

# Priority areas for the conservation of tree species in a neotropical seasonal dry forest under deforestation and climate change scenarios

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## HIGHLIGHTS

- Deforestation reduced by 11–20% the potential distribution of three dominant species.
- Protected areas harbor <10% of the potential distribution of these species in current and future climate scenarios.
- In future scenarios, potential distribution of these species can occur in stable climatic areas.
- Measures need to be taken to reduce deforestation and increase protected areas.

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## ABSTRACT

The Piedmont Forest in northwest Argentina, like most Neotropical seasonal dry forests, is one of the world's most threatened ecosystems due to deforestation and climate change. To plan conservation strategies aimed at sustaining this forest type, the response to projected changes in habitat conditions must be anticipated. Our objectives were to determine the potential distribution and identify priority areas for conservation that remain stable for saplings and mature trees of three dominant species (*Anadenanthera colubrina*, *Calycophyllum multiflorum*, and *Phyllostylon rhamnoides*) in land use plan categories, protected areas, and forest types under current and two future climate scenarios in northwest Argentina. *Calycophyllum multiflorum* has the smallest current potential distribution of the three species, but expands to have the largest potential distribution under future climate scenarios. Deforestation reduced by 11–20 % and protected areas harbor < 10 % of the potential distribution of the three species in both age classes in current and future scenarios. In future scenarios, and compared to the current period, the overlap of the potential distribution will increase in the highest protection category, but also for areas categorized as low conservation value that can be transformed according to the land use plan. Half or more of the co-occurring potential distribution of each species, in each age class in current and future scenarios occurs in the Piedmont Forest. Three priority areas for conservation were identified totaling 5483 km<sup>2</sup> of which 9 % are currently within protected areas. Thus, at the end of this century the Piedmont Forest is likely to maintain its structure and function if measures are taken to ensure that natural tree regeneration can occur. In the face of future climate change, management policies can satisfy long-term conservation planning necessary to ensure persistence of Piedmont Forest function by protecting priority areas identified in this study.

## 1. Introduction

Since the 1960 s global forest area has decreased dramatically and anthropogenic climate change is altering the local, regional and global

climatic conditions of forests (FAO, 2020). These changes have resulted in biodiversity loss at an unprecedented rate, severely impacting ecosystem service provision and therefore the well-being of societies (Diaz et al., 2018). Biodiversity loss results from the transformation of

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natural environments that reduces the area of suitable habitat for species and disrupts connectivity of habitat, making species more vulnerable to extinction (Newbold et al., 2015). Exacerbating this problem, the pace of anthropogenic climate change is faster than the ability of many species to adapt, especially those with long lifespans, such as trees, and many species are rapidly losing suitable climatic ranges (Thurman et al., 2020).

Trees represent the largest source of biomass within forests. To date approximately 58,000 tree species have been described, of which 30 % are threatened with extinction in the short term (BGCI, 2021). Currently, deforestation is the main threat to tree species, while climate change is becoming a growing threat (Tejedor Garavito et al., 2015; BGCI, 2021). Tree species extinctions are in some cases immediate, but in other cases there may be a lag effect, which is referred to as extinction debt (Vellend et al., 2006). Extinction debts are more likely in long-lived species (Kuussaari et al., 2009) such as tree species with life spans of hundreds of years, that may have become established during favorable environmental conditions, and once established are able to persist in areas that no longer have suitable conditions for future regeneration (Talluto et al., 2017). Changes induced by climatic conditions overlap with deforestation, therefore to ensure successful regeneration it is necessary to implement landscape scale conservation and land use planning efforts that mitigate or avoid tree extinctions (Dunckel et al., 2017).

Protecting forests and adequate forest management are the most effective strategies for biodiversity conservation, in general, and tree species conservation, in particular, under given climate change (Griscom et al., 2017). Most countries have committed to protect at least 30 % of their land by 2030 under the Kunming-Montreal Global Biodiversity Framework: 30 × 30 strategy (Eckert et al., 2023). Climate change represents a challenge for biodiversity conservation as suitable habitat conditions for species shift location, potentially moving outside of protected areas where they are currently found (Shrestha et al., 2021). Therefore, a fundamental step in designating protected area systems that halt biodiversity loss despite climate change is to determine species' potential future distributions (Dobrowski et al., 2021). Identifying priority areas that are currently occupied by a given desired species and will continue to be in the future (i.e., climatic refugia; Keppel et al., 2012; Keppel et al., 2015) is a key strategy. Climatic refugia are critical when conditions in the broader landscape are not adequate to ensure species persistence (e.g., due to deforestation, global warming, increase in frequency and intensity of fires), and can be a source of individuals that continue to reproduce, with some young trees potentially adapted to new conditions (Keppel et al., 2012). Prioritization of climatic refugia is important because not all species will be able to disperse or migrate to follow suitable environmental conditions, either because of the rapid rate of change or because of fragmentation of natural environments creating barriers that some species cannot cross (Carroll et al., 2010; Dobrowski et al., 2021). Another key consideration in sustaining biodiversity is the management of the human-dominated matrix within which protected areas are embedded (Arroyo-Rodríguez et al., 2020). Land use plans are particularly relevant in countries or regions with high levels of biodiversity that are being transformed at high rates allowing to achieve different trade-offs between social, economic and conservation objectives (Martinuzzi et al., 2021).

Seasonal dry forests are deciduous or semi-deciduous forests with pronounced precipitation seasonality (Collevatti et al., 2013) and are considered among the most threatened forest types in the world due to the combination of deforestation and climate change (Portillo-Quintero and Sanchez-Azofeifa, 2010). Piedmont Forest, located in the foothills of the eastern sub-Andean ranges in northwest Argentina and southern Bolivia, forms one of the twelve floristic cores of Neotropical seasonal dry forests (Banda et al., 2016). The Piedmont Forest is located between the dry temperate-subtropical lowlands of Chaco Forest and the wetter Southern Yungas (Prado, 2000). The Piedmont Forest has three dominant tree species in the provinces of Jujuy and Salta, Argentina: Elm, *Phyllostylon rhamnoides* (family Ulmaceae), Madder, *Calycophyllum*

*multiflorum* (family Rubiaceae) and Cebil, *Anadenanthera colubrina* (family Fabaceae) (Prado, 2000). The species composition of Piedmont Forest should remain stable as long as climate conditions within the existing forested areas remain suitable for regeneration. However, if climate conditions shift, and climatic suitability for regeneration declines in current forests and increases in transformed areas, then this will create a barrier to regeneration, and ultimately will result in loss of tree species from future forests (Aguirre et al., 2017). Given the scarce information about the factors determining the distribution and survival of the three dominant tree species of Piedmont Forest, species distribution models are a useful tool for estimating the risk of future range contraction or shift of these species (Fremout et al., 2020). Species distribution models predict the relationship between species occurrences and environmental conditions and can be used to extrapolate the extent of suitable conditions to unsurveyed areas and periods (Guisan et al., 2013). The ability to anticipate the response of species to projected anticipated changes in habitat conditions makes it possible to plan conservation strategies (Fremout et al., 2020).

Our objectives in this study were to (1) determine the current potential distribution of Elm, Madder, and Cebil in two age classes (i.e., sapling and mature tree) in the forests, in the protected area system, and in forest land use plans of the provinces of Salta and Jujuy, Argentina, (2) generate predictions about their potential distribution under current conditions and two climate change scenarios, (3) identify priority areas for conservation of the potential distribution that will remain suitable under future climate scenarios. The results of this research can serve as input for land use planning that will ensure the persistence of these three tree species as dominant components of Piedmont Forest in future decades and centuries.

## 2. Materials and methods

### 2.1. Study area

The study area, located in the provinces of Jujuy and Salta, northwest Argentina, covers a total area of 124245 km<sup>2</sup> with three forest types: Chaco Forest, Piedmont Forest, and Southern Yungas (Fig. 1). Chaco Forest occurs < 400 m asl, Piedmont Forest between 400 and 900 m asl and Southern Yungas from 900 to 2800 m asl (Prado, 2000). Mature forest in the Piedmont Forest of northwest Argentina harbor approximately 40 tree species. Basal area of trees > 10 cm diameter at breast height (DBH) is 25 m<sup>2</sup> ha<sup>-1</sup> (Tallei et al., 2023). The three tree species with highest relative importance value (RIV) are Elm (RIV ≈ 20 %), Cebil (RIV ≈ 20 %), and Madder (RIV ≈ 10 %) (Table S1).

According to Argentina's native forest land use plan (National Law N° 26331, enacted in 2007) all the native forests in each province must be assigned to one of three categories: category I includes areas of high conservation value forests where no productive activities can be carried out, category II includes areas of intermediate conservation value where productive activities can be carried out in a sustainable manner, and category III includes areas of low conservation value that can be transformed to other land uses (Alcañiz and Gutierrez, 2020). Provinces have assigned to category I all governmental protected areas, and have included additional key forests (such as riparian corridors) that are under other jurisdictions (such as private owners). Provincial governments pay compensation to land-owners whose forest lands are under category I. Funds are also provided to land-owners whose properties are assigned to category II so that they can pursue economic activities through sustainable management of the forests, but cannot transform the forests to other cover types (Alcañiz and Gutierrez, 2020).

### 2.2. Focal species

The three focal tree species have intermediate economic value in the forestry industry and therefore are desirable in logging operations (Nazaro et al., 2021). (1) *Calycophyllum multiflorum* has a restricted

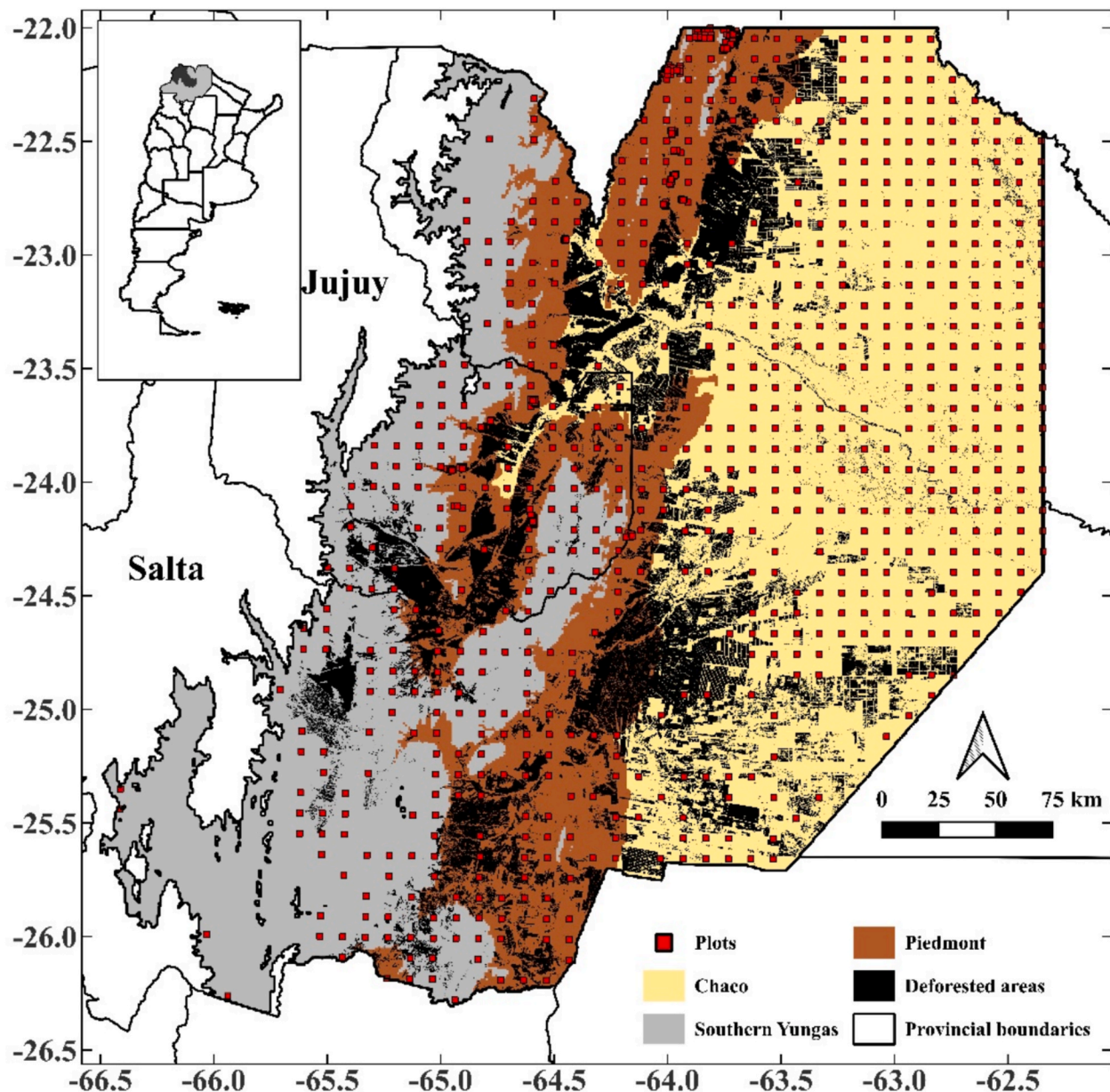


Fig. 1. Vegetation plot locations within the three forest types in the provinces of Jujuy and Salta, in northwestern Argentina (shown in upper left insert).

range throughout Bolivia, southwestern Brazil, Paraguay and northern Argentina along the narrow belt of the Neotropical seasonal dry forests. (2) *Phyllostylon rhamnoides* is distributed from Mexico to northern Argentina, especially in xerophytic and seasonally dry forests. (3) *Anadenanthera colubrina* is widely distributed in tropical and subtropical dry forests of the Neotropics, where it is one of the most common tree species. These three tree species are deciduous, the fruits are wind dispersed, and small flowers that are pollinated by insects and, to a lesser extent, by wind.

### 2.3. Data acquisition and preparation

To model species distribution, records of presence and absence of mature trees (i.e., diameter at breast height: DBH  $\geq 10$  cm) from 1209 circular plots and of saplings (i.e., DBH  $< 10$  cm and height  $\geq 1.5$  m) from 1040 circular plots obtained from 2016 to 2020 (Fig. 1) from the database of Dirección Nacional de Bosques (2021) and Alabar et al. (2022). To minimize sample bias, records of each species and age class were thinned to randomly select plots with the restriction of been

spaced  $\geq 1$  km apart (Table S2; Table S3) using the spThin library (Aiello-Lammens et al., 2015) within R statistical software v 4.1.3.

We obtained spatially explicit monthly mean values of precipitation and maximum and minimum temperatures for three periods (i.e., 1970–2018, 2000–2018, and 2081–2100) from WorldClim 2.1 (<https://worldclim.org>), with a pixel of 1-km resolution (Fick and Hijmans, 2017). We used the period 1970–2018 to model the current potential distribution for mature trees, and the period 2000–2018 to model current potential distribution of saplings (Alabar et al., 2022). The time period used to calculate the bioclimatic variables of saplings and mature trees represents the approximate number of years for the three species to reach 5 and 10 cm diameter at breast height, respectively, according to the growth rate of the tree species studied (Humano, 2020). For the future scenario period (2081–2100) we considered 23 climate models (Table S4) in two shared socioeconomic pathways (SSPs): SSP2-4.5 and SSP5-8.5 (Tu et al., 2021). The SSP2-4.5 pathway scenario (best case scenario) assumes the adoption of policies that mitigate greenhouse gas emissions and results in a temperature increase of between 0.3 and 1.8 °C by the end of the 21st century, while the SSP5-8.5 scenario (worst



case scenario) assumes that emissions will continue to increase, resulting in an increase of between 4.0 and 4.8 °C by the end of the 21st century (IPCC, 2021).

We used `biovars` function of the `dismo` library in R (Hijmans et al., 2017) to derive 19 bioclimatic variables for 1970–2018 and 2000–2018, and for the two scenarios for the projected period 2081–2100 (Table S5) from the downloaded precipitation and temperature data. For each of the two emission scenarios, we took the arithmetic average of the 23 climate models of projected data for 2081–2100, to reduce the uncertainty of distributions predicted under future climatic conditions (Zhou et al., 2021). In addition, we derived slope and aspect from the WordClim 2.1 digital elevation model (Fick and Hijmans, 2017) with a 1-km resolution using QGIS v.3.3 software (Table S5). Multicollinearity was evaluated to select the bioclimatic and topographic variables to use in the distribution modelling of each species and age class (Cruz-Cárdenas et al., 2014). For multicollinearity, a threshold of 0.6 Pearson correlation coefficient and < 10 variance inflation factor was used with the `corSelect` function of the `fuzzySim` library in R (Barbosa, 2015). If a pair of variables were correlated, we removed the variable with the largest variance inflation factor to avoid the prediction error induced by multicollinearity among environmental variables (Naimi and Araújo, 2016).

#### 2.4. Modeling potential distribution

We performed distribution modeling for each of the species and age classes in the current period and for the two future scenarios using the `biomod2` v.3.5 package in R (Thuiller et al., 2016). We used the ten algorithms in the default model settings in the `biomod2` package (Table S6) (Li et al., 2020). We used a buffer size of 200 km distance and generated 2000 pseudo-absences spaced  $\geq 1$  km apart in the buffer area around plots. Because this pseudo-absence generation process is a stochastic procedure using random selection, it was repeated three times to address possible bias in pseudo-absence generation (Wani et al., 2022). For model calibration 80 % of the records (presence and absence) were used for training and the remaining 20 % were used as the validation set in three iterations. Therefore, a total of 90 individual models (10 algorithms  $\times$  3 replicate pseudo-absence data sets  $\times$  3 iterations) were obtained for saplings and mature trees (Table S6). Model performance was evaluated using cross-validation with two evaluation metrics: true skill statistics (TSS) and area under the receiver operating characteristic (ROC) curve (AUC) (Wani et al., 2022). For both evaluation metrics the mean and standard deviation of the individual models formed was determined. The importance of variables for the mature tree and sapling models was quantified using the `get_variables_importance` function within the `biomod2` library, which calculates the Pearson correlation ( $r$ ) between model predictions including all remaining variables (“full model”) and predictions excluding the variable being tested (“reduced model”). If a variable contributes little to a model the two output models are similar, while the opposite is true for important variables (Navarro-Cerrillo et al., 2018; Blanco-Cano et al., 2022). The mean and standard deviation of the importance of each variable was estimated. For saplings and mature trees, the final ensemble model was constructed from the individual modelling results using the weighted mean approach to reduce uncertainty among species distribution algorithms (Erfanian et al., 2021). Only models with a TSS score  $\geq 0.70$  were included in the final ensemble predictions for each species in each age class in each period and climate scenario. Ensemble models were converted to binary presence-absence predictions using the threshold maximizing TSS (Erfanian et al., 2021) with the `Find.Optim.Stat` function of the `biomod2` library.

We calculated a) the areal extent of the potential distribution for each species at each age class, b) the areal extent of overlap among the three species, and finally, c) the areal extent of overlap among the three species in both age classes. Thereafter, we conducted this procedure a second time, with deforested areas (data obtained from <https://geoportal.idesa.gob.ar/>) removed from the potential distributions to

estimate the suitable habitat that will be available under future climate conditions. The resulting potential distribution models of forested land cover were summarized by forests type (i.e., Southern Yungas, Piedmont Forest, and Chaco Forest), zoning categories of the native forest land use plan, and the protected areas system in the provinces of Jujuy and Salta, Argentina (data obtained from <https://www.ign.gob.ar/>). We calculated the area of potential distribution in the future scenario models that remained stable, decreased or increased in extent with respect to the current potential distribution (Wani et al., 2022). Finally, we overlapped the potential distribution of the area that remained stable for the three species in both age classes in both climate change scenarios and from this area selected polygons that had  $> 500$  km<sup>2</sup> which we identify as priority areas for conservation.

### 3. Results

#### 3.1. Variables explaining species distributions.

We retained seven of our 22 (19 bioclimatic + 3 topographic) variables to model mature tree and sapling distributions (Table 1). The variable `bio02` (mean diurnal range of temperature) appeared in all the potential distribution models of tree species in the two age classes (Table 1). Individual models of the potential distribution for tree species in the two age classes had TSS scores  $> 0.64$  and the ensemble models had TSS scores  $> 0.74$  (Table 1).

#### 3.2. Current and future potential distribution and transformed area

Of the three tree species, Madder had the smallest area of current potential distribution in the study area, while its potential distribution doubled under the SSP2-4.5 and the SSP5-8.5 scenarios (Fig. 2; Table S7). In the current and the future scenarios 11 to 20 % of the potential distribution of sapling and mature trees of the three species were found in areas that have already been deforested (Fig. 2). Under current conditions, 10 % of the potential distribution of mature trees of the three tree species overlap spatially, and under the SSP2-4.5 and SSP5-8.5 scenarios, there is a 15 and 14 % overlap, respectively (Fig. 2, Fig. 3). Seven percent of the current potential distribution of saplings of all three tree species overlap and in the future scenarios SSP2-4.5 and SSP5-8.5 the overlap is 12 and 13 %, respectively (Fig. 2, Fig. 3). In both future scenarios, the area that remains stable for mature trees of all three species is greater ( $> 52$  %) than for saplings ( $< 43$  %) (Fig. 2). The overlap of the area that remains stable in future scenarios for all three species of both age classes was 42 % and 40 %, respectively for SSP2-4.5 and SSP5-8.5 (Fig. 2).

#### 3.3. Potential distribution by forest type

Half or more of the current potential distribution of each species, in each age class and of their co-occurring potential distribution (‘overlap’) in the study area, occurred in the Piedmont Forest (Table S8). In the SSP2-4.5 scenario the largest area of overlap of the three species (58 % of mature trees and 60 % of saplings) will also be in the Piedmont Forest (Fig. 3). However, in the SSP5-8.5 scenario the largest area of overlap (53 % of both mature trees and of saplings) of three tree species will be approximately half in the Piedmont Forest and the other half in the Southern Yungas (Fig. 3).

#### 3.4. Representation in protected areas and land use plan categories and priority areas for conservation

Less than 11 % of the potential distribution of the three tree species in both age classes is represented in protected areas, both under current and future scenarios (Fig. 4; Table S9). Under future emissions scenarios, approximately 23 % of the overlap of the potential distribution of the three tree species will be included in category I (highest protection level)

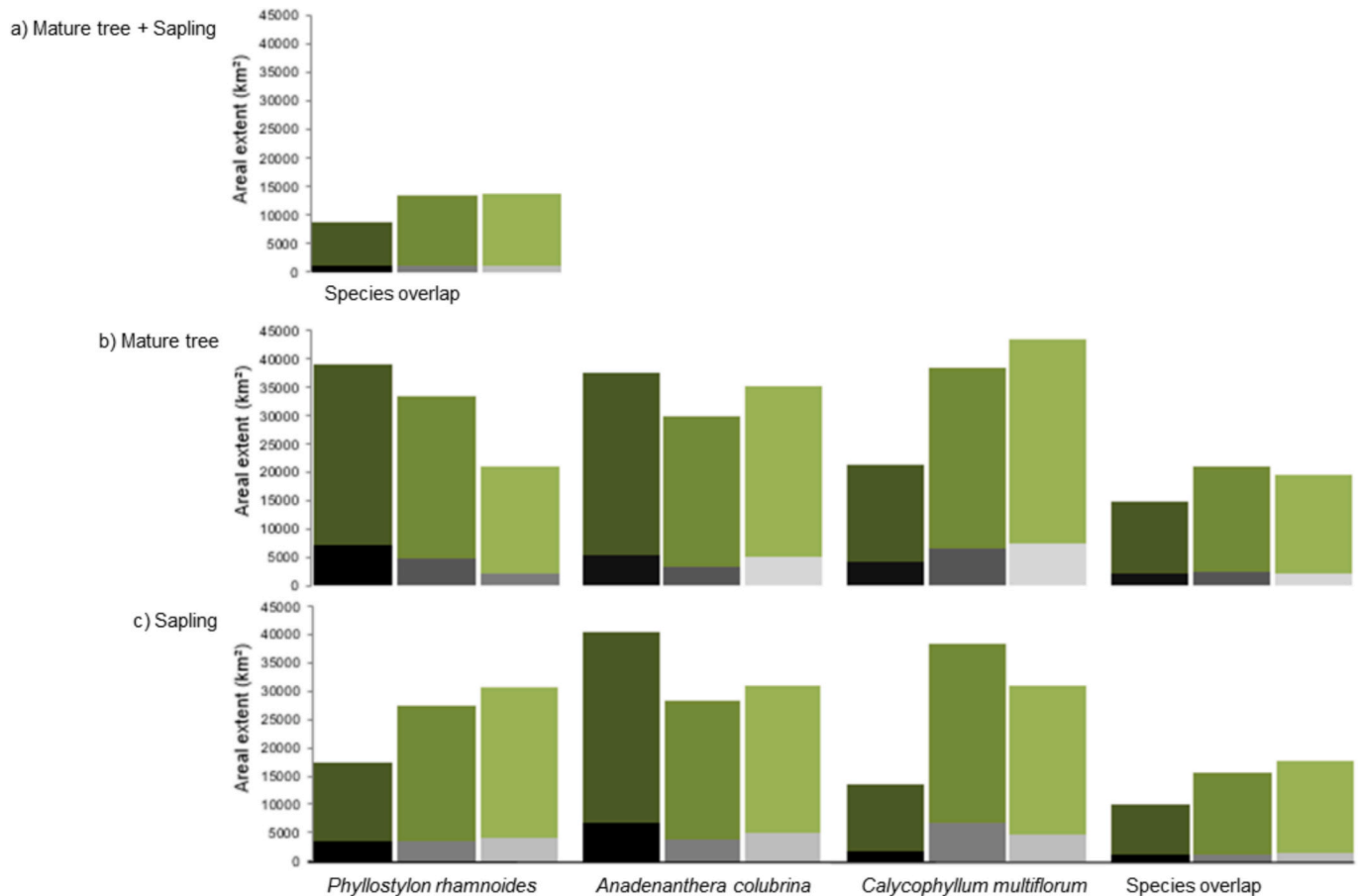


**Table 1**

Importance values of the variables (%) and evaluation metrics (TSS and ROC) for individual and ensemble models of the current potential distribution for saplings and mature trees of three species in forests of the provinces of Salta and Jujuy, Argentina. Values are shown as mean  $\pm$  standard deviation.

| Age class   | Species | Variables <sup>a</sup> |        |         |        |         |         |         | Individual models |             | Ensemble models |      |
|-------------|---------|------------------------|--------|---------|--------|---------|---------|---------|-------------------|-------------|-----------------|------|
|             |         | bio02                  | bio03  | bio04   | bio09  | bio14   | bio18   | slope   | TSS               | ROC         | TSS             | ROC  |
| Mature tree | Elm     | 35 ± 12                | 11 ± 7 |         | 12 ± 6 | 9 ± 6   | 32 ± 13 |         | 0.67 ± 0.11       | 0.87 ± 0.06 | 0.84            | 0.97 |
|             | Cebil   | 60 ± 18                |        |         | 9 ± 6  |         | 20 ± 9  | 10 ± 11 | 0.75 ± 0.05       | 0.97 ± 0.04 | 0.83            | 0.97 |
| Sapling     | Madder  | 18 ± 6                 | 10 ± 6 |         | 15 ± 5 | 17 ± 7  | 40 ± 13 |         | 0.67 ± 0.10       | 0.87 ± 0.06 | 0.89            | 0.98 |
|             | Elm     | 39 ± 13                |        | 14 ± 8  | 14 ± 7 | 7 ± 6   | 26 ± 15 |         | 0.70 ± 0.09       | 0.88 ± 0.05 | 0.89            | 0.98 |
|             | Cebil   | 85 ± 13                |        |         |        | 15 ± 13 |         |         | 0.64 ± 0.08       | 0.84 ± 0.05 | 0.74            | 0.92 |
|             | Madder  | 25 ± 15                |        | 18 ± 10 | 21 ± 6 | 7 ± 7   | 29 ± 15 |         | 0.65 ± 0.15       | 0.84 ± 0.08 | 0.95            | 0.99 |

<sup>a</sup> bio02: mean diurnal range ( $^{\circ}\text{C}^{\circ}\text{10}$ ); bio03: Isothermality; bio04: Temperature seasonality ( $^{\circ}\text{C}^{\circ}\text{10}$ ); bio09: Mean temperature of the driest quarter ( $^{\circ}\text{C}^{\circ}\text{10}$ ); bio14: Precipitation of the driest month (mm); bio18: Precipitation of the warmest quarter (mm); slope: mean slope (degree).

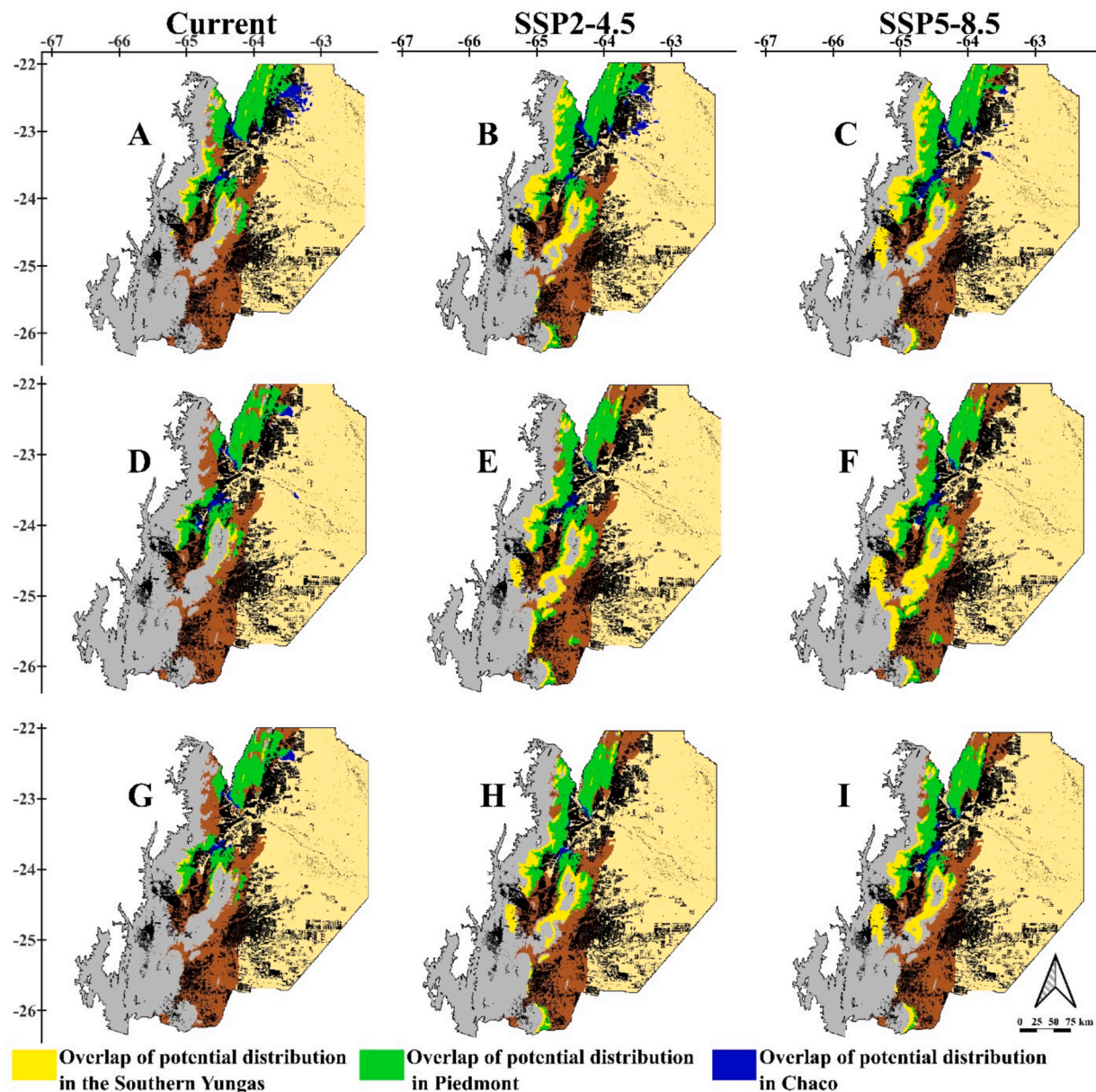


**Fig. 2.** Areal extent ( $\text{km}^2$ ) of the total (considering transformed areas and remaining forest shown as dark, mid and light green bars) and forest (considering only remaining forest shown as black, dark and light grey bars) potential distribution in current (dark green and black bars), SSP2-4.5 (mid green and dark grey bars), and SSP5-8.5 (light green and grey bars) future climate change scenarios (and) for (a) overlap of both age classes, (b) mature trees, and (c) and saplings of three species in the provinces of Salta and Jujuy, Argentina. For mature trees, the current period is from 1970 to 2018 and for saplings from 2000 to 2018, and the future scenarios are projected for the period from 2081 to 2100. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of the native forest land use plan, 73 % in category II, and 4 % in category III (Fig. 4). In future scenarios, and compared to the current period, the area of overlap of the potential distribution will increase in category I, and in category III (Table S9). Within the existing protected area system, only 9 % of the overlap of the potential distribution of the three species will remain stable in the future scenarios, while 21 % will remain stable in category I, 72 % in category II, and 5 % in category III of the land use plan (Fig. 4). Three priority areas for conservation were identified totaling 5483  $\text{km}^2$  (i.e., 547  $\text{km}^2$ , 2121  $\text{km}^2$ , and 2815  $\text{km}^2$ ) of which 475  $\text{km}^2$  (9 %) are represented within protected areas (Fig. 4).

#### 4. Discussion

Our species distribution models provide evidence that under future climate scenarios the Piedmont Forest will have adequate climatic conditions to allow potential regeneration of the three dominant tree species and thus maintaining viable populations. Given the numerical importance of the three tree species in the Piedmont Forest (Tallei et al., 2023) and that their potential distribution are likely to be maintained in the future, it is probable that the Piedmont Forest will maintain its structure and function even if climate change reorganizes the species composition due to differential responses of other tree species, as has



**Fig. 3.** Overlap of potential distribution of mature trees (A, B, and C), saplings (D, E and F), and both stages superimposed (G, H, I) of three species (Elm: *Phyllostylon rhamnoides*, Cebil: *Anadenanthera colubrina* and Madder: *Calycophyllum multiflorum*) in current and future emissions scenarios SSP2-4.5 and SSP5-8.5 in three forest types of the provinces of Salta and Jujuy, Argentina.

been reported for other forest ecosystems (Williams and Jackson, 2007; Mtsetfwa et al., 2023). Focusing on these dominant tree species is key to understanding the impacts of anthropogenic changes as they can serve as proxies for the entire community or ecosystem (Avolio et al., 2019). However, the persistence of these dominant tree species is not guarantee in the long term since there are numerous examples where common species had substantial decline or even have become extinct (Fensham et al. 2015; Pau and Dee, 2016).

By examining the potential distribution of both saplings and mature trees, we were able to identify areas where suitable conditions will exist for regeneration of the three tree species. This approach is particularly important given the longevity and slow development of trees, which means that different life stages may be subject to different environmental conditions. Because of this, it becomes important to consider the regeneration stage, given that this stage determines the recruitment capacity of the next generation of trees and is more sensitive to climatic extremes than mature trees (Bell et al., 2014; Petrie et al., 2017). The

loss of priority areas for conservation implies the loss of source populations, limiting the ability of species to persist or recover (Beaumont et al., 2019; Pang et al., 2021). Therefore, we recommend that the areas identified as priority that are currently in native forest land use plan as category III should be revised to category I or II.

Future projections of the overlap of the potential distribution of the three species show an increase in Southern Yungas, which is at higher elevation and currently has more humid forests than Piedmont and Chaco Forests. This projected shift suggests that the Southern Yungas will become drier, a pattern similar also found in Amazonian forests (Esquivel-Muelbert et al., 2019). The migration of tree species to higher elevations has also been reported for tropical Andean forests as a response to climate change (Urrutia and Vuille, 2009; Feeley et al., 2011; Rehm and Feeley, 2013). For the Chaco Forest, our results indicate a future reduction in the potential distribution of Cebil saplings and mature trees, similar to what has been previously been reported for the species in the seasonal dry forests of northwestern Argentina

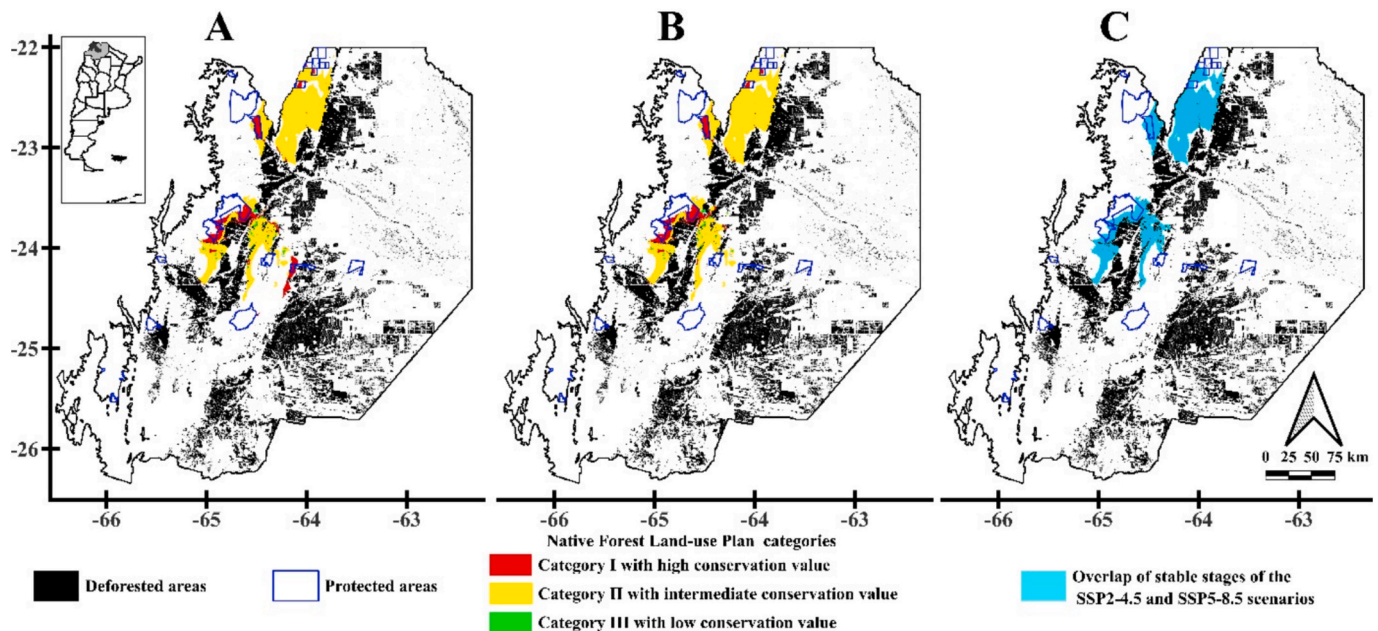


Fig. 4. Overlap of potential distribution of saplings and mature trees of three species (Elm: *Phyllostylon rhamnoides*, Cebil: *Anadenanthera colubrina* and Madder: *Calycophyllum multiflorum*) that remains stable within the protected areas network and the native forest land use plan categories under future climate conditions (A) SSP2-4.5 and (B) SSP5-8.5 emissions scenarios, and priority areas of conservation (C) identified in the provinces of Salta and Jujuy, Argentina.

(Giamminola et al., 2020). In contrast, the future potential distribution area of saplings and mature trees of Elm and Madder increase their distribution towards the current location of the Chaco Forest (except for a decrease in area of mature trees of Elm in the SSP5-8.5 scenario). The Chaco Forest is projected to be warmer and wetter in the future (Marengo et al., 2010; Barros et al., 2015) transforming this ecosystem into a closed forest ecosystem more similar to the current Piedmont Forest (Pennington et al., 2004). The difference in species responses (Cebil vs. Madder and Elm) could be explained by the importance of the mean diurnal range of temperature (bio02) in the potential distribution models of Cebil, Madder, and Elm. Cebil, which is a pioneer and strictly heliophilous species (Justiniano and Fredericksen, 1998), is dependent on bio02, as is typical for other dry forest species (Rodrigues et al., 2015; Lohbeck et al., 2015). While Madder and Elm are limited by bio02 and the precipitation of the warmest quarter (bio18). The potential distribution of these species in the future indicates that there will be an expansion into what is currently known as Southern Yungas and as Chaco Forest, changing the composition of forest communities. This will lead to novel conditions and could have consequences for species interactions and the provisioning and regulation of ecosystem services (Williams and Jackson, 2007; Pecl et al., 2017).

From our results it is clear that the most important threat to the conservation of these three tree species in the study area is deforestation, which has already reduced between 10 and 20 % of the potential distribution in current and future scenarios. Deforestation has also been reported in other developing countries as the most immediate threat to trees and to other taxonomic groups, representing the main driver of population declines of numerous species by favoring mortality or lack of recruitment that manifests as extirpations or functional extinctions (Collevatti et al., 2013; Pang et al., 2021). Given climate change, deforestation decreases the possibility of species to colonize new areas to compensate these changes (Pecl et al., 2017; Manchego et al., 2017). Removing deforested areas is a particularly important step in estimating remaining species habitat, especially in tropical and subtropical regions that are experiencing rapid and recent changes in land cover (Feeley et al., 2011). The native forest land use plan of the provinces of Salta and Jujuy designate which forest areas can legally be transformed and if this were to occur, according to our results, this would decrease the current

and future potential distribution area of these species by 3 to 25 %. Therefore, avoiding deforestation of these and other forests is one of the most urgent measures to be taken to mitigate climate change since, in addition, deforestation releases greenhouse gas emissions producing positive feedback on climate change (Lawrence et al., 2022).

We found a lack of adequate representation of the three tree species within the protected area system, which covers < 10 % of their current and future potential distribution. Our research makes it possible to identify currently unprotected areas that will remain as suitable habitat in the future, and whose protection are a priority for ensuring that Piedmont Forests persists over time as climate changes. These protection gaps occur mainly in the central and northern parts of the Piedmont Forest, where the creation of new protected areas or the expansion of existing protected areas should be a priority. Expansion of the protected area system would also contribute to Argentina's international commitments, since currently < 3 % of the study area is represented in the protected area system, far less than the target set in the 30 × 30 strategy. To achieve this target in the study area it would be necessary to add 25000 km<sup>2</sup> to the protected area system (currently only 2700 km<sup>2</sup> of forests are protected). Therefore, our results could be used to reach this goal, starting with the protection of the priority areas we identified (ca. 5000 km<sup>2</sup>). Designation of new protected areas and improved implementation of existing ones would also foster climate change mitigation through carbon sequestration and storage (Dinerstein et al., 2020). In some cases, land ownership (or other reasons) makes it difficult to designate new protected areas, so there may be other designations and management actions that can help achieve these objectives (Maxwell et al., 2020). For example, in the native forest land use plan areas designated in category I or II sustainable management could complement the protected area system by contributing to a landscape that ensures the continuation of ecological and evolutionary processes (Edwards et al., 2014; Hannah et al., 2020).

## 5. Conclusion

Overall, we found that deforestation is a greater threat than climate change to three dominant tree species of Piedmont Forest in northwest Argentina. Climatic conditions for regeneration of these species under



two near-term future scenarios are generally adequate, but representation of these species is low within the protected area network and within the strongest protection zone of the National Native Forest Law, leaving their future status unclear. The information generated in this research can then be used to guide and improve management policies for conservation planning to achieve the desired conditions in the future in the face of climate change (Busch et al., 2012). This is particularly relevant given that the Piedmont Forest, like most Neotropical seasonal dry forests, is one of the most threatened ecosystems in the world and has been neglected in research, which has limited decision-making to ensure adequate management, leading to a severe degradation of forest remnants (Sánchez-Azofeifa et al., 2005).

## CRediT authorship contribution statement

**Fabio David Alabar:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Natalia Politi:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Formal analysis, Conceptualization. **Anna M. Pidgeon:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization. **Paula Názaro:** Writing – review & editing, Methodology, Funding acquisition, Data curation. **Ashley Olah:** Writing – review & editing, Formal analysis. **Silvana Yanina Tejerina:** Writing – review & editing, Formal analysis, Data curation. **Volker C. Radeloff:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization. **Sebastián Martinuzzi:** Writing – review & editing, Methodology, Formal analysis. **Mariano M. Amoroso:** Writing – review & editing, Supervision. **Luis Rivera:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Conceptualization.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2025.105422>.

## Data availability

Data will be made available on request.

## References

- Aguirre, N., Eguiguren, P., Maita, J., Ojeda, T., Sanamiego, N., Furniss, M., & Aguirre, Z. (2017). Potential impacts to dry forest species distribution under two climate change scenarios in southern Ecuador. *Neotrop. Biodivers.*, 3(1), 18–29.
- Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., & Anderson, R. P. (2015). spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, 38, 541–545.
- Alabar, F., Politi, N., Názaro, P., Amoroso, M., & Rivera, L. (2022). Changes in the potential distribution of valuable tree species based on their regeneration in the Neotropical seasonal dry forest of north-western Argentina. *Environ. Conserv.*, 49(2), 83–89.
- Alcañiz, I., & Gutierrez, R. A. (2020). Between the global commodity boom and subnational state capacities: Payment for environmental services to fight deforestation in Argentina. *Global Environ. Polit.*, 20(1), 38–59.
- Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J. L., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I. R., Melo, F. P. L., Morante-Filho, J. C., Santos, B. A., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M. J., Cudney-Valenzuela, S., Galán-Acedo, C., San-José, M., Vieira, I. C. G., Ferry Slik, J. W., Nowakowski, A. J., & Tschamtk, T. (2020). Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecol. Lett.*, 23(9), 1404–1420.
- Avolio, M. L., Forrestel, E. J., Chang, C. C., La Pierre, K. J., Burghardt, K. T., & Smith, M. D. (2019). Demystifying dominant species. *New Phytol.*, 223(3), 1106–1126.
- Banda, K., Delgado-Salinas, A., Dexter, K. G., Linares-Palomino, R., Oliveira-Filho, A., Prado, D., Pullan, M., Quintana, C., Riina, R., Rodríguez, G. M., Weintritt, J., Acevedo-Rodríguez, P., Adarve, J., Álvarez, E., Aranguren, A. B., Arteaga, J. C., Aymard, G., Castaño, A., Ceballos-Mago, N., Cogollo, Á., Tablas, H., Delgado, F., Devia, W., Duenas, H., Fajardo, L., Fernández, A., Fernández, M.Á., Franklin, J., Freid, E. H., Galetti, L. A., Gonto, R., González-M, R., Graveson, R., Helmer, E. H., Idárraga, Á., López, R., Marciano-Vega, H., Martínez, O. G., Maturo, H. M., McDonald, M., McLaren, K., Melo, O., Mijares, F., Moggi, V., Molina, D., Moreno, N. P., Nassar, J. M., Neves, D. M., Oakley, L. J., Oatham, M., Olvera-Luna, A. R., Pezzini, F. F., Reyes Domínguez, O. J., Ríos, M. E., Rivera, O., Rodríguez, N., Rojas, A., Särkinen, T., Sánchez, R., Smith, M., Vargas, C., Villanueva, B., & Pennington, R. T. (2016). Plant diversity patterns in Neotropical dry forests and their conservation implications. *Science*, 353, 1383–1387.
- Barbosa, A. M. (2015). fuzzySim: Applying fuzzy logic to binary similarity indices in ecology. *Methods Ecol. Evol.*, 6(7), 853–858.
- Barros, V. R., Boninsegna, J. A., Camilloni, I. A., Chidiak, M., Magrín, G. O., & Rusticucci, M. (2015). Climate change in Argentina: Trends, projections, impacts and adaptation. *Wiley Interdiscip. Rev. Clim. Chang.*, 6, 151–169.
- BGCI (Botanic Gardens Conservation International). (2021). State of the World's trees. Disponible en: <https://www.bgci.org/wp/wp-content/uploads/2021/08/FINAL-GTARReportMedRes-1.pdf>.
- Beaumont, L. J., Esperón-Rodríguez, M., Nipperess, D. A., Wauchope-Drumm, M., & Baumgartner, J. B. (2019). Incorporating future climate uncertainty into the identification of climate change refugia for threatened species. *Biol. Conserv.*, 237, 230–237.
- Bell, D. M., Bradford, J. B., & Lauenroth, W. K. (2014). Early indicators of change: Divergent climate envelopes between tree life stages imply range shifts in the western United States. *Glob. Ecol. Biogeogr.*, 23(2), 168–180.
- Blanco-Cano, L., Navarro-Cerrillo, R. M., & González-Moreno, P. (2022). Biotic and abiotic effects determining the resilience of conifer mountain forests: the case study of the endangered Spanish fir. *For. Ecol. Manage.*, 520, Article 120356.
- Busch, J., Dave, R., Hannah, L. E. E., Cameron, A., Rasolohery, A., Roehrdanz, P., & Schatz, G. (2012). Climate change and the cost of conserving species in Madagascar. *Conserv. Biol.*, 26(3), 408–419.
- Carroll, C., Dunk, J. R., & Moilanen, A. (2010). Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific Northwest, USA. *Glob. Chang. Biol.*, 16(3), 891–904.
- Collevatti, R. G., Ribeiro, M. D. S. L., Diniz Filho, J. A. F., Oliveira, G. D., Dobrowski, R., & Terribile, L. C. (2013). Stability of Brazilian seasonally dry forests under climate change: Inferences for long-term conservation. *Am. J. Plant Sci.*, 4(4), 29705.
- Cruz-Cárdenas, G., Villaseñor, J. L., López-Mata, L., Martínez-Meyer, E., & Ortiz, E. (2014). Selección de predictores ambientales para el modelado de la distribución de especies en Maxent. *Revista Chapingo. Serie ciencias forestales y del ambiente*, 20(2), 187–201.
- Díaz, S., Pascual, U., Stenseke, M., Martín-Lopez, B., Watson, R. T., Molnár, Z., Hill, R., Chan, K. M. A., Baste, I. A., Brauman, K. A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P. W., van Oudenhoven, A. P. E., van der Plaats, F., Schröter, M., Lavorel, S., Aumeeruddy-Thomas, Y., Bukvareva, E., Davies, K., Demissew, S., Erpul, G., Failler, P., Guerra, C. A., Hewitt, C. L., Keune, H., Lindley, S., & Shirayama, Y. (2018). Assessing nature's contributions to people. *Science*, 359(6373), 270–272.
- Dinerstein, E., Joshi, A. R., Vynne, C., Lee, A. T. L., Pharand-Deschênes, F., França, M., Fernando, S., Birch, T., Burkart, K., Asner, G. P., & Olson, D. (2020). A “Global Safety Net” to reverse biodiversity loss and stabilize Earth's climate. *Sci. Adv.*, 6(36), Article eabb2824.
- Dobrowski, S. Z., Littlefield, C. E., Lyons, D. S., Hollenberg, C., Carroll, C., Parks, S. A., Abatzoglou, J. T., Hegewisch, K., & Gage, J. (2021). Protected-area targets could be undermined by climate change-driven shifts in ecoregions and biomes. *Commun. Earth Environ.*, 2(1), 198.
- Dunckel, K., Weiskittel, A., & Fiske, G. (2017). Projected future distribution of *Tsuga canadensis* across alternative climate scenarios in Maine. *US. Forests*, 8(8), 285.
- Eckert, I., Brown, A., Caron, D., Riva, F., & Pollock, L. J. (2023). 30× 30 biodiversity gains rely on national coordination. *Nat. Commun.*, 14(1), 7113.
- Edwards, D. P., Tobias, J. A., Sheil, D., Meijaard, E., & Laurance, W. F. (2014). Maintaining ecosystem function and services in logged tropical forests. *Trends Ecol. Evol.*, 29(9), 511–520.
- Erfanian, M. B., Sagharyan, M., Memariani, F., & Ejtehadi, H. (2021). Predicting range shifts of three endangered endemic plants of the Khorassan-Kopet Dagh floristic province under global change. *Sci. Rep.*, 11(1), 9159.
- Esquivel-Muelbert, A., Baker, T. R., Dexter, K. G., Lewis, S. L., Brienen, R. J., Feldpausch, T. R., Jon Lloyd, J., Monteagudo-Mendoza, A., Arroyo, L., Álvarez-Dávila, E., Higuchi, N., Marimon, B. S., Marimon-Junior, B. H., Silveira, M., Vilanova, E., Gloor,

- E., Malhi, Y., Chave, J., Barlow, J., Bonal, D., Davila Cardozo, N., Erwin, T., Fauset, S., Hérault, B., Laurance, S., Poorter, L., Qie, L., Stahl, C., Sullivan, M. J. P., ter Steege, H., Vos, V. A., Zuidema, P. A., Almeida, E., Almeida de Oliveira, E., Andrade, A., Aparecida Vieira, S., Aragão, L., Araujo-Murakami, A., Arets, E., Aymard, C. G. A., Baraloto, C., Barbosa Camargo, P., Barroso, J. G., Bongers, F., Boot, R., Camargo, J. L., Castro, W., Chama Moscoso, V., Comiskey, J., Cornejo Valverde, F., Lola da Costa, A. C., del Aguila Pasquel, J., Di Fiore, A., Duque, L. F., Elias, F., Engel, J., Llambazo, G. F., Galbraith, D., Herrera Fernández, R., Honorio Coronado, E. H., Hubau, W., Jimenez-Rojas, E., Nogueira Lima, A. J., Umetsu, R. K., Laurance, W., Lopez-Gonzalez, G., Lovejoy, T., Melo Cruz, O. A., Morandi, P. S., Neill, D., Núñez Vargas, P., Pallqui Camacho, N. C., Parada Gutierrez, A., Pardo, G., Peacock, J., Peña-Claros, M., Peñuela-Mora, M. C., Petronelli, P., Pickavance, G. C., Pitman, N., Prieto, A., Quesada, C., Ramírez-Angulo, H., Réjou-Méchain, M., Restrepo Correa, Z., Roopsind, A., Rudas, A., Salomão, R., Silva, N., Silva Espejo, J., Singh, J., Stropp, J., Terborgh, J., Thomas, R., Toledo, M., Torres-Lezama, A., Valenzuela Gamarra, L., van de Meer, P. J., van der Heijden, G., van der Hout, P., Vasquez Martinez, R., Vela, C., Guimarães Vieira, I. C., & Phillips O. L. (2019). Compositional response of Amazon forests to climate change. *Global Change Biology*, 25(1), 39–56.
- FAO. (2020). Global Forest Resources Assessment 2020: Main Report. Rome: FAO. <https://www.fao.org/documents/card/en?details=ca9825en>.
- Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., Meir, P., Salinas Revilla, N., Raurau Quisiquipanki, M. N., & Saatchi, S. (2011). Upslope migration of Andean trees. *J. Biogeogr.*, 38(4), 783–791.
- Fensham, R. J., Fraser, J., MacDermott, H. J., & Firn, J. (2015). Dominant tree species are at risk from exaggerated drought under climate change. *Glob. Chang. Biol.*, 21(10), 3777–3785.
- Fick, S. E., & Hijmans, R. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.*, 37(12), 4302–4315.
- Fremout, T., Thomas, E., Gaisberger, H., Van Meerbeek, K., Muenchow, J., Briers, S., Gutierrez-Miranda, C. E., Marcelo-Peña, J. L., Kindt, R., Atkinson, R., Cabrera, O., Espinosa, C. L., Aguirre-Mendoza, Z., & Muys, B. (2020). Mapping tree species vulnerability to multiple threats as a guide to restoration and conservation of tropical dry forests. *Glob. Chang. Biol.*, 26(6), 3552–3568.
- Giamminola, E. M., Urtasun, M. M., Lamas, C. Y., & De Viana, M. L. (2020). Will global change modify the distribution of the *Anadenanthera colubrina* (Fabales: Fabaceae) plant, a key species in dry tropical forest? *Rev. Biol. Trop.*, 68(2), 517–527.
- Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., Schlesinger, W. H., Shoch, D., Siikamäki, J. V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R. T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M. R., Herrero, M., Kiesecker, J., Landis, E., Laestadius, L., Leavitt, S. M., Minnemeyer, S., Polasky, S., Potapov, P., Putz, F. E., Sanderman, J., Silvius, M., Wollenberg, E., & Fargione, J. (2017). Natural climate solutions. *Proc. Natl. Acad. Sci.*, 114(44), 11645–11650.
- Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. T., Regan, T. J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T. G., Rhodes, J. R., Maggini, R., Setterfield, S. A., Elith, J., Schwartz, M. W., Wintle, B. A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M. R., Possingham, H. P., & Buckley, Y. M. (2013). Predicting species distributions for conservation decisions. *Ecol. Lett.*, 16(12), 1424–1435.
- Hannah, L., Roehrdanz, P. R., Marquet, P. A., Engquist, B. J., Midgley, G., Foden, W., Lovett, J. C., Corlett, R. T., Corcoran, D., Butchart, S. M., Boyle, B., Feng, X., Maitner, B., Fajardo, J., McGill, B. J., Merow, C., Morueta-Holme, N., Newman, E. A., Park, D. S., Raes, N., & Svenning, J. C. (2020). 30% land conservation and climate action reduces tropical extinction risk by more than 50%. *Ecography*, 43(7), 943–953.
- Hijmans, R. J., Phillips, S., Leathwick, J., Elith, J., & Hijmans, M. R. J. (2017). Package ‘dismo’. *R J.*, 9(1), 1–68.
- Humano, C. (2020). Modeladodelcrecimiento de especies nativas forestales de la Selva Pedemontana de Yungas. *Argentina. Quebracho*, 28, 5–19.
- IPCC (Intergovernmental panel on climate change). (2021): Summary for policymakers. In: Climate Change 2021: The physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change. IPCC, Switzerland. [www.ipcc.ch](http://www.ipcc.ch).
- Justiniano, M. J., & Fredericksen, T. S. (1998). Ecología y silvicultura de especies menos conocidas: Curupaú *Anadenanthera colubrina* (Vell. Conc.) Benth. Mimosoideae. Proyecto de Manejo Forestal Sostenible. Justiniano, M. J. y T. S. Fredericksen (Eds). Santa Cruz, Bolivia. 30 pp.
- Keppel, G., Mokany, K., Wardell-Johnson, G. W., Phillips, B. L., Welbergen, J. A., & Reside, A. E. (2015). The capacity of refugia for conservation planning under climate change. *Front. Ecol. Environ.*, 13(2), 106–112.
- Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., Antonius, G. T., Schut, A. G. T., Hopper, S. D., & Franklin, S. E. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Glob. Ecol. Biogeogr.*, 21(4), 393–404.
- Kuusaaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Ockinger, E., Partel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., & Steffan-Dewenter, I. (2009). Extinction debt: A challenge for biodiversity conservation. *Trends Ecol. Evol.*, 24(10), 564–571.
- Lawrence, D., Coe, M., Walker, W., Verchot, L., & Vandecar, K. (2022). The unseen effects of deforestation: Biophysical effects on climate. *Front. For. Global Change*, 5, 49.
- Li, J., Fan, G., & He, Y. (2020). Predicting the current and future distribution of three Coptis herbs in China under climate change conditions, using the MaxEnt model and chemical analysis. *Sci. Total Environ.*, 698, Article 134141.
- Lohbeck, M., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J. A., Poorter, L., & Bongers, F. (2015). Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession. *PLoS One*, 10(4), Article e0123741.
- Manchego, C. E., Hildebrandt, P., Cueva, J., Espinosa, C. I., Stimm, B., & Günter, S. (2017). Climate change versus deforestation: Implications for tree species distribution in the dry forests of southern Ecuador. *PLoS One*, 12(12), Article e0190092.
- Marengo, J. A., Ambrizzi, T., da Rocha, R. P., Alvez, L. M., Cuadra, S. V., Valverde, M. C., Torres, R. R., Santos, D. C., & Ferraz, S. E. T. (2010). Future change of climate in South America in the late twenty-first century: Intercomparison of scenarios from three regional climate models. *Clim. Dyn.*, 35, 1073–1097.
- Martinuzzi, S., Radeloff, V. C., Pastur, G. M., Rosas, Y. M., Lizarraga, L., Politi, N., Rivera, L., Huertas Herrera, A., Silveira, E. M. O., Olah, A., & Pidgeon, A. M. (2021). Informing forest conservation planning with detailed human footprint data for Argentina. *Global Ecol. Conserv.*, 31, Article e01787.
- Maxwell, S. L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A. S., Stolton, S., Visconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, N., Strassburg, B. B. N., Wenger, A., Jonas, H. D., Venter, O., & Watson, J. E. (2020). Area-based conservation in the twenty-first century. *Nature*, 586(7828), 217–227.
- Mtsefwa, F. P., Kruger, L., & McCleery, R. A. (2023). Climate change decouples dominant tree species in African savannas. *Sci. Rep.*, 13(1), 7619.
- Naimi, B., & Araújo, M. B. (2016). sdm: A reproducible and extensible Rplatform for species distribution modelling. *Ecography*, 39, Article 368–375. <https://doi.org/10.1111/ecog.01881>.
- Navarro-Cerrillo, R. M., Duque-Lazo, J., Delgado Manzanedo, R., Sanchez-Salguero, R., & Palacios-Rodriguez, G. (2018). Climate change may threaten the southernmost *Pinus nigra* subsp. *salzmannii* (Dunal) Franco populations: An ensemble niche-based approach. *iForest-Biogeosci. Forest.*, 11(3), 396–405.
- Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Choimes, A., De Palma, A., Díaz, S., Echeverría-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., Ingram, D. J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Laginha Pinto Correia, D., Martin, C. D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H. R. P., Purves, D. W., Robinson, A., Simpson, J., Tuck, S. L., Weiher, E., White, H. J., Ewers, R. M., Mace, G. M., Scharlemann, J. P. W., & Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520(7545): pp. 45–50.
- Pang, S. E., De Alban, J. D. T., & Webb, E. L. (2021). Effects of climate change and land cover on the distributions of a critical tree family in the Philippines. *Sci. Rep.*, 11(1), 276.
- Pau, S., & Dee, L. E. (2016). Remote sensing of species dominance and the value for quantifying ecosystem services. *Remote Sens. Ecol. Conserv.*, 2(3), 141–151.
- Pecl, G. T., Araujo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffiths, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., Lenoir, J., Linnetved, H. L., Martin, V. Y., McCormack, P. C., McDonald, J., Mitchell, N. J., Mustonen, T., Pandolfi, J. M., Petrotelli, N., Popova, E., Robinson, S. A., Scheffers, B. R., Shaw, J. D., Sorte, C. J. B., Strugnell, J. M., Sunday, J. M., Tuanmu, M.-N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E., & Williams, S. E. (2017). Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science*, 355(6332), Article eaai9214.
- Pennington, R. T., Lavin, M., Prado, D. E., Pendry, C. A., Pell, S. K., & Butterworth, C. A. (2004). Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. *Philosoph. Trans. Roy. Soc. Lond. Ser. B: Biol. Sci.*, 359(1443), 515–538.
- Petrie, M. D., Bradford, J. B., Hubbard, R. M., Lauenroth, W. K., Andrews, C. M., & Schlaepfer, D. R. (2017). Climate change may restrict dryland forest regeneration in the 21st century. *Ecology*, 98(6), 1548–1559.
- Portillo-Quintero, C. A., & Sanchez-Azofeifa, G. A. (2010). Extent and conservation of tropical dry forests in the Americas. *Biol. Conserv.*, 143(1), 144–155.
- Prado, D. E. (2000). Seasonally dry forests of tropical South America: From forgotten ecosystems to a new phytogeographic unit. *Edinb. J. Bot.*, 57(3), 437–461.
- Rehm, E. M., & Feeley, K. J. (2013). Forest patches and the upward migration of timber line in the southern Peruvian Andes. *For. Ecol. Manage.*, 305, 204–211.
- Rodrigues, P. M. S., Silva, J. O., Eisenlohr, P. V., & Schaefer, C. E. G. R. (2015). Climate change effects on the geographic distribution of specialist trees of the Brazilian tropical dry forests. *Braz. J. Biol.*, 75(3), 679–684.
- Sánchez-Azofeifa, G. A., Quesada, M., Rodríguez, J. P., Nassar, J. M., Stoner, K. E., Castillo, A., Garvin, T., Zent, E. L., Calvo-Alvarado, J. C., Kalacska, M. E. R., Fajardo, L., Gamon, J. A., & Cuevas-Reyes, P. (2005). Research priorities for Neotropical dry forests. *Biotropica*. *J. Biol. Conservat.*, 37(4), 477–485.
- Shrestha, N., Xu, X., Meng, J., & Wang, Z. (2021). Vulnerabilities of protected lands in the face of climate and human footprint changes. *Nat. Commun.*, 12(1), 1632.
- Tallei, E., Rivera, L., Schaaf, A., Vivanco, C., & Politi, N. (2023). Post-logging changes in a Neotropical dry forest composition and structure modify the ecosystem functioning. *For. Ecol. Manage.*, 537, Article 120944.
- Talluto, M. V., Boulangeat, I., Vissault, S., Thuiller, W., & Gravel, D. (2017). Extinction debt and colonization credit delay range shifts of eastern North American trees. *Nat. Ecol. Evol.*, 1(7), 0182.
- Tejedor Garavito, T. N., Newton, A. C., Golicher, D., & Oldfield, S. (2015). The relative impact of climate change on the extinction risk of tree species in the montane tropical Andes. *PLoS One*, 10(7), Article e0131388.
- Thuiller, W., Georges, D., Engler, R., Breiner, F., Georges, M. D., & Thuiller, C. W. (2016). Package ‘biomod2’. Species distribution modeling within an ensemble forecasting framework.

- Thurman, L. L., Bruce Stein, B., Beever, E. A., Foden, W., Geange, S., Verde, N., Gross, J. E., Lawrence, D., LeDee, O., Olden, J., Thompson, L., & Young, B. L. (2020). Persist in place or shift in space? Evaluating the adaptive capacity of species to climate change. *Front. Ecol. Environ.*, 18(9), 520–528.
- Tu, W., Xiong, Q., Qiu, X., & Zhang, Y. (2021). Dynamics of invasive alien plant species in China under climate change scenarios. *Ecol. Ind.*, 129, Article 107919.
- Urrutia, R., & Vuille, M. (2009). Climate change projections for the tropical Andes using a regional climate model: temperature and precipitation simulations for the end of the 21st century. *J. Geophys. Res. Atmos.*, 114(D2).
- Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., & Hermy, M. (2006). Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology*, 87, 542–548.
- Wani, I. A., Khan, S., Verma, S., Al-Misned, F. A., Shafik, H. M., & El-Serehy, H. A. (2022). Predicting habitat suitability and niche dynamics of *Dactylorhiza hatagirea* and *Rheum webbianum* in the Himalaya under projected climate change. *Sci. Rep.*, 12(1), 13205.
- Williams, J. W., & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.*, 5(9), 475–482.
- Zhou, Y., Zhang, Z., Zhu, B., Cheng, X., Yang, L., Gao, M., & Kong, R. (2021). Maxent modeling based on cmip6 models to project potential suitable zones for *Cunninghamia lanceolata* in China. *Forests*, 12(6), 752.