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Dynamic seed zones to guide climate-smart seed sourcing for tropical dry forest restoration in Colombia

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Abstract

Tree-based forest landscape restoration interventions require knowledge on the suitability and origin of seed sources and planting material. A common recommendation is to select locally sourced material based on the assumption that it is well adapted to local environmental conditions and to avoid introduction of maladapted genes. However, faced with accelerating climate change, it may be prudent to supplement local provenances with ‘climate-matched’ provenances, i.e. where current climate conditions are similar to those anticipated in the future at the planting site. Restoration practitioners usually do not have access to the necessary information to implement such climate-smart seed sourcing. Here, we combine genetic data of 11 socio-economically important tree species of the tropical dry forests of Colombia with spatial environmental data to inform the delineation of dynamic seed zones for the restoration of this highly threatened ecosystem. Analysis of Molecular Variance (AMOVA) indicates significant population genetic differentiation within all 11 species. We fitted linear mixed effects models to evaluate if the genetic distance between trees was mainly related to geographic distance (i.e. isolation by distance; IBD), environmental distance (i.e. isolation by environment; IBE), or both. Observed scales of genetic differentiation were best explained by the model including both geographic and environmental distance (IBD + IBE) for 6 out of 11 species, and by the IBE model for the remaining species, suggesting that the observed differentiation is at least partly driven by adaptive processes. Aiming at capturing as much as possible of the observed genetic differentiation, we propose a set of 36 provisional seed zones that are applicable across species and dynamic under climate change, based on the clustering of environmental data and geographical coordinates. We project these seed zones to future climate conditions using five general circulation models and two emission scenarios, and discuss how they can be used to implement different climate-smart seed sourcing strategies in a pragmatic way. The seed zone maps are made available in a user-friendly online tool.

1 Introduction

In times of unprecedented anthropogenic pressure on ecosystems worldwide, the restoration of degraded lands has become a global priority (Aronson and Alexander, 2013; FAO, 2020; Suding et al., 2015). Restoration efforts often include tree planting, in which case decisions need to be made on the species to be planted, but also on the provenance of the planting material (also called forest reproductive material; typically seeds but may also consist of cuttings, stakes, wildlings, etc.. we use ‘seeds’ here for simplicity). Many provenance trials, also called common garden trials, have found evidence of adaption of tree species populations to local environmental conditions, although most have been carried out in temperate regions (e.g., Isaac-Renton et al., 2018; Kreyling et al., 2014; St. Clair, 2006; Vitasse et al., 2009) and knowledge on adaptive variation in tropical tree species remains scarce (Alberto et al., 2013, but see for example Barton et al., 2020). As a result of these findings, it is frequently recommended to source seeds or seedling planting material for restoration locally to avoid maladaptation, while also reducing the risk of outbreeding depression or erosion of intraspecific genetic diversity (Bischoff et al., 2010; Hufford and Mazer, 2003; Krauss and He, 2006; McKay et al., 2005; Montalvo and Ellstrand, 2001; Vander Mijnsbrugge et al., 2010).

The importance of using local seed for tree planting activities remains a crucial principle to guide seed sourcing decisions (Pedrini and Dixon, 2020). However, implementing a seed sourcing strategy purely focussed on local sources may be problematic for a number of reasons. Populations closest to a planting site may be small and fragmented, resulting in inbred seeds of low genetic diversity (Aguilar et al., 2006; Breed et al., 2012; Vranckx et al., 2012), making it difficult or impossible to capture sufficient genetic diversity to establish self-sustaining populations (Broadhurst et al., 2008). In addition, several studies have found evidence that the geographic distance between individuals or populations is not always the best indicator of their genetic dissimilarity, which is sometimes more correlated to environmental distance (i.e. isolation by environment; IBE) than to geographic distance (i.e. isolation by distance; IDB) (Montalvo and Ellstrand, 2001; Sexton et al., 2014). Furthermore, the magnitude and rate of climate change is increasingly raising concerns about the ability of local populations to adapt to future climate conditions (Aitken et al., 2008; Hancock and Hughes, 2014; Vitt et al., 2010) and has sparked an intense debate on what constitutes an appropriate seed sourcing strategy.

Several alternative ‘climate-smart’ or ‘climate-proof’ seed sourcing approaches have been proposed, often involving the collection of at least a part of the seeds in areas where current climate conditions are most similar to those anticipated at the planting site under climate change, i.e. ‘climate matching’ or ‘predictive provenancing’ (e.g., Booth, 2016; Broadmeadow et al., 2005; Crowe and Parker, 2008; Gray and Hamann, 2011; Harrison et al., 2017; Shryock et al., 2018; Thomson et al., 2010). Other alternative approaches put more focus on increasing genetic diversity and thereby adaptive potential. These include the ‘composite provenancing’ approach, in which seeds from several local provenances are mixed with progressively smaller amounts of seeds from more distant provenances (Broadhurst et al., 2008), the 'admixture provenancing' approach, in which seeds from different populations are mixed without considering the geographic or environmental distance to the planting site (Breed et al., 2013), the 'regional admixture' approach, in which seeds are sourced from different populations within a biogeographic region (or seed zone) (Bucharova et al., 2018), and the 'climate-adjusted provenancing' approach, in which seeds are collected in several localities along a gradient coinciding with the direction of predicted climatic changes (Prober et al., 2015). Although the debate continues, several authors have provided guidance on how to select the most appropriate strategy depending on species characteristics, the expected impacts of climate change and the local context (Breed et al., 2013; Havens et al., 2015; Ramalho et al., 2017; Sgrò et al., 2011).

Most of previously proposed climate-smart seed sourcing strategies developed based on temperate species are not easily implemented in a tropical context, given the large local species pools, scarcity of data on scales of adaptive variation, generally limited logistic capacity of restoration practitioners and lack of government incentives to obtain appropriate planting material (Atkinson et al., 2018; Jalonen et al., 2018). To support climate-smart seed sourcing for a tropical context, we propose a more pragmatic approach using dynamic seed zones to guide seed sourcing decisions. Seed zones (also called seed transfer zones, seed provenance zones, or breeding zones) are geographic areas in which planting material can be moved freely while minimizing the risk for a loss of population fitness and the disruption of population genetic patterns (Hufford and Mazer, 2003; Miller et al., 2011). Ideally, they should be informed by insights on intraspecific adaptation patterns (Hufford and Mazer, 2003), traditionally obtained using provenance trials (Hamann et al., 2000; Kramer et al., 2015; Miller et al., 2011). While provenance trials remain crucial to inform seed sourcing decisions (Brancalion et al., 2015; Breed et al., 2018), they do not exist for most species used in restoration, especially in the tropics, prompting researchers to delineate provisional seed zones using proxies for local adaptation.

Based on the notion that seed zones are assumed to reflect genetic differentiation between populations, several studies have used genetic markers to inform seed sourcing decisions, including both adaptive markers (e.g., Hufford et al. 2016, Shryock et al. 2017), which are directly under natural selection, and neutral markers (e.g., Jorgensen et al. 2016, Durka et al. 2017, Listl et al. 2018). While neutral markers are not directly linked to adaptation, meta-analyses have found that population differentiation in neutral markers tends to be correlated with differentiation in adaptive markers (Leinonen et al., 2008; Merilä and Crnokrak, 2001). Other proxies purely based on environmental characterization data have also been used, such as ecoregions (e.g., Kramer et al., 2015; Miller et al., 2011), selected climate variables (e.g., Bower et al. 2014, Castellanos-Acuña et al. 2018), or a wide range of environmental variables (e.g., Potter and Hargrove 2012, Crow et al. 2018). These have the advantage that they do not rely on detailed species-specific data, but it remains uncertain how representative environmentally delimited seed zones are for mapping genetic and adaptive variability across a species range. In addition, they are not likely to accurately reflect differences in biotic interactions, which may also drive local adaptation, especially in the tropics (Hargreaves et al., 2020). Nonetheless, one great advantage of environmentally-based delimitation of seed zones is that it permits to predict how zones are expected to shift under climate change, i.e. 'dynamic' seed zones (Kramer and Havens, 2009; Vitt et al., 2010). Hence, the combination of environmentally-based limitation of seed zones and species-specific estimates of population genetic differentiation based on genetic marker data seems a promising approach to develop such dynamic seed zones.

Tropical dry forests (TDFs), also called seasonally dry tropical forests (SDTFs), are among the most threatened of ecosystems worldwide (Fremout et al., 2020; Hoekstra et al., 2005; Janzen, 1988). In the Americas, only around one-third of the original TDF cover remains (Portillo-Quintero and Sánchez-Azofeifa, 2010). Despite this, TDFs receive less scientific attention than more humid tropical forests and there is a pressing need to step up science-based restoration and conservation efforts in this ecosystem (Pennington et al., 2018; Schröder et al., 2021). The situation is especially critical in Colombia, where only around 8% of the original TDF cover remains (García et al., 2014), making it a national priority for restoration and conservation (Norden et al., 2020; Vargas and Ramírez, 2014).

In this study, we used neutral genetic marker data of 11 socio-economically important tree species of the TDFs of Colombia combined with spatial environmental data to inform the delineation of dynamic seed zones for guiding climate-smart provenance decisions for the restoration of this highly threatened ecosystem. First, we use these markers to evaluate if tree species populations are genetically differentiated, and, whether genetic differences between trees are driven by isolation by distance (IBD), isolation by environment (IBE), or both. Next, we propose a set of seed zones based on the clustering of environmental data and geographical coordinates, and project these seed zones to future climate conditions using different climate models and emission scenarios. Finally, we discuss how these seed zones can be used to implement several previously proposed climate-smart seed sourcing strategies in a pragmatic way.

2 Methods

2.1 Study region

The study region comprises the potential distribution of TDF in Colombia, i.e. all areas that would be covered by TDF in the absence of human disturbance, as delimited by the Instituto Alexander von Humboldt (Rodríguez-Buritacá et al., 2016), building on the work of Etter et al. (2008). The Colombian TDFs are located mainly along the Caribbean coast and the Inter-Andean valleys of the Cauca, Magdalena, Chicamocha and Patía rivers. Some authors also include a number of deciduous or semi-deciduous forest types embedded in a mosaic of savannah and grassland of the Los Llanos region in the Orinoquia department of north-eastern Colombia, which show similarity with other Colombian TDFs due to drought stress caused by topographic and soil conditions (e.g., rocky outcrops and calcareous soils) (Pizano et al., 2016), but these forests are not included here. The Caribbean and Inter-Andean TDFs can be considered as floristically distinct from each other (Banda et al., 2016; González-M et al., 2018).

To avoid any possible omission errors, we slightly extended the potential TDF distribution to include all areas falling within the climatic definition of TDF, for which we considered a maximum annual precipitation of 1600 mm, at least 5 months with less than 100 mm precipitation, and a mean annual temperature of at least 17°C (Murphy and Lugo, 1986; Pennington et al., 2000). Average precipitation and temperature data were obtained from the WorldClim database at a resolution of 30 arcsec (ca. 0.9 km at the equator) (Hijmans et al., 2005). We did not set a lower limit for precipitation, which resulted in the inclusion of the entire Guajira peninsula, the driest part of the Colombian TDFs, which in reality consists of a mosaic of TDF, shrublands, and desert. The reason for this is that populations from the Guajira peninsula may be useful for climate-smart seed sourcing (see below) to restore areas that are expected to become drier in the future.

2.2 Study species

The study species consist of 11 socio-economically important tree species native to the TDFs of Colombia, comprising 5 species mostly known for their high-quality timber (*Astronium graveolens*, *Aspidosperma polyneuron*, *Caesalpinia ebano*, *Cedrela odorata*, *Platymiscium pinnatum*) and 6 multipurpose tree species (*Albizia saman*, *Bursera simaruba*, *Ceiba pentandra*, *Enterolobium cyclocarpum*, *Hura crepitans*, and *Hymenaea courbaril*). Information on their life history traits (dispersal, pollination, sexual system, and mating system) is given in Table 1. All 11 species are diploid.

Table 1: Study species with their life history traits. Note that 'monoecious' is used in the strict sense here, only referring to species with separate male and female flowers on the same plant.

Species	**Dispersal**	**Pollination**	**Sexual system**	**Mating system**
Albizia saman (Jacq.) F. Muell. (Fabaceae)	Terrestrial mammals*	Bees and moths	Hermaphrodite	Outcrossing (self-incompatible) [1]
Aspidosperma polyneuron Müll.Arg. (Apocynaceae)	Wind (samara fruit)	Moths and butterflies	Hermaphrodite	Mostly outcrossing [2]
Astronium graveolens Jacq. (Anacardiaceae)	Wind (samara-like fruit)	Small bees	Dioecious	Outcrossing (dioecious) [3]
Bursera simaruba (L.) Sarg. (Burseraceae)	Birds, bats	Bees, wasps and wind	Dioecious	Outcrossing (dioecious) [1]
Caesalpinia ebano H.Karst (Fabaceae)	Terrestrial mammals*	Insects	Hermaphrodite	Unknown [4]
Cedrela odorata L. (Meliaceae)	Wind (samara fruit)	Bees and moths	Monoecious	Mostly outcrossing [5]
Ceiba pentandra (L.) Gaertn. (Malvaceae)	Wind (cottony seeds)	Bats	Hermaphrodite	Mixed [6]
Enterolobium cyclocarpum (Jacq.) Griseb. (Fabaceae)	Terrestrial mammals*	Bees and moths	Hermaphrodite	Outcrossing (self-incompatible) [1]
Hura crepitans L. (Euphorbiaceae)	Autochory	Bats	Monoecious	Mostly outcrossing [6]
Hymenaea courbaril L. (Fabaceae)	Terrestrial mammals*	Bats	Hermaphrodite	Outcrossing (self-incompatible) [1]
Platymiscium pinnatum (Fabaceae)	Wind (samara fruit)	Bees	Hermaphrodite	Unknown

* *A. saman*, *E. cyclocarpum*, and *H. courbaril* were primarily dispersed by now extinct megafauna (Janzen and Martin, 1982), the same is possibly true for *C. ebano*, which fruits are also hard pods. *H. courbaril* and *E. cyclocarpum* were part of the diet of Precolumbian societies (Iriarte et al., 2020; Zizumbo-Villarreal et al., 2016) and may have undergone considerable human dispersal as a consequence, the same is possibly true for *A. saman* which also has edible fruits. Similarly, *A. saman* and *E. cyclocarpum* have been used traditionally as pasture trees for centuries (Aguirre-Morales et al., 2020; Thomas et al., 2016).

[1] (Bawa, 1974)

[2] (Chaves et al., 2016)

[3] (Sanchez-Gomez et al., 2020)

[4] No info on *C. ebano* was found. Bullock (1985) report mating systems of several *Caesalpinia* species in Mexico, but these include entirely outcrossing, mostly outcrossing and mixed reproduction (both selfing and outcrossing).

[5] (James et al., 1998)

[6] (Murawski and Hamrick, 1992)

2.3 Field sampling

Field sampling was carried out across the TDFs of Colombia in a total of 18 localities (Figure 1; Table S1), covering all Colombian TDF regions except the TDFs of the Orinoquia department. Within each locality, adult trees were sampled within a circular area with radius of ca. 10 km, with selected trees standing at least 50 meters apart to avoid sampling closely related individuals. The number of sampled populations per species varied between 4 (*C. ebano*) and 12 *(C. pentandra*). A total of 725 trees was sampled, with the number of sampled trees per species varying between 37 (*H. courbaril)* and 96 (*A. saman*, *A. graveolens*, *C. pentandra*) (Table 2). All biological materials were collected in collaboration with the Instituto Alexander von Humboldt following the Colombian Decreto 302 of 2003.

Table 2: Number of sampled trees per population for the tree species included in this study. The species codes refer to the following species: Asa: *Albizia saman*; Apo: *Aspidosperma polyneuron*; Agr: *Astronium graveolens*; Bsi: *Bursera simaruba*, Ceb: *Caesalpinia ebano*, Cod: *Cedrela odorata*, Cpe: *Ceiba pentandra*; Ecy: *Enterolobium cyclocarpum*; Hcr: *Hura crepitans*; Hco: *Hymenaea courbaril*, Ppi: *Platymiscium pinnatum*. The central coordinates and average climatic conditions of the populations are given in Table A.1 (Supplementary material).

		Species										
Region	**Population**	**Asa**	**Apo**	**Agr**	**Bsi**	**Ceb**	**Cod**	**Cpe**	**Ecy**	**Hcr**	**Hco**	**Ppi**
Caribbean Coast	Santa Marta N	3	12	9		9			4	5		9
	Santa Marta S	7	1	9	10	12			4	9		7
	El Guamo			10		13		14	10	10		10
	Zambrano	14	9	10		8		11		11		
	Colosó		9	9	11		10	8	3	15		3
Cauca Valley	Ituango	10		9	9				10	10		
	Santa Fe de Antioquia	7		12	11			10	13	9	11	
	La Pintada	12		9	11		11	11	16		10	10
	La Paila	12						12	3	3		
	Mata de Guadua	10			1			4		3	1	
	CIAT						2	3	2			
	Jamundí										7	
Magdalena Valley	Tolima N		5				4					
	Tolima S		9		1			2				
	Tatacoa N			10	10							
	Tatacoa S	6						3				
Patía Valley	Patía	10						8			8	
Chicamocha Valley	Chicamocha	5		9	10		13	12		10		10
	N° of populations	11	6	10	9	4	5	11	9	10	5	6
	Total n° trees	96	45	96	74	42	40	96	65	85	37	49

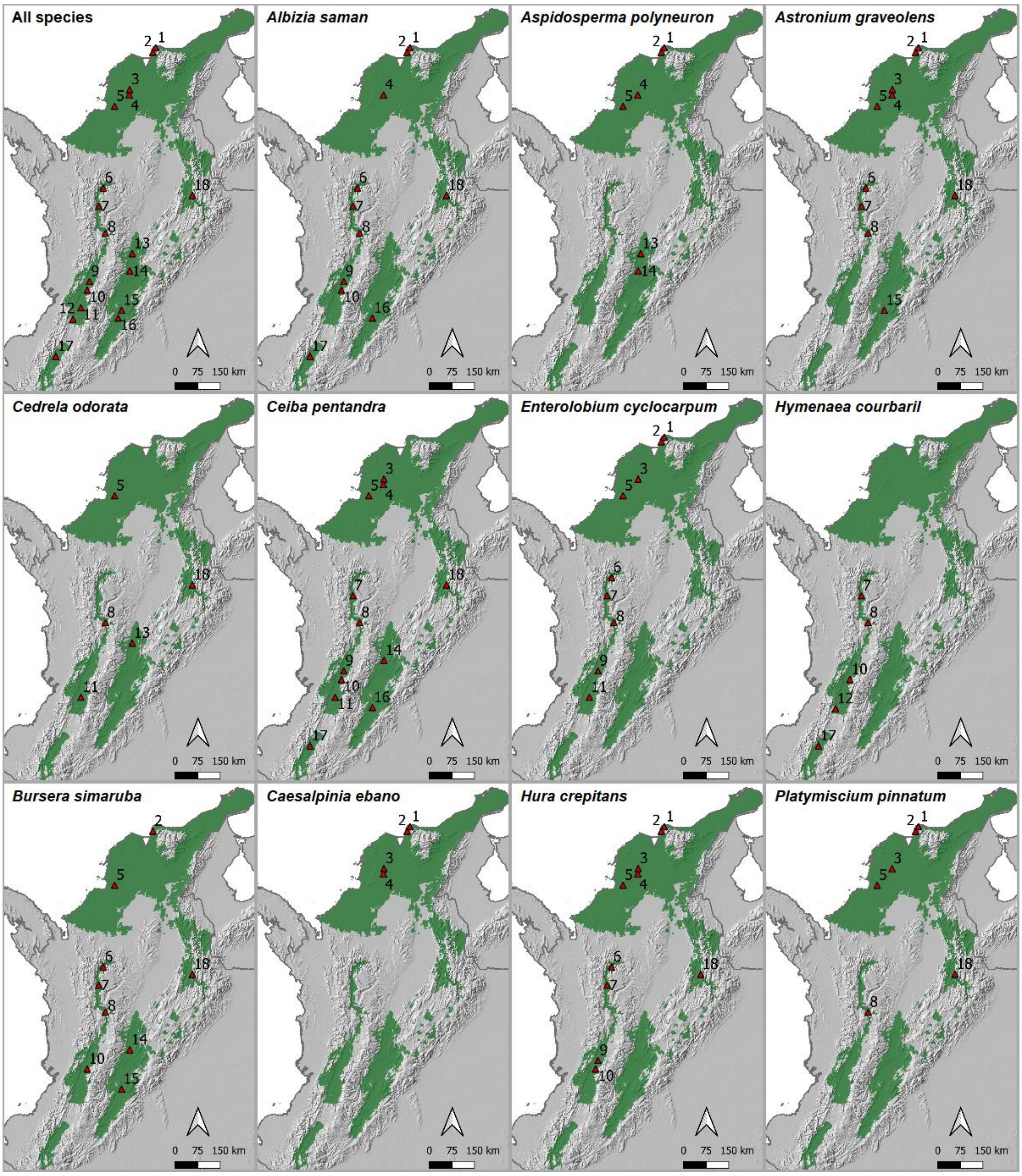

Figure 1: Sampling locations for all species (first panel 1) and individual species (remaining panels). The potential tropical dry forest (TDF) distribution (see section 2.1) is shown in green. Populations are indicated with red triangles and are numbered as follows: 1. Santa Marta Norte; 2. Santa Marta Sur; 3. El Guamo; 4. Zambrano; 5. Colosó; 6. Ituango; 7. Santa Fe de Antioquia; 8. La Pintada; 9. La Paila; 10. Mata de Guadua; 11. Centro Internacional de Agricultura Tropical (CIAT); 12. Jamundí; 13. Tolima Norte; 14. Tolima Sur; 15. Tatacoa Norte; 16. Tatacoa Sur; 17. Patía; 18. Chicamocha. Populations 1-5 are located along the Carribean coast, localities 6-12 in the Cauca Valley, localities 13-16 in the Magdalena Valley, locality 17 in the Patía Valley, and locality 18 in the Chicamocha Valley.

2.4 Genetic markers

Total genomic DNA was extracted from leaf material using the CTAB procedure (Doyle, J. J. and Doyle, 1987), with modifications described by Novaes et al. (2009), and was amplified using polymerase chain reactions (PCR). Seven of the study species (*A. saman*, *A. polyneuron*, *A. graveolens*, *C. odorata*, *C. pentandra*, *E. cyclocarpum* and *H. courbaril*) were characterized using simple sequence repeat markers (SSRs), also called microsatellite markers, with the number of loci per species ranging from 7 (*A. graveolens*) to 12 (*A. saman*) (Table A.2, Supplementary material), whereas the four remaining species (*B. simaruba*, *C. ebano*, *H. crepitans*, *P. pinnatum*), were characterized using inter-simple sequence repeat markers (ISSRs), with the number of loci per species ranging from 44 (*H. crepitans*) to 67 (*B. simaruba*) (Table A.2, Supplementary material). SSR markers are codominantly inherited whereas ISSR markers are dominantly inherited, which means that ISSR markers do not allow to distinguish between heterozygosity and homozygosity. The data of the species characterized with ISSR markers have been published by Bocanegra-González et al. (2019), those of *A. saman* by Aguirre-Morales et al. (2020), those of A. *graveolens* by Morillo-Paz (2019), those of *C. odorata* by Aguirre-Morales (2017), those of *C. pentandra* by Bocanegra-González et al. (2018), and those of *E. cyclocarpum* by Thomas et al. (2016). Those of *A. polyneuron* and *H. courbaril* have not yet been published. Although similar, SSR and ISSR markers may result in different estimates of population genetic differentiation (Ganopoulos et al., 2011; Li et al., 2017; Rawat et al., 2014), but comparisons between species were not a primary objective of this study.

2.5 Environmental variables

A set of 30 climate and soil variables were selected to evaluate IBE (see section 2.6) and to construct seed zones (see section 2.7) (Table A.1, Supplementary material). These comprise 19 bioclimatic variables from the WorldClim v1.4 database (Hijmans et al., 2005), aridity (i.e. annual precipitation divided by annual potential evapotranspiration), which was calculated using WorldClim temperature and precipitation data and the Hargreaves formula for estimating potential evapotranspiration (Hargreaves and Allen, 2003), and 9 continuous soil variables from the ISRIC SoilGrids250m v1 database (Hengl et al., 2017). All variables were used at a spatial resolution of 30 arcsec (ca. 0.9 km at the equator).

Future climate data were downloaded from the CCAFS Climate Data Portal (http://www.ccafs-climate.org/). Data were downloaded for the 2050s and 2070s time horizons and two greenhouse gas emission scenarios, using the representative concentration pathway RCP8.5 as the worst-case scenario and RCP4.5 as a more optimistic scenario, as forecasted by five general circulation models (GCMs). These GCMs were selected using the same approach as in Fremout et al. (2020), first selecting all GCMs that perform better than the median GCM performance (against observed temperature and precipitation values) following Knutti et al. (2013) and that are available at the CCAFS Climate Data Portal and next maximizing 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.

2.6 Population genetic structure and isolation by distance and environment

To assess whether populations were genetically differentiated, we first calculated the genetic distance between sampled trees. The simple matching coefficient was used to express genetic distance for the species characterized by ISSR markers, whereas the Kosman-Leonard distance was used for the species characterized by the codominant SSR markers, for which traditional genetic distance measures are not appropriate (Kosman and Leonard, 2005). We calculated these genetic distances using the ‘ade4’ and ‘mmod’ packages for R (Dray and Dufour, 2007; Winter, 2012). Next, these distances were used to test for genetic differentiation between the sampled populations by carrying out an Analysis of Molecular Variance (AMOVA; Excoffier et al. 1992) for each of the species, using the ‘adegenet’ and ‘ade4’ packages for R (Dray and Dufour, 2007; Jombart and Ahmed, 2011). AMOVA, which results in Φ_{ST} statistics analogous to F_{ST} statistics (Wright, 1949), accommodates both dominant and codominant marker data and works relatively well with limited numbers of loci (Nelson and Anderson, 2013). Statistical significance of population genetic differentiation was assessed with a permutation test (n = 1000) using the ‘randtest’ function of the ‘ade4’ package, which involves the random permutation of the rows of the genetic distance matrix (Excoffier et al., 1992). When overall differentiation was significant, pairwise AMOVA analyses were carried out to evaluate differentiation between individual populations.

To evaluate IBD and IBE, we compared the pairwise genetic distances between trees described above with the corresponding geographical and environmental distances. To remove multicollinearity between environmental variables, environmental distances between trees were calculated as the Euclidean distance in the multi-dimensional space made up by the first n PCs (principal components) derived from a principal component analysis (PCA) on the entire set of environmental variables, with n the number of PCs having an eigenvalue higher than one (i.e. the Kaiser-Guttman criterion; Guttman, 1954). Geographical distance was calculated as the Euclidean distance between tree locations. Next, we used linear mixed effects models (LMMs) to regress genetic distance against geographic distance and environmental distance. LMMs have been found to outperform other regression methods for landscape genetic analysis (Shirk et al., 2018), including Mantel tests, which have been criticized in the context of spatial analysis (Guillot and Rousset, 2013; Legendre et al., 2015). Following the maximum likelihood population effects framework (MLPE; Clarke et al. 2002), we accounted for the non-independence of pairwise comparisons using random effects, with tree identity and population as nested random effects. Geographic distance and environmental distance were included as fixed effects.

For each species, three LMMs were fit using the ‘lme4’ package for R (Bates et al., 2015), using (i) geographic distance, (ii) environmental distance, and (iii) both geographic and environmental distance as fixed effects. Each of these LMMs was then compared with a null model including only random effects, using the Akaike Information Criterion (AIC) corrected for small sample sizes (Hurvich and Tsai, 1989). Models were with fit with maximum likelihood (ML) rather than REML (restricted maximum likelihood) to obtain valid AIC scores (Clarke et al., 2002; Shirk et al., 2018). Models with AIC scores less than ten units lower than the AIC score of the null model were considered to have insufficient support (Burnham and Anderson, 2004). For each species, the best performing model (IBD, IBE, or IBD + IBE) was selected based on the AIC scores. In addition, the marginal R-squared (i.e. the proportion of variance explained by the fixed effects) was estimated for each of the fitted LMMs following Nakagawa et al. (2017), using the ‘MuMIn’ package for R (Barton, 2016).

2.7 Seed zones

To guide seed sourcing decision in the TDFs of Colombia, we aimed at constructing seed zones that are (i) applicable across tree species, (ii) dynamic in the light of ongoing climate change, and (iii) able to capture as much as possible of the observed population genetic differentiation of the study species, but large enough to keep it practically feasible to implement the seed zones on the ground. We constructed geo-environmental seed zones with the CLARA (Clustering Large Applications) approach, an extension for large datasets of the partitioning-around-medoids (PAM) algorithm, which represents a more robust alternative of the k-means algorithm (Kaufman and Rousseeuw, 1990). To reflect both environmental conditions and geographical location, the environmental variables, which were represented by the same PCs described in the previous section, were clustered along with longitude and latitude. Longitude and latitude were rescaled to have a variance equal to the average variance of the first six PCs. The number of clusters (i.e. number of seed zones) was varied between 5 and 50. To evaluate the performance of the resulting seed zone maps, we carried out additional AMOVAs to estimate the percentage of molecular variance explained by each of these seed zone scenarios. The optimal number of seed zones for each of the species was estimated as the number that explained most of the molecular variance. In order to obtain a seed zone map applicable across species, we selected the seed zone map with the highest number of zones among these optima. To reduce the occurrence of isolated patches in this proposed seed zone map, it was subject to a modal filter with a window of 3x3 grid cells (i.e. each grid cell was assigned to the most common seed zone in the 3x3 window).

To project the current seed zones to future climate conditions, the predicted future environmental conditions of every grid cell within the potential TDF distribution were projected to the same PCs as those used for the clustering of the current seed zones (i.e. the variables describing the future environmental conditions were recombined using the same linear combinations of variables as defined by the PCA that was carried out based on the current environmental variables), after which each grid cell was assigned to the closest cluster medoid, using the 'cl_predict' function of the 'clue' package for R (Hornik, 2019). In this way, the current seed zones were projected to future climate conditions as predicted by each of the selected GCMs under emission scenarios RCP4.5 and RCP8.5 for the 2050s and 2070s (section 2.5).

3 Results

We found significant genetic differentiation between populations for all 11 species, with the percentage of genetic variance between populations ranging from only 4% for *E. cyclocarpum* to 28% for *P. pinnatum.* Overall population differentiation was highly significant (P<0.001) for all species except for *E. cyclocarpum* (P=0.02). For most species, at least half of pairwise comparisons between populations was significant, except for *E. cyclocarpum* (5 out of 36 comparisons) and *A. saman* (23 out of 55 comparisons). *C. ebano* was the only species for which all pairwise combinations of populations were significantly differentiated (6 out of 6 comparisons) (Table 3).

Table 3: AMOVA (Analysis of Molecular Variance) partitioning of genetic variance for the tree species included in this study, showing the results of the overall AMOVA in the second column and results of the pairwise AMOVA analyses in the third column. All overall AMOVA analyses were statistically significant (P<0.05). SSR and ISSR stand for simple sequence repeats and inter-simple sequence repeats, respectively.

Species	% Variance between populations (Φ_{ST})	Number of significant pairwise comparisons
SSR markers		
Albizia saman (B)	14	24/55
Aspidosperma polyneuron (A)	15	16/28
Astronium graveolens (A)	7	26/45
Cedrela odorata (A)	18	5/10
Ceiba pentandra (A)	10	38/66
Enterolobium cyclocarpum (B)	4	6/36
Hymenea courbaril (B)	10	5/10
ISSR markers		
Bursera simaruba (B)	19	18/21
Caesalpinia ebano (B)	19	6/6
Hura crepitans (A)	25	31/45
Platymiscium pinnatum (A)	27	11/15

Table 4 presents the results of the pairwise AMOVA analyses in more detail. Genetic differentiation not only occurred between the five biogeographic regions where sampling was carried out but also within these regions, with 47% of the pairwise population combinations within regions being significantly differentiated. For example, the Santa Fe de Antioquia and Ituango populations, despite being separated by only ca. 100 km and being both located in the Cauca river valley, were genetically differentiated for 3 out of 5 species (Table 4). This is further illustrated by the significant differentiation between all four populations of *C. ebano,* which are all located in the same region (Caribbean coast). Further, Table 4 shows that the Patía population was clearly the most differentiated from the other sampled populations, with significant pairwise differentiation for all but two of the pairwise comparisons, and high percentages of genetic variance between populations, as high as 50% and higher (Table 4). While genetic differentiation between the five sampling regions was often significant, this was not always the case. For example, the populations in the south of the Magdalena valley (TAN: Tatacoa N; TAS: Tatacoa) were only differentiated from the populations in the Cauca valley in 50% of the comparisons.

Table 4: Pairwise AMOVA (Analysis of Molecular Variance) results. The lower triangular matrix shows the number of species for which each of the pairwise comparisons indicated significant genetic differentiation (P<0.05), as the fraction of the total number of species for which pairwise comparisons were made. The upper triangular matrix indicates the average percentage of variance situated between the two populations (calculated from all the pairwise comparisons, not only those that were statistically significant). Dashes ("-") indicate pairs of populations for which no comparisons could be made. Populations are abbreviated as follows: SMN: Santa Marta N; SMS: Santa Marta S; GUA: El Guamo; ZAM: Zambrano; COL: Colosó; ITU: Ituango; SFE: Santa Fe de Antioquia; PIN: La Pintada; PAI: La Paila; MAT: Mata Guadua; CIA: Centro Internacional de Agricultura Tropical; JAM: Jamundí; TON: Tolima N; TOS: Tolima S; TAN: Tatacoa N; TAS: Tatacoa S; PAT: Patía; CHI: Chicamocha.

Biogeographic region		SMN	SMS	GUA	ZAM	COL	ITU	SFE	PIN	PAI	MAT	CIA	JAM	TON	TOS	TAN	TAS	PAT	CHI
Carribean coast	SMN		11	12	15	15	17	8	14	21	35	0	-	27	22	2	4	59	20
	SMS	3/7		10	10	13	15	11	11	9	15	0	-	23	11	10	5	49	19
	GUA	2/5	3/5		10	5	13	2	11	18	13	9	-	-	26	0	1	35	13
	ZAM	4/5	2/5	4/4		11	15	10	12	15	16	16	-	22	22	4	1	44	18
	COL	2/5	4/6	1/5	2/4		21	8	14	13	6	3	-	18	12	7	0	28	19
	ITU	2/4	4/5	2/3	3/3	3/4		13	11	17	14	0	-	-	-	19	11	50	25
Cauca valley	SFE	0/4	3/5	0/4	2/4	2/5	3/5		7	11	-7	5	15	-	17	4	-3	29	15
	PIN	2/4	2/5	3/4	3/3	3/6	1/4	2/6		14	12	9	20	5	13	14	5	31	18
	PAI	1/3	1/3	2/3	3/3	2/3	3/3	2/4	3/3		0	0	-	-	24	-	12	45	16
	MAT	1/2	0/2	1/2	2/3	1/2	1/2	1/4	0/3	0/3		0	35	-	21	-	13	25	15
	CIA	0/1	0/1	1/2	1/1	0/3	0/1	0/2	0/3	0/2	0/1		-	2	18	-	10	34	7
	JAM	-	-	-	-	-	-	1/1	1/1	-	0/1	-		-	-	-	-	12	-
Magdalena valley	TON	1/1	1/1	-	1/1	2/2	-	-	0/1	-	-	0/1			6	-	-	-	13
	TOS	1/1	0/1	1/1	2/2	1/2	-	1/1	0/1	1/1	1/1	0/1	-	0/1		29	21	29	20
	TAN	0/1	1/2	0/1	0/1	1/2	2/2	0/2	1/2	-	-	-	-	-	-		-	-	8
	TAS	0/1	0/1	0/1	0/2	0/1	1/1	0/2	1/2	2/2	0/2	0/1	-	-	1/1	-		50	7
Patía valley	PAT	1/1	1/1	1/1	2/2	1/1	1/1	2/3	3/3	2/2	2/3	1/1	1/1	-	1/1	-	2/2		43
Chicamocha valley	CHI	2/4	4/5	3/4	3/4	4/6	3/4	4/5	4/6	3/3	1/3	0/2	-	1/1	0/1	1/2	0/2	2/2	

The first six PCs resulting from the PCA of the environmental variables (n = 30) together explained 85% of the total variance. Already 60% was explained by the first two PCs only, mainly reflecting variation in temperature and precipitation, respectively. The loadings of the environmental variables of the first six PCs are given in Table A.4 and the scree plot is given in Figure A.1 (Supplementary material).

The results of the LMMs that were fit to evaluate IBD and IBE are given in Table 5. For 6 out of 11 species, the model with the lowest AIC was the model including both geographic distance and environmental distance (IBD + IBE) as explanatory variables, whereas the IBE model had the lowest AIC for the 5 remaining species (Table 5). On average, environmental distance was a better predictor of genetic distance, according to both the AIC and R^2 values (Table 5).

Table 5: Results of the linear mixed effects models (LMMs) evaluating the relationship between genetic distances between trees and corresponding geographical distances (isolation by distance; IBD) and environmental distances (isolation by environment; IBE). LMMs were fitted within a maximum likelihood population effects (MLPE) framework, using trees and population as nested random effects and geographical and environmental distance as fixed effects. The reported R^2 values are marginal R^2 values only reflecting the variance explained by the fixed effects. ΔAIC scores refer to the difference between the AIC score of the fitted model and the AIC score of a null model with only random effects. All AIC scores were corrected for small sample sizes. Models with ΔAIC scores higher than -10 were not considered to have sufficient support and are not shown. For each species, the best model (last column) was identified based on the lowest ΔAIC.

	Isolation by distance (IBD)		**Isolation by environment (IBE)**		**IBD + IBE**		**Best model**
	ΔAIC	**R^2**	**ΔAIC**	**R^2**	**ΔAIC**	**R^2**	
SSR markers							
Albizia saman	-118.7	0.03	-12.3	0.00	-156.1	0.05	IBD + IBE
Aspidosperma polyneuron	-79.0	0.10	-20.2	0.03	-79.2	0.10	IBD + IBE
Astronium graveolens	-11.3	0.00			-13.3	0.00	IBD + IBE
Cedrela odorata	-36.5	0.06	-77.3	0.11	-75.7	0.11	IBE
Ceiba pentandra	-101.7	0.02	-12.3	0.00	-113.1	0.03	IBD + IBE
Enterolobium cyclocarpum	-38.1	0.02	-34.0	0.02	-41.8	0.02	IBD + IBE
Hymenea courbaril			-18.8	0.03	-17.5	0.03	IBE
ISSR markers							
Bursera simaruba	-11.4	0.01	-198.5	0.17	-196.9	0.17	IBE
Caesalpinia ebano	-60.4	0.11	-65.2	0.13	-64.2	0.13	IBE
Hura crepitans	-62.4	0.04	-118.7	0.07	-116.8	0.07	IBE
Platymiscium pinnatum	-85.3	0.19	-93.0	0.20	-98.0	0.22	IBD + IBE
Average	-55.7	0.05	-60.0	0.07	-88.4	0.08	

The performance of the seed zone maps with different number of seed zones was evaluated by means of AMOVAs (Table 6; full results in Table A.5 in Supplementary material). The optimal number of seed zones, determined as the number of seed zones explaining most of the genetic variance, ranged from 5 (*A. polyneuron*) to 36 (*C. pentandra*). In order to obtain a conservative, risk-minimizing seed zone map applicable across species, we selected the base map with 36 zones for further analysis. In addition, this approach has the advantage that seed zones could be merged for species with known genetic variance which can be explained by fewer zones.

Table 6: Optimal number of seed zones per species as estimated by the AMOVAs, also showing the percentage of genetic variance situated between zones at these numbers, and the percentage of genetic variance situated between populations for comparison.

	Optimal n° seed zones	**% variance between seed zones**	**% variance between populations**
SSR markers			
Albizia saman	26	17	14
Aspidosperma polyneuron	5	16	15
Astronium graveolens	27	7	7
Cedrela odorata	8	18	18
Ceiba pentandra	36	11	10
Enterolobium cyclocarpum	26	5	4
Hymenea courbaril	20	10	10
ISSR markers			
Bursera simaruba	24	19	19
Caesalpinia ebano	19	18	19
Hura crepitans	27	23	25
Platymiscium pinnatum	27	27	27

The seed zones under present climatic conditions are shown in Figure 2. Panel b, depicting the seed zones with colours reflecting environmental similarity, shows that some seed zones located far apart have similar environmental conditions, as illustrated for example by the purple colors in both the central part of the Caribbean TDFs and the Magdalena valley. However, by adding longitude and latitude as input variables in the clustering, these areas were assigned to different seed zones, as would be expected under an IBD scenario. Figure 3 depicts the seed zones under both present (panel a) and future climate conditions (2050s; panels b and c), showing the expected expansion and contraction of seed zones under future climatic conditions, as illustrated for example by the predicted southward expansion of the pink seed zone of the Guajira peninsula in the northernmost part of Colombia.

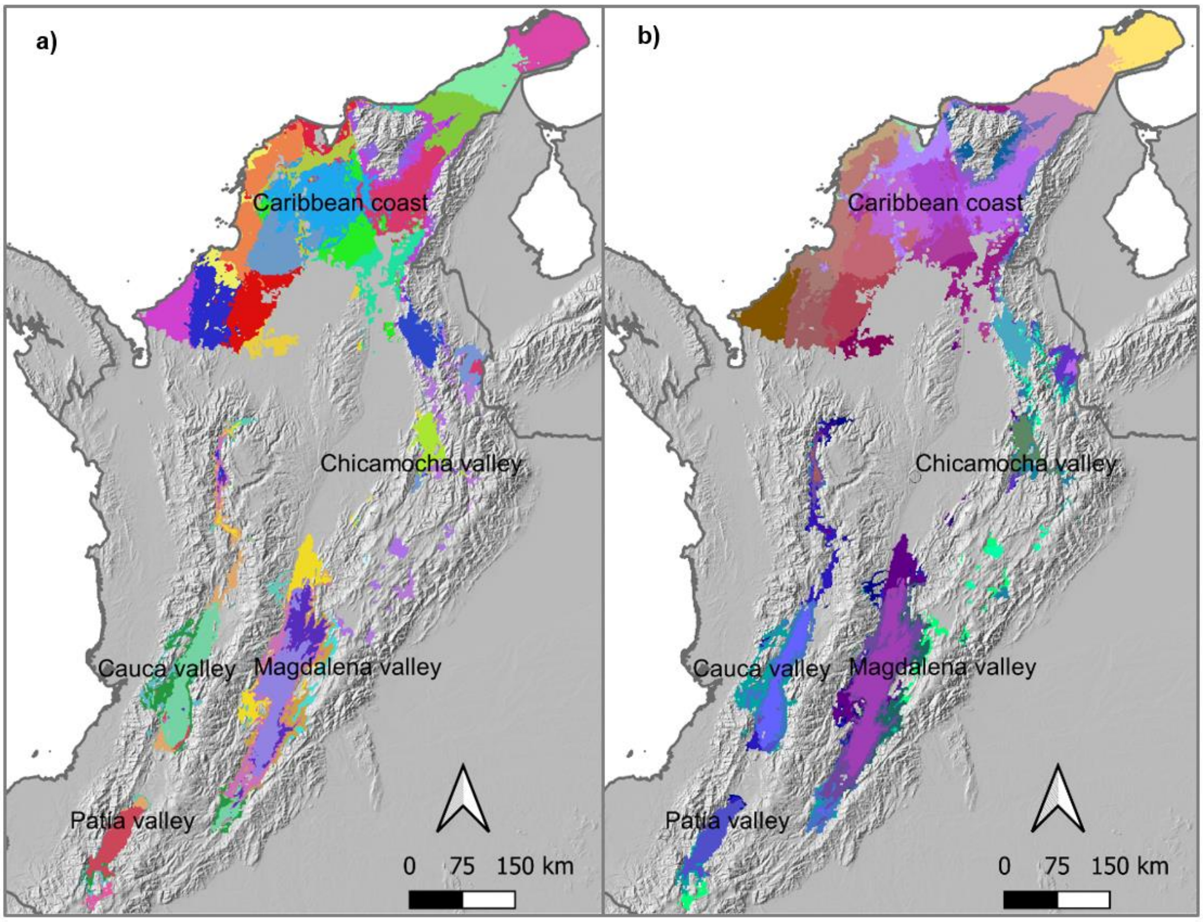

Figure 2: Seed zones (n = 36) for the tropical dry forests (TDFs) of Colombia under present climate conditions. The colours of the seed zones in panel a were randomly chosen, whereas the colours in panel b reflect the environmental similarity between seed zones, using a red-green-blue colouring scheme determined by the average scores of the three first principal components (PCs) of the environmental variables, as proposed by Hargrove and Hoffman (2005).

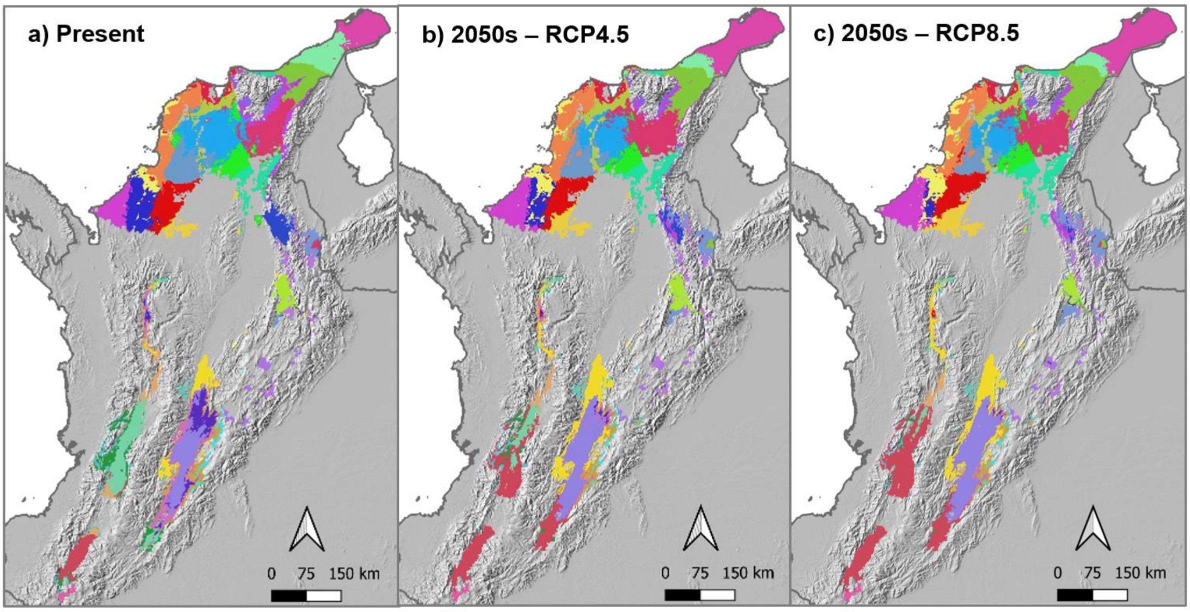

Figure 3: Seed zones (n = 36) for the tropical dry forests (TDFs) of Colombia under present climate conditions (panel a) and future climate conditions for the 2050s under the representative concentration pathways RCP4.5 and RCP8.5 (panel b and c). The future seed zones shown here are those predicted by the HadGEM2-ES model, one of the five selected GCMs (section 2.5), but note that the tool in which the seeds zones are integrated (www.diversityforrestoration.org/) combines the predictions of all five GCMs.

4 Discussion

4.1 Population genetic differentiation

All of the 11 study species showed significant genetic differentiation between populations, with the percentage of variance situated between populations (Φ_{ST}) ranging from 4% to 28% (Table 3). These figures are similar to other neutral marker characterizations of Neotropical tree species at similar spatial scales (e.g., Chase et al. 1995, Lacerda et al. 2001, Lowe et al. 2003, Cerón-Souza et al. 2005) and within the range of expected values for outcrossing long-lived species, which tend to retain most of the genetic variability within populations (Hamrick and Godt, 1996; Nybom, 2004; Reisch and Bernhardt-Römermann, 2014). The marked differences between species, also between species characterized by the same type of markers, suggest that species-specific seed zones may be more appropriate than general seed zones. However, collecting genetic data on all the species used in restoration of the Colombian TDFs, which are home to several hundreds of tree species, would be a daunting task, and it may be unrealistic to expect restoration practitioners to implement different seed zones for each of the species used, given the generally limited logistic capacity and lack of incentives to obtain appropriate planting material (Atkinson et al., 2018; Jalonen et al., 2018). Trait-based generalizations provide one possible solution, but previous research has shown that predicting the degree of population genetic differentiation using life history traits is far from an easy undertaking, as relationships between both are generally weak (Duminil et al., 2007). We therefore adopted a more pragmatic approach and aimed to construct a single set of seed zones applicable across species, drawing on genetic marker data of 11 species with differing life history traits (Table 1).

The current difference in population genetic structure between the study species are the result of a complex interplay of different factors. Past climatic changes are likely to have led to different degrees of range contraction and expansion and possibly convergence of different genetic groups in some areas (Aguirre-Morales et al., 2020; Bocanegra-González et al., 2018; Thomas et al., 2016). Using Bayesian genetic clustering, these studies furthermore suggest that exchange of tree genetic resources across the Inter-Andean valleys may have taken place during or prior to the Last Glacial Maximum (LGM) (Aguirre-Morales et al., 2020; Bocanegra-González et al., 2018), which may explain why genetic differentiation between populations in the Magdalena valley and those in the Cauca valley was often not significant (Table 4).

Other important factors influencing the genetic differentiation between populations are species' seed dispersal modes, pollination modes, and mating systems (Ballesteros-Mejia et al., 2016; Hamrick et al., 1993; Lowe et al., 2018), which result in differences in the degree of gene flow. For example, our findings partly followed the expected pattern that populations of animal-dispersed species tend to be less genetically differentiated (average Φ_{ST} =13.2%) than those of abiotically dispersed species (e.g. wind, autochory; average Φ_{ST} = 15.0%) as a consequence of gene flow over larger distances in animal-dispersed species (Hamrick et al. 1993, Lowe et al. 2018, but see Duminil et al. 2007), although some wind-dispersed seeds can be dispersed over extremely large distances (e.g., *C. pentandra*; Dick et al., 2007). The species with the lowest degree of differentiation, *E. cyclocarpum* (Table 3), used to be dispersed by Pleistocene horses (Janzen and Martin, 1982), but has long been widely planted in pasture lands and is now mainly dispersed by introduced cattle and horses (Gonzales et al., 2010; Janzen, 1982), resulting in large distance dispersal when these animals are moved around by humans. Human-mediated dispersal may also have become the dominant dispersal mode of other species originally dispersed by megafauna, including *H. courbaril* and *A. saman* (Janzen and Martin, 1982). *E. cyclocarpum* and *H. courbaril* also have a long history as human food (Iriarte et al., 2020; Zizumbo-Villarreal et al., 2016) and the same is possibly true for *A. saman*. However, as each of the factors mentioned above may have affected the genetic structure of each of the species differently, it is difficult to explain the findings of the AMOVAs (Table 3). In addition, the differences between species in our study should be interpreted with care because not all species were present in all sampling sites and because two different marker types were used. Rigorous hypothesis testing on the relationship between life history traits and population genetic structure was therefore not part of the scope of the present study. Rather, the value of the selected set of species lies in the broad range of life history traits they represent, increasing the likelihood that the obtained results are applicable across many tree species of the Colombian TDFs.

For more than half (6 out of 11) of the study species, genetic differences between trees was best explained using both geographical and environmental distance, while they were best explained by environmental distance for the remaining species (Table 5), suggesting that the observed genetic differentiation is a consequence of both neutral and adaptive processes, in line with similar findings elsewhere (Sexton et al. 2014). The obtained R^2 values were relatively low for most species, which was expected since the studied species retain the majority of genetic variability within populations, within which both geographic and environmental distances are limited. As discussed by Sexton et al. (2014), IBE results from reduced gene flow between populations growing under divergent environmental conditions, which may be the consequence of natural selection, with maladapted immigrants or offspring of local and immigrant parents failing to germinate, survive or reproduce, and hence failing to introduce their genes in the local population. It may also be caused by nonrandom mating resulting from different environmental conditions, both as a consequence of genetic adaptation (e.g., flowering period mismatch between immigrants and locals) or phenotypic plasticity (e.g., plants growing at different altitudes flowering at different times). Without provenance trials, it is difficult to determine the relative importance of these different mechanisms (Sexton et al., 2014).

Neutral markers have been used extensively to inform provenancing decisions (Durka et al., 2017; Jorgensen et al., 2016; Krauss et al., 2013; Krauss and He, 2006; Listl et al., 2018; Malaval et al., 2010; Massatti et al., 2020). However, they are not directly linked to local adaptation (Holderegger et al., 2006), which has led to criticism on their use in guiding seed provenancing (McKay et al., 2005). Nevertheless, meta-analyses have found that differentiation in adaptive and neutral markers tends to be correlated (Leinonen et al., 2008; Merilä and Crnokrak, 2001). Divergent natural selection (i.e. selection acting in different directions on different populations) can not only lead to population differentiation by acting on specific loci or those physically associated with them, but can also promote barriers to gene flow as discussed above. This results in genome-wide neutral divergence via genetic drift, which is readily detectable by neutral markers (Nosil et al., 2009).

4.2 Seed zones

The population genetic differentiation we found in all the study species (Table 3) supports the need for establishing seed zones to promote adaptedness of seeds used in tree planting activities and to avoid disruptions of genetic patterns. Pairwise genetic differentiation between populations within the five sampled biogeographic regions was often significant (47% of within-region comparisons were significant; Table 4), indicating that population differentiation occurs at a finer scale than these five regions, which should be reflected in a sufficiently high number of seed zones. Further, as our results indicate that the genetic differences between trees are related to both geographic distance and environmental differences (Table 5), we included longitude and latitude along with the PCs derived from environmental variables in the PAM clustering, seeking to construct seed zones that are environmentally homogeneous while also avoiding large geographic distances between locations within the same seed zone. This reduces the probability that isolated areas with similar environmental conditions would be grouped in the same seed zone, which is a disadvantage of seed zones based on clustering environmental variables only (Potter and Hargrove, 2012).

Non-hierarchical clustering methods such as k-means clustering or PAM have been used before to delineate seed zones (Potter and Hargrove, 2012; Shryock et al., 2018) or ecoregions (Hargrove and Hoffman, 2005). Compared to hierarchical clustering, these methods have the advantage that they result in similar environmental heterogeneity within different seed zones (Hargrove and Hoffman, 2005). We followed Shryock et al. (2018) by submitting the environmental variables to a PCA prior to clustering, which is more robust against the inclusion of correlated variables, and does not require prior knowledge about which environmental variables are most closely linked to local adaptation of tree species populations. We generated seed zone maps with differing number of seed zones, ranging from 5 to 50, and determined the optimal number of zones by carrying out an AMOVA for each of these numbers of zones. However, it should be noted that the sampling density was relatively low, and that the number of seed zones proposed here should be seen as the optimal scenario based on currently available information. In order to more thoroughly study the spatial scale of genetic differentiation, a more dense sampling scheme is recommended, in analogy with Malaval et al. (2010) or Michalski and Durka (2012).

We projected the proposed set of seed zones to the climate conditions anticipated in the 2050s and 2070s by assigning the future conditions of each of the grid cells to the closest cluster medoid resulting from the CLARA algorithm using the present environmental conditions as an input. As such, a grid cell is assigned to another seed zone under future climate conditions only if its distance in PCA space to the cluster medoid of that other seed zone is shorter than to the medoid of the present seed zone. By also including longitude and latitude in the clustering, the probability that grid cells are assigned to another seed zone under future climate conditions decreases with the geographic distance to the grid cell representing the cluster medoid of the latter zone. Grid cells changing from one seed zone to another result in the contraction and expansion of seed zones under future climate conditions, for example seed zones that are currently already characterized by high temperatures are likely to expand under future conditions.

Our approach to predict shifts in seed zones from present to future climate condition is similar to the multivariate spatiotemporal clustering (MSTC) approach proposed by Hargrove and Hoffman (2005), with the difference that in MSTC, predicted future environmental conditions are used directly as input variables in the clustering along with the present environmental conditions. Consequently, when some of the predicted future conditions are very dissimilar to any of the current conditions, some clusters in MSTC may only exist under future conditions (i.e. represent novel climates). While such novel climates are likely to occur in the future, in the context climate-smart seed sourcing, we considered it more important to identify the current seed zone where conditions are most similar to the expected novel climate.

The aim of the seed zones presented here is to promote the use of planting material that is well-adapted to present and future climate conditions in the TDFs of Colombia. To facilitate their use, the zones have been integrated into a map-based online decision-support tool (DiversityForRestoration, available at www.diversityforrestoration.org; Thomas et al. 2017a). The tool recommends to supplement planting material from the present seed zone with material from areas currently located in the seed zone that is anticipated at the planting site under future climate conditions, i.e. combining local provenancing with predictive provenancing. While the tool recommends a 50/50 ratio, some restoration planners may consider the risk of introducing 50% material from a non-local seed zone too high, and may opt for only introducing only a smaller amount of non-local seeds, coinciding with the ‘genetic enrichment’ approach proposed by Lefèvre et al. (2013). Both local and predictive provenancing may include one or more source populations (more is better to increase adaptive potential, but logistical costs may be a constraint).

While all five GCMs predict marked increases in temperature in the TDFs of Colombia, the direction of predicted precipitation changes is not always consistent. As a result, we found that different GCMs did not always coincide in the future seed zone projections, in which case the tool recommends sourcing proportional parts of the planting material in each of the future seed zones as predicted by different GCMs. This approach coincides with the risk-minimizing portfolio approach proposed by Crowe and Parker (2008), directly incorporating the uncertainty of future climate predictions, as illustrated in Figure 4.

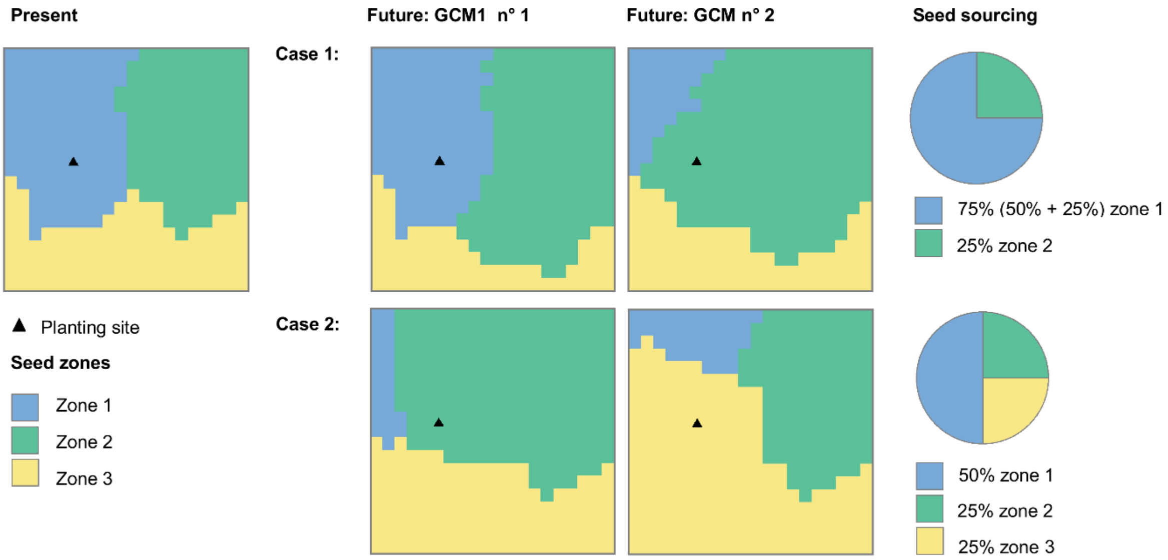

Figure 4: Illustration of the risk-minimizing seed sourcing strategy ('portfolio approach') proposed in the DiversityForRestoration decision support tool (www.diversityforrestoration.org), which involves sourcing 50% of the seeds in the present seed zone, and 50% in the future seed zones as predicted by different General Circulation Models (GCMs), recommending to source from different future seed zones if different GCMs do not coincide in their predictions of future seed zones. This is illustrated here with two GCMs for simplicity, but note that 5 GCMs were used (section 2.5).

4.3 Final considerations and prospects

Climate-smart seed sourcing is a complex issue and the 'local + predictive' strategy we adopted in the DiversityForRestoration tool is only one of several possible strategies. The seed zones presented here can be used to implement other strategies too, as illustrated in Figure 5. While the inclusion of longitude and latitude in the clustering ensures that seed zones do not expand over very large geographic distances, limiting the distances over which predictive provenancing is recommended, some restoration planners may prefer to not carry out any assisted gene flow at all, as experimental evidence of its potential remains limited and some concerns remain about the risk of outbreeding depression and mismatches in biotic interactions (Aitken and Whitlock, 2013; Bucharova, 2017; Bucharova et al., 2018). To increase adaptive capacity, these restoration planners may opt to only focus on the collection of genetically diverse and locally adapted planting material instead. In this case, the proposed seed zones can be used as boundaries within which seeds of several populations may be mixed, coinciding with the regional admixture approach proposed by Bucharova et al. (2018), which we termed 'zonal admixture' for consistency with the seed zones terminology. Similarly, seed zones can be used as boundaries for composite provenancing (Breed et al., 2013), which we termed 'zonal composite' provenancing, while combining seeds from different seed zones coincides with an admixture provenancing strategy (Broadhurst et al., 2008). Lastly, when sourcing seeds for restoration in the long term (many restoration objectives will typically go beyond the 2050s; e.g. biodiversity conservation, slow-growing timber species), an approach similar to the climate-adjusted provenancing approach (Prober et al., 2015; Ramalho et al., 2017) could be implemented by sourcing from both the seed zone predicted for the 2050s and the seed zone predicted for the 2070s, if different (Figure 5). In this way, seed zones provide a useful tool to implement different previously proposed climate-smart seed sourcing strategies in a pragmatic way. It is important to note that restoration should not be considered a onetime activity, and that adaptive management may include assisted migration only at a later stage, for example when it has become more clear that local populations are not able to adapt fast enough, or when the uncertainty about future climatic changes has become lower. Other climate-smart adaptive management strategies are discussed in Lefèvre et al. (2013).

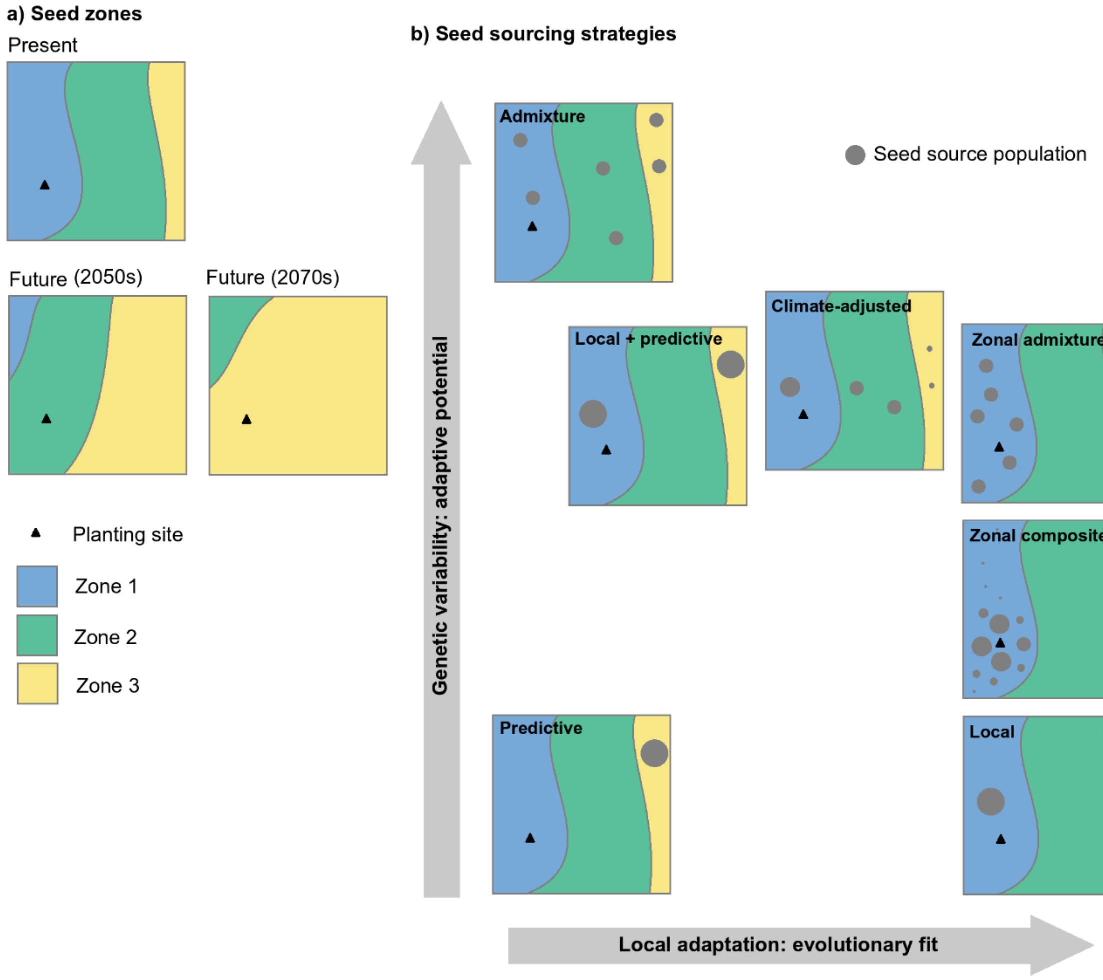

Figure 5: Use of dynamic seed zones for different seed sourcing strategies, in relation to the trade-off between local adaptation vs. genetic variability, modified from Bucharova et al. (2018) (climate gradient replaced by seed zones and some seed sourcing strategies added or modified). The sizes of the grey circles reflect the relative contributions of different seed source populations. The 'regional admixture' approach proposed by Bucharova et al. (2018) is termed 'zonal admixture' here to fit with the seed zone terminology. The climate-adjusted provenancing follows Ramalho et al. (2017) by making the amount of seed smaller further along the climate change gradient and was therefore placed higher on the local adaptation axis than in Bucharova et al. (2018). Note that with 'local' seed sourcing we refer to any seed source population within the local seed zone under current climate conditions. We assume that all populations in the local seed zone are equally well adapted to local conditions; the local seed sourcing strategy is therefore put at the same level of local adaptation as the 'zonal admixture' and 'zonal composite' seed sourcing strategies. Similarly, we assume that the 'local + predictive' and the 'zonal admixture' approaches result in a similar level of total genetic variability (the 'local + predictive' approach consists of a lower number of provenances but from more different environmental conditions). Note that the seed sourcing strategies shown here are not exhaustive and that more variations are possible, for example the predictive provenancing approach may involve sourcing seeds from more than one source population.

Once restoration practitioners have identified the appropriate seed zones, they need to identify at least one seed source or seed provider in each of these zones. Hence, it is clear that any seed sourcing strategy should go hand in hand with a strategy for the conservation of viable seed sources. The seed zone approach we presented here can also be used as a proxy for the identification of ‘management units’ or ‘evolutionary significant units’ that should be subject of gene conservation efforts (Azpilicueta et al., 2013; Potter and Hargrove, 2012; Soliani et al., 2017). Identifying protected areas in each of the seed zones provides one way forward, but only 5% of the remaining Colombian TDFs is currently protected (i.e. less than 1% of the original TDF cover; García et al., 2014). While this underlines the pressing need to step up conservation efforts, it also indicates that protected areas alone will not be sufficient to underpin an efficient and climate-smart national seed sourcing strategy in Colombia. Experiences from the restoration of the Atlantic Forest in Brazil have shown that involving local communities and private landowners in seed collection is a promising way forward for large-scale seed collection (Brancalion et al., 2012; Schmidt et al., 2019). This can provide local communities and private landowners with alternative income sources and serve as an economic incentive for conserving local tree populations. However, it is important that seed providers are trained in proper seed collection practices (Basey et al., 2015; Thomas et al., 2017), to ensure that the planting material has a sufficient broad genetic basis promoting the evolutionary potential of established populations (Broadhurst et al., 2008; Thomas et al., 2014).

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