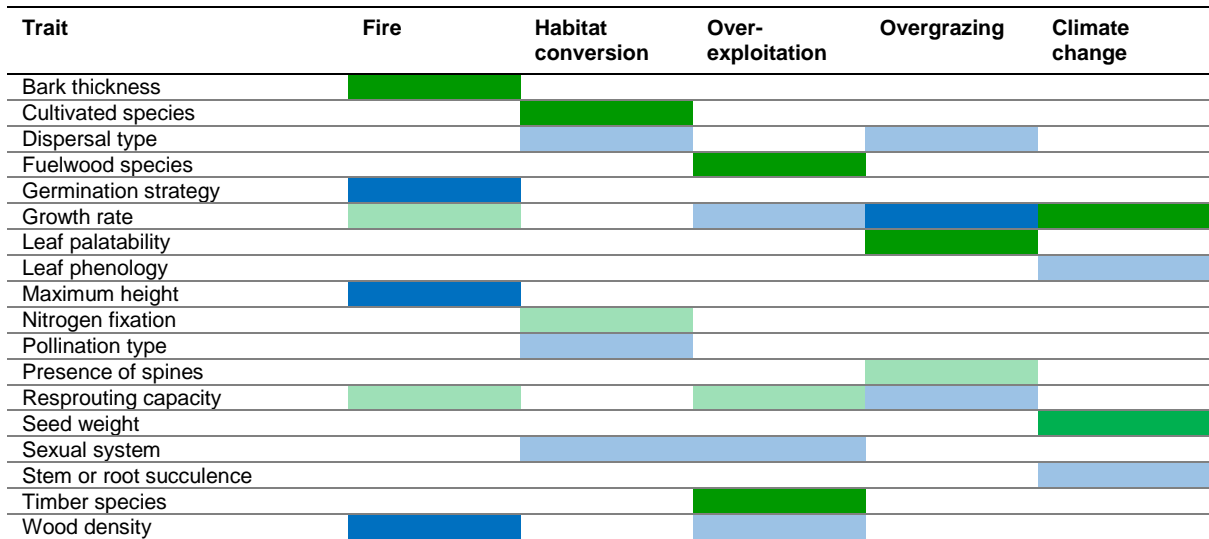
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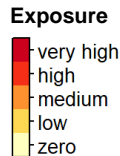
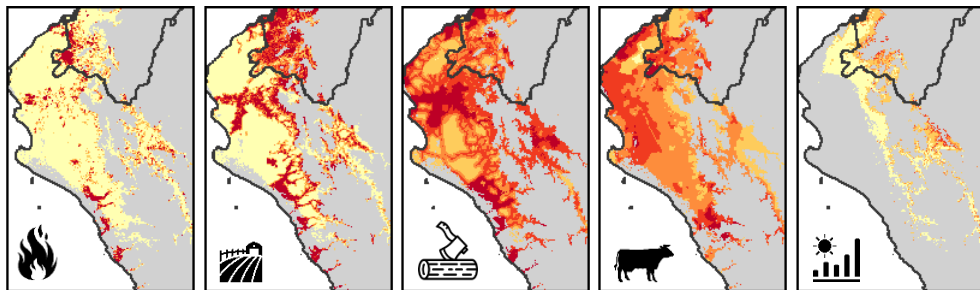


Trait importance (weight):

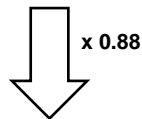
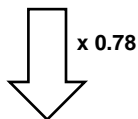
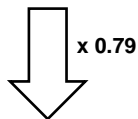
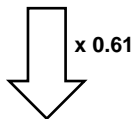
Very low (1) Low (2) Medium (3) High (4) Very high (5)



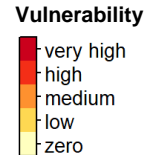
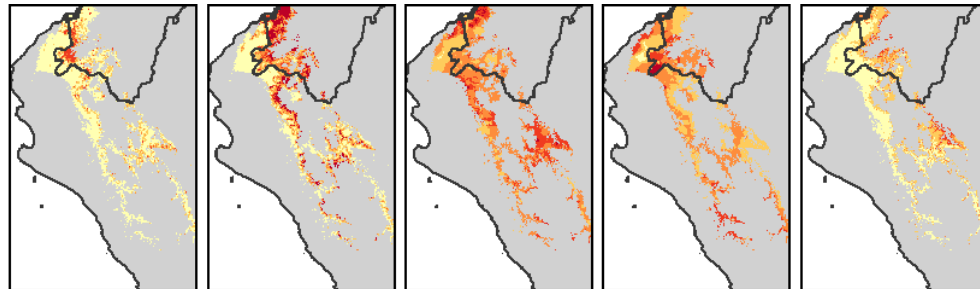
Exposure maps



Mask by distribution range and multiply by trait-based sensitivity estimates



Vulnerability maps



Fire

Habitat conversion

Overexploitation

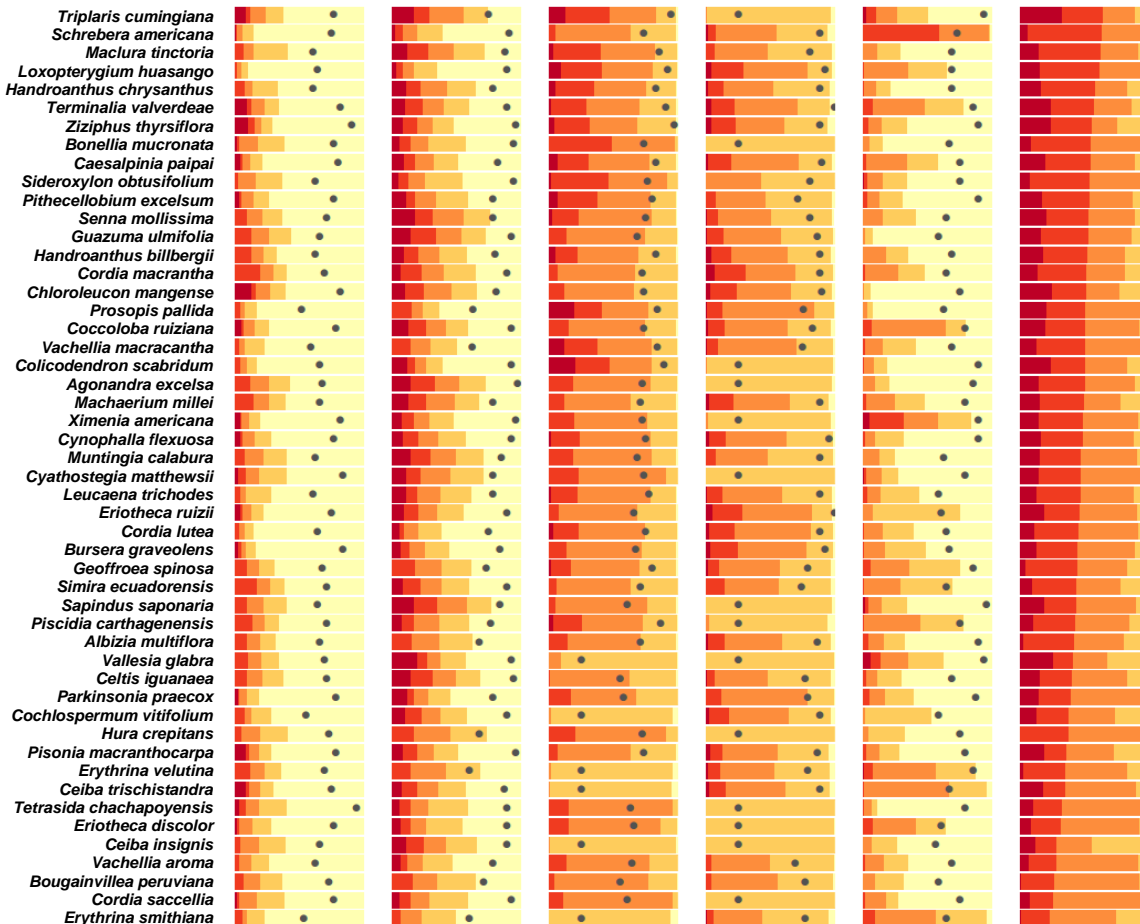
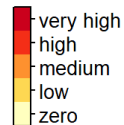
Overgrazing

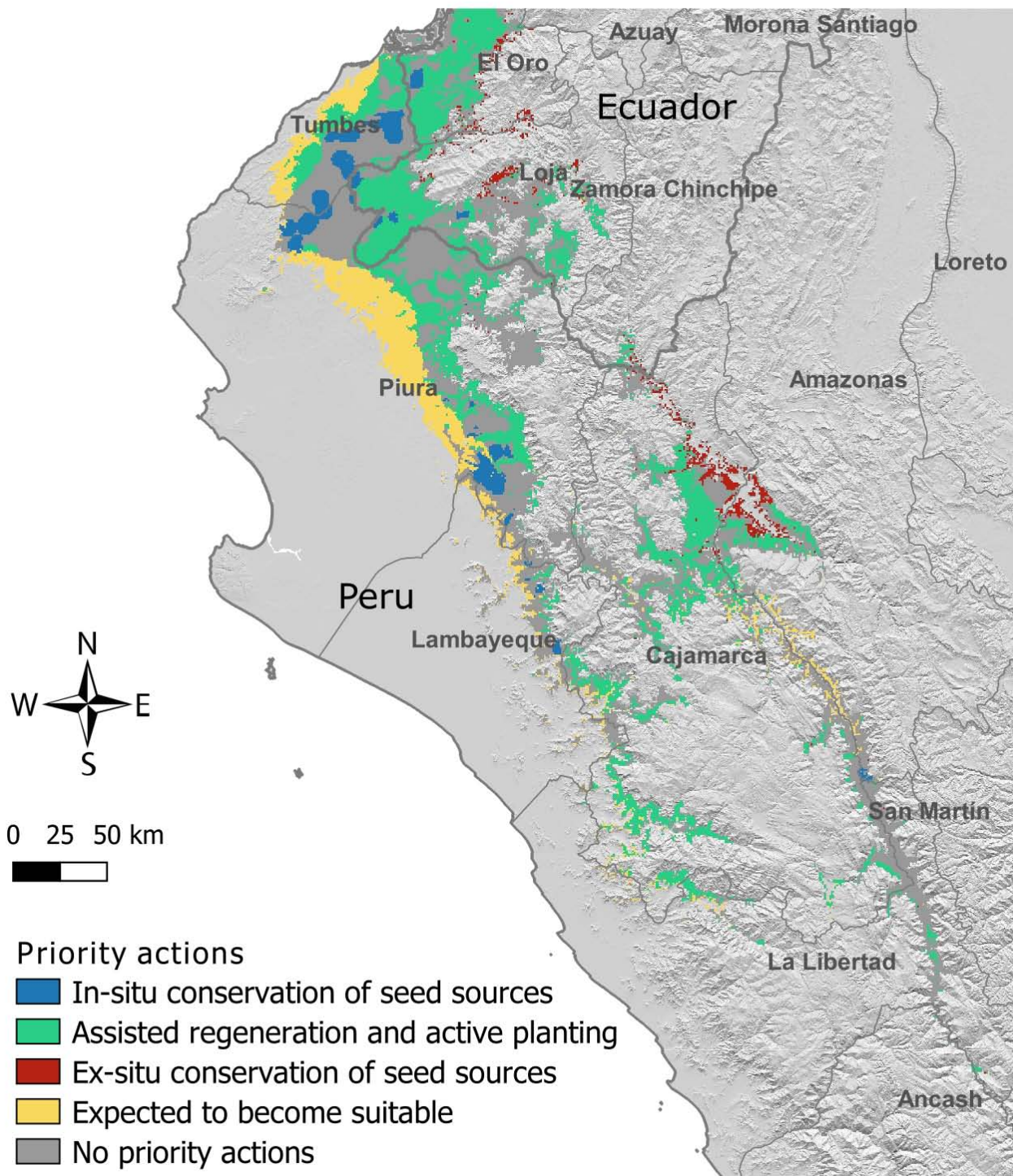
Climate change



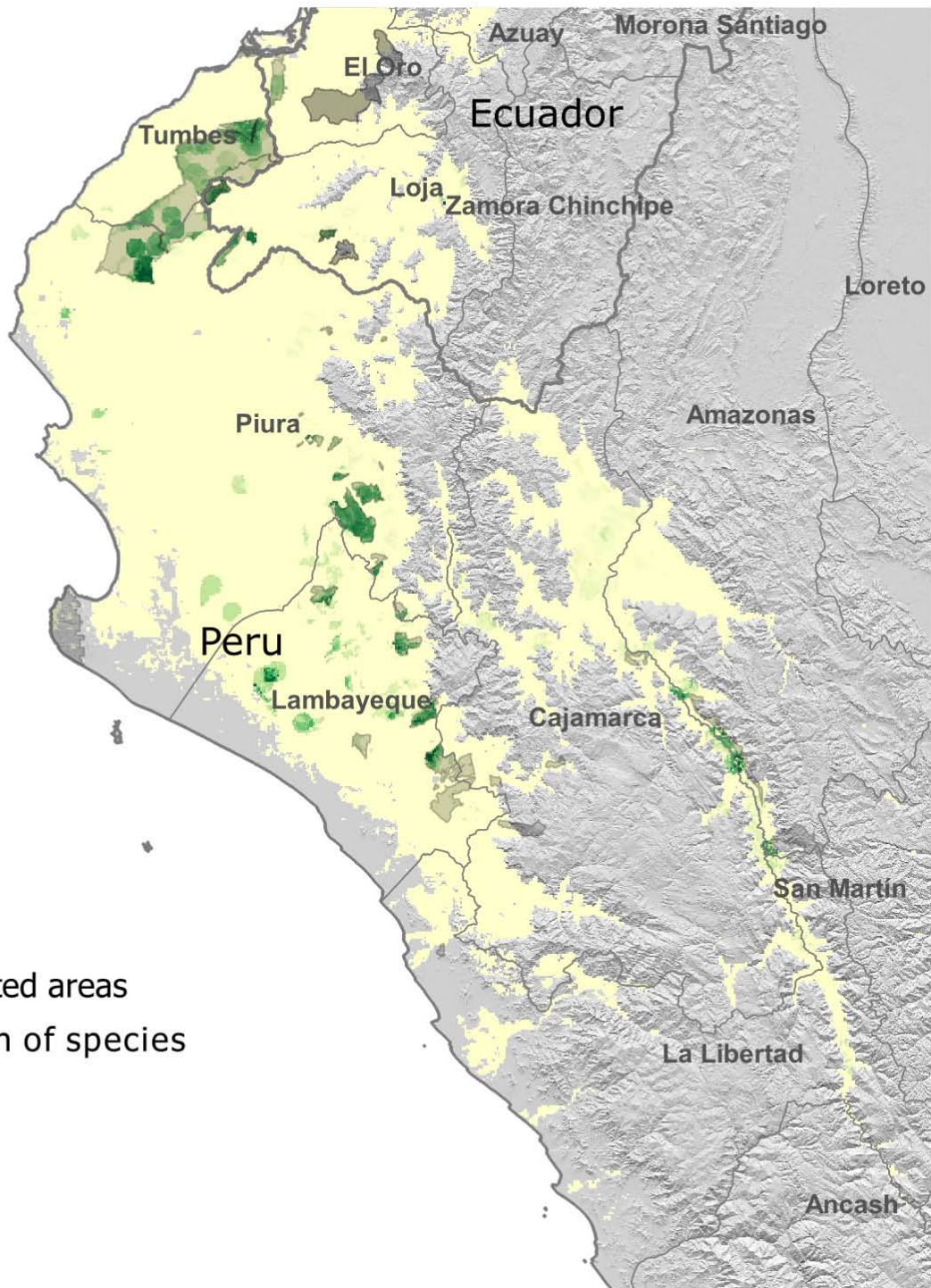
Max.

Vulnerability





(a)



(b)

