Ecological niche modeling, niche overlap, and good old Rabinowitz's rarities applied to the conservation of gymnosperms in a global biodiversity hotspot

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Title: Ecological niche modeling, niche overlap, and good old Rabinowitz's rarities applied to the conservation of gymnosperms in a global biodiversity hotspot

Short title: Vegetation suitability and rarities in the conservation of gymnosperms

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ABSTRACT

Context

Biodiversity hotspots harbor 77% of endemic plant species. Patagonian Temperate Forest (PTF) is a biodiversity hotspot, but over the past centuries, has been over-exploited, fragmented and replaced with exotic species plantations, lately plus the threat of climate change.

Objectives

Our aim is to better understand patterns of habitat suitability and niche overlap of nine endemic gymnosperm species, key elements of the PTF, complementing traditional approaches of biodiversity conservation.

Methods

Using R packages and 3024 occurrence data, we deployed ecological niche models (ENM) in MaxEnt via KuENM, and classified species according to Rabinowitz's types of rarity. We then overlapped their niches calculating Schoener's D index, and considered types of rarity in a spatial ecological context. Finally, we overlay high species' suitability and protected areas and detect conservation priorities using GapAnalysis.

Results

We generated simplified ENMs for nine Patagonian gymnosperms and found that most niches overlap, and only one species displayed a unique niche. Surprisingly, we found that three species have divergent suitability of habitats across the landscape. We showed that the rarer a species is the smaller niche volume tend to have, that six out of nine studied species have high conservation priority, and that there are conservation gaps in the PTF.

Conclusion

Our approach showed that there are unprotected suitable areas for native key species at high risk in Patagonian forests. Suggesting that integrating habitat-suitability models of multiple species, types of rarity, and niche overlap, can be a handy tool to identify potential conservation areas in global biodiversity hotspots.

Keywords: Araucariaceae, evolutionary potential, conservation, Cupressaceae, ENM, niche volume, Podocarpaceae

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Introduction

Biodiversity hotspots of the planet harbor 77% of endemic plant species, have high levels of species richness, but are highly threatened (Mittermeier et al. 2011). High species diversity in these hotspots is often attributed to an accumulation of narrow-ranged species via high speciation rates and/or preservation of species over time, via low extinction rates (Jetz et al. 2004), usually hosting ancient and young species (Harrison and Noss 2017). *Patagonian Temperate Forest* (PTF) runs through the spine of the Southern Andes in Argentina and Chile, where it has been declared a global biodiversity hotspot, however over the past centuries, has been over-exploited, fragmented and replaced with exotic species plantations (Miranda et al. 2014), lately also threatened by climate change. This forest is frequently dominated by an ancient group of phylogenetically related gymnosperm species, whose gene pool has shown its ability to keep pace with past climatic changes. Although some of them have been focus of ecological and genetic studies, either for their cultural or economic value, others are relatively understudied, due to their remote distribution and inaccessibility (Donoso 2006; Premoli et al. 2000; Premoli et al. 2002; Allnutt et al. 2001; Quiroga and Premoli 2010; Souto et al. 2015a). Since many of its native species are considered rarities, included in the IUCN red list, urgent conservation actions are in need (Smith-Ramirez et al. 2004; Alaniz et al. 2016; Miranda et al. 2017). Given limited resources, conservation efforts should arguably be directed toward taxa and/or areas that represent the greatest amount of unique evolutionary history (Scherson et al. 2014). Currently new aims in conservation contemplate large geographic areas and/or long-time scales, to preserve evolutionary potential. Highly diverse groups that share a set of ecological adaptations along an environmental gradient, are exemplar opportunities to test and develop specific actions and target areas aimed to protect a biome. Such studies might shed light to understand ecological niche differences and handy to develop conservation and mitigation actions against global change impacts (Aguirre-Gutierrez et al. 2015).

Current approaches to the conservation of biodiversity hotspots include the application of biogeographical principles, theories, and analyses, concerned with range shifting of taxa (Whittaker et al. 2005). Species distribution models (SDMs), which describe both, a species' niche and habitat suitability that supports it (Richardson and Whittaker 2010), and ecological niche models (ENM) that identify potential areas of distribution (Soberón and Nakamura 2009), constitute essential tools in conservation biogeography (Franklin 2010; Scoble and Lowe 2010). In these studies, the niche conservatism concept allows to infer species responses to climate changes in the past and how they might shift species' distribution, especially regarding changes in their habitat specificity (Wiens et al. 2010). Also, similarities and differences in niche characteristics among populations within a species can be statistically analyzed using ENM (Wiens and Graham 2004). Advances in studies on how global climate change affects species have highlighted the importance of knowing the differences between species in terms of their environmental requirements in a geographical context and in an extension comparable to that of the species' ranges (Warren et al. 2008). ENMs are correlative models unrelated to the biological processes underlying genetic differentiation and adaptation of a species to its environment (Morente-López et al. 2020), so they can identify areas with different levels of environmental suitability for a species within its range. In this way, ENMs allow, not only to estimate the distribution of a species and identify putative important environmental variables that shape it (Searcy and Shaffer 2016), but also to postulate hypotheses on divergent selection within a species' range (Blanquart et al. 2013). The niche overlap framework has been shown as a robust statistical method to test

between-species niches' differences, as well as subspecies or different populations of the same species which are therefore likely to experience different climatic conditions (Broennimann et al. 2012).

Species conservation depends on the preservation of their habitats (Dengler et al. 2008), and its goals have evolved over time from a more species-centric approach to one that considers keystone species and their role in the ecosystem (Lacher 2018), including rare ones. Types of rarity theory, states that range size, habitat specificity, and local population size, are environmental constraints that generate many ways in which a species can be rare (Rabinowitz 1981). There are eight forms of rarity, defined according to three species' characteristics: 1. Range size, so species can be Widespread or Narrow; 2. Habitat specificity, classifying species in Broad or Restricted, and 3. Local population size, then species have, either Large, somewhere dominant, or Small, non-dominant populations. Current, online abundant occurrence records could potentially be used to define plant species types of rarity and their level of endemism, adding a new tool to the design of conservation plans (Fleishman et al. 2006; Choe et al. 2019). Geographic ranges of closely related species can vary dramatically, yet we do not fully grasp the mechanisms underlying such variation. Niche volume hypothesis posits that species that have evolved broad environmental tolerances can achieve larger geographic ranges than species with narrow environmental tolerances (Slatyer 2013). This assumption has been used in multiple studies of conservation and distribution of dissimilar lineages (Yu and Dobson 2000; Choe et al. 2019; Ramírez-Bautista et al. 2020), giving a conceptual framework to make multiple comparisons.

In this study we combine the background presented above to deploy patterns of habitat suitability and niche overlap of nine gymnosperm species, key elements of the PTF biodiversity hotspot, complementing traditional approaches of biodiversity conservation. Particularly, we aim to: 1) Define ENM for focal species; 2) Test pairwise niche overlap to detect shared environmental constraints among focal gymnosperms, and within a species' range as indication of divergent selection; 3) Classify each species according to Rabinowitz's types of rarity and test niche volume hypothesis that widespread species with low habitat specificity, and continuous populations have larger niche volume compared to narrow species, with high habitat specificity and scattered populations; finally 4) Combining ENM, niche overlap and forms of rarity, to pinpoint and prioritize conservation gaps in a global biodiversity hotspot.

Materials and methods

Patagonian Temperate Forest have a high number of endemism, making it a global biodiversity hotspot (Smith-Ramirez 2004; Scherson et al. 2014), with sectors of high genetic diversity evidencing a complex evolutionary history (Souto et al. 2015b; Scherson et al. 2017). Product of these events, PTF is considered a biogeographic island, arisen along several geological/climatic events (Armesto et al. 1998), with a dynamic history, undergoing almost continuous changes since the Paleocene, establishing the current species' associations (Hinojosa and Villagrán 1997; Barreda and Palazzesi 2007).

Studied species and presence records

We focus our study in an endemic phylogenetically related group of species of biogeographical interest, the Coniferophyta II (here after gymnosperms) from PTF. This group includes nine species from three families: Araucariaceae, with one species (*Araucaria araucana*); Cupressaceae, with three monotypic genera (*Austrocedrus chilensis*, *Fitzroya cupressoides* and *Pilgerodendron uviferum*); and Podocarpaceae with five

species (*Lepidothamnus fonkii*, *Podocarpus nubigenus*, *Podocarpus salignus*, *Prumnopitys andina* and *Saxegothaea conspicua*). These are all ancient taxa that have long successfully navigated climate and geology, been confined to a narrow strip of land in Southwest South America. Araucariaceae and Podocarpaceae diverged between 176-230 Ma ago (Leslie et al. 2012, Quiroga et al. 2016), while *Austrocedrus*, *Pilgerodendron*, and *Fitzroya* diverged circa 120 Ma ago (Yang et al. 2012). All these species are emblematic either for being taxonomic rarities, relict lineages, long-lived or dominant species. The Cupressaceae and *Saxegothaea* are mono-specific and unique in the world. The other species have many related taxa within the continent, as is the case of *Araucaria*, *Prumnopitys* and *Podocarpus*, as well as in other former Gondwanan continents.

Climatic variables and ecological niche models

We completed our personal data collection of focal species' presence records, with available occurrence sources: GBIF repository, Concepcion (Chile) regional herbarium, and CONAF territorial information system (<http://sit.conaf.cl/>). We checked each datum before including it in our data base and cleaned all species' data sets with a minimum distance of 30 seconds among records using NicheToolBox (NTB) R-script (Osorio-Olvera et al. 2020). After removing duplicates and neighbors, we obtained a total of 3024 presence records (Table 1).

In order to define the fundamental niche of the nine gymnosperms of the PTF, we clipped 19 bioclimatic variables from the present-day WorldClim database at 30 seconds resolution (1970 -2000) (Fick and Hijmans 2017; <http://www.worldclim.org>), representing summaries of means and variation in temperature and precipitation. For each species, a background area (M zone) was delimited using Qgis v. 3.14.0.Pi (2019), covering the entire range and potential areas of colonization. Then we performed suitability models using MaxEnt v3.3.3 (Phillips et al. 2017), including: linear, quadratic, and product with or without threshold and hinge features, recording in all cases the logistic output. To estimate bioclimatic variable's relevance in each model, we run a jackknife procedure. We cross validate each model with 10 replicates, 500 iterations, 10 percentile training presence, and regularization multiplier of 1. Exceptionally, we doubled the number of iterations for *L. fonkii*, an extremely rare species, with only 37 available records. Once we obtained each species' general model in MaxEnt, we applied dimension-reduction techniques to minimize strong covariance among environmental variables and to avoid over fitted models that reduce accuracy (Synes and Bsborne 2011; Boria et al. 2014). Since each species has its own M zone, we performed Pearson's correlations among the 19 bioclimatic variables for each species, and eliminated highly correlated variables using the function `correlation_finder` using a threshold of $r \leq 0.85$, in NTB R-package. For each species we tested several models and sets of variables considering (1) statistical significance, (2) predictive power, and (3) model complexity. We used jackknifing procedures in MaxEnt and bioclimatic variables correlation matrixes to build alternative models for each species selecting different sets of variables that contributed the most to each model. Then, we applied model calibration, which is a Bayesian procedure that finds the combination of parameters that best represents the phenomenon of interest fitting with the data. For each species, we compared alternative models using KuENM R-script (Cobos et al. 2019), that automates important calibration and evaluation steps in ENMs. Each comparison included different sets of variables, multipliers (0.5, 1, 1.5, 2, 4, 6, 8) and features (lineal, quadratic, product, hinges and threshold). For each

species we test all possible models until obtaining a statistically significant simplified ecological niche model (S3ENM).

Niche overlap

We estimated niche overlap, to test shared environmental constraints between pairs of species or between two different sets of populations within a species' range when they showed different niches across their range as an indication of divergent selection. For each pairwise comparison we run scripts provided in Broennimann et al. (2012) using R v3.5, including each particular set of bioclimatic variables selected in S3ENM, and both species occurrences were pooled and randomly split into two datasets, maintaining the number of occurrences as in the original dataset. Then the niche overlap statistic Schoener's D was calculated, which shows values that range from 0 (no overlap) to 1 (complete overlap) (Schoener 1968). This method uses cell-by-cell comparisons of geographical predictions of occurrences and randomization tests to quantify niche differences and assess their statistical significance (Warren et al. 2008), with 100 repetitions, to ensure that the null hypothesis can be rejected with high confidence, building a histogram of simulated values. If the observed D value falls within the 95% density of simulated values, the null hypothesis of niche equivalency cannot be rejected. We also performed a PCA, applying to this multivariate approach a smoothers kernel to densities of species occurrence in gridded environmental space, in order to calculate metrics of niche overlap (Broennimann et al. 2012).

Rabinowitz' rarities and niche volume

We classified focal species according to Rabinowitz' forms of rarity. A species was considered "**widespread**" if its range spans more than 8 degrees of latitude, while a species was "**narrow**" when its range is 8 degrees of latitude or less. Regarding habitat specificity, we assigned each species either to a "**broad**" group, when it occurs in several habitats, or to a "**restricted**" group if it shows high fidelity to its habitat. Finally, we classified species according to its local population size and continuity, in "**large-dominant**" or "**small-isolated**". Habitat specificity and population size classifications were made based on our personal observations in the field, along with species' descriptions from the literature (Donoso 1995, Donoso 2006).

We also estimate each species' Euclidian niche volume in NTB R-package using bioclimatic variables selected in S3ENM, except for *L. fonkii* north and south populations, where we included the three variables with higher percent of contribution in MaxEnt models, performed without hinges or threshold features. For each species, we ran 10 replicas of Euclidian niche volume calculation. Then, we tested differences in niche volume between rarity types via lineal models, with range width, habitat specificity, and population size as explanatory variables. We also assigned an increasing rarity score to each of the eight cells of the Rabinowitz's classification of species: 1 → common (wide, broad, dominant), 2 → predictable, 3 → sparse, 4 → discontinuous, 5 → unlike, 6 → endemic, 7 → rare, 8 → maximum rarity (narrow, restricted, small/isolated). With these values, we tested if increasing rarity is related with niche volume, deploying lineal models using niche volume as response variable performed in lmer package R 3.4.4 (R Development Core Team 2017).

Conservation priorities and gap areas

We produce metrics that estimate the degree of representation of each species in protected natural areas and identified their conservation priorities applying ecogeographic methods and tools using GapAnalysis R package (Carver et al. 2021). We performed the option *in situ* using our occurrence records data set for each species, each species' S3ENM, a moderate suitability value of 0.5, and WDPA protected areas layer (UNEP-WCMC 2021 retrieved from www.protectedplanet.net). This package calculates four scores for each species: a sampling representativeness score (SRS), a geographical representativeness score (GRS), an ecological representativeness score (ERS), and, a final conservation score (FCS), averaging all previous scores. All scores are bound between 0 and 100, with 0 representing an extremely poor state of conservation, and 100 representing comprehensive protection. Also, to graphically identify potential conservation gap areas, we overlaid suitability areas with values above 0.5 for all species together and the above mentioned regional protected areas layer in QGIS Development Team (2019). Considering this conservation gap map, the degree of representation of each species in protected natural areas, ENMs, niche overlap results and forms of rarity, we discuss an integrated prioritization scheme.

Results

Niche modelling

We obtained reliable suitability maps using the full set of bioclimatic variables in MaxEnt for six out of nine gymnosperm species endemics of PTF, and then we deployed S3ENM delivering credible suitability maps (Fig. 1, and Supplementary Information S1 for detailed model results). Each S3ENM included 3 to 4 low correlated bioclimatic variables (Supplementary Information S2) representing main environmental constraints for these species (Supplementary Information S1). Precipitation seasonality (BIO15) was a recurrent environmental constrain, contributing between 21 to 41% in four out of the six models deployed (Supplementary Information S1, S3).

The three remaining species delivered unreliable suitability maps, when using the full set of bioclimatic variables in MaxEnt. *Pilgerodendron uviferum* and *L. fonkii* showed ENMs with relatively low AUC values (0.848 and 0.721 respectively) and *S. conspicua*, although displayed an AUC value of 0.917, the percentage contribution and permutation importance of climatic variables exhibited discrepant response curves. In order to overstep observed inconsistencies, and based in our observations in the field, we split the records of these three species into two geographic sectors each. For *P. uviferum* and *L. fonkii*, we split the records in a latitudinal fashion, separating north and south of -44°30'L and 47°L, respectively. And for *S. conspicua* we split the records longitudinally, distinguishing between coastal (west) and Andean (east) localities (Fig. 1). For each sector, we obtained ecological niche models with higher AUC values than those obtained with complete sets of records, and also more reliable suitability maps (Supplementary Information S3). We identified different climatic drivers within each sector, as well as accurate response curves, and jackknifing values (Supplementary Information S3). We assume these results as two divergent ecological sectors for these three species, and tested specific S3ENMs for each sector, using the same background zone to model both sectors, and the projection of one sector did not predict the species' presence in the other (Supplementary Information S1). Once we partitioned *L. fonkii* data, the reduced model analysis test lack convergence, due to low number of records, so for further analysis we retain the three bioclimatic variables with higher percent of contribution in MaxEnt models performed without hinges and threshold features (Supplementary Information S3). Precipitation seasonality (BIO15) was also a recurrent environmental

constrain, contributing between 24.4 to 51.4% in five out of these six models deployed (two for each species) (Supplementary Information S1, S3).

Niche overlap

We pairwise compared the overlap of S3ENMs for all focal species, and found that 17% of the niches overlapped, with eleven statistically significant pairs (Table 2, Fig. 2). *Araucaria araucana* niche showed no overlap with any other studied species (Table 2), even when it is sympatric with three of them (*A. chilensis*, *P. andina*, and *P. salignus*). We found that the following pairs occupy the same portion of the niche space: *P. andina* and *A. chilensis* (Fig. 2a), *F. cupressoides* and *P. andina* (Fig. 2b), *F. cupressoides* and *S. conspicua* east, and also the northern sectors of *P. uviferum* and *L. fonkii* (Table 2, Fig. 2a-a', c-c'). Many of the studied species are partially sympatric, however their niches do not overlap, this is the case of *A. araucana* and *P. andina* (Fig. 2c). In addition, *P. uviferum* north overlaps niche with *P. nubigenus*, *P. salignus* and *S. conspicua* west; while *P. uviferum* south overlaps niche with *L. fonkii* south and *P. nubigenus*, and *L. fonkii* south niche is overlapped with *P. nubigenus*. Finally, *P. andina* and *S. conspicua* east have overlapped niches. For the three species showing two divergent ecological sectors across their range as *S. conspicua* east and west, *P. uviferum* north and south and *L. fonkii* north and south (Fig. 2d-d'); pairwise niche equivalence test yielded no niche overlap between sectors (Table 2).

Comparison of species considering Rabinowitz' rarities

We classified the nine focal species of this study following Rabinowitz's types of rarity (Table 3), and tested the difference in niche volume between rarity categories (Supplementary Information S4). We found statistically significant differences in niche volume between species with wide and narrow range, with widespread species showing bigger niche volume ($F= 16.55$; $p< 0.001$) than narrow species. We also found statistical differences in niche volume between species with broad and restricted habitat specificity ($F= 4.54$; $p= 0.03$), showing that species with restricted habitat specificity present smaller niche volume. Also, we saw significantly larger niche volume in species with large dominant populations than species with small isolated populations ($F= 18.38$; $p< 0.001$). Finally, we tested the relationship between niche volume and types of rarity, finding that niche volume significantly decreases with increasing rarity ($t= -7.48$, $p< 0.01$, $r^2= 0.32$).

Conservation priorities and gap areas

Using metrics that estimate the degree of representation of each species in protected natural areas we found that species with high conservation priority (HP) are *F. cupressoides*, *P. uviferum* north, *L. fonkii* north, *P. nubigenus*, *P. salignus* and *S. conspicua* west, with low final conservation scores (FCS) ranging from 0.46 to 24.25. We obtained intermediate scores of conservation priority for *P. andina* (FCS= 41.20), and *A. araucana*, *A. chilensis* and *P. uviferum* south presented low conservation priority ($50<FCS<75$). Meanwhile, *L. fonkii* south and *S. conspicua* east are sufficiently conserved (SC) with $FCS>75$ (Table 4). We identified areas of high suitability among nine native gymnosperm species of PTF (Fig. 3). One conservation gap area is located between -35° to -40° S latitude in the Costal Range, where the *P. salignus* has the higher suitability values (Fig. 3a). A second conservation gap area is located southward, between -40° to -43° S latitude,

including a suitability hot spot in central Chiloé island, where *S. conspicua* west and *F. cupressoides* showed concordant high suitability along the coastal range (Fig. 3b). When overlapping protected areas layer, we detected few, very small natural sanctuaries scattered within this high suitability hot spot (Fig. 3a, b). The southernmost region of the PTF, between -43° to -55°S latitude is well conserved in vast protected areas, where *P. uviferum* south, *L. fonkii* south, and *P. nubigenus* showed concordant high suitability values (Fig. 3c).

Discussion

Studying ENMs of nine species of gymnosperms and integrating niche overlap and estimation of levels of rarity, allowed us to prioritize species and identify conservation gap areas in a global biodiversity hotspot. We generated reliable ENMs for nine Patagonian gymnosperms and found that some of their niches overlap, and only one species displayed a unique niche. Unexpectedly, we found that three species have divergent suitability of habitats along their range. We showed that the rarer a species is the smaller niche volume tend to have, and that there are unprotected suitable areas for key species of the PTF. We suggest that urgent conservation actions are needed, if we aim to preserve gymnosperms' niches in this global biodiversity hotspot.

ENM for focal species

We obtained reduced ENMs that suggested both temperature and precipitation seasonality, as constrain factors depicting the environmental envelope of vegetation in PTF. Although, precipitation seasonality (BIO15) is present in nine out of twelve models deployed and in the region gymnosperms are usually considered to define the forest type (i.e. *Araucaria* forest) (Donoso 2006, Luebert and Pliscoff 2006), here we showed that each species can also harbor its particular set of environmental constrains. This species-specific set of constrains might be relevant to guide climate change mitigation projects through assisted migration programs for focal species in this hotspot (Casazza et al. 2021). This strategy can be especially relevant for endemic species that might not be able to follow rapid changes in climate, as they may have little dispersal capacity (Essl et al., 2011), and/or a reduced climatic niche, so negative effects of warming and climate change deepen their survival (Ozinga et al. 2009), particularly for cold tolerant species. Species that already show a narrow range may increase their vulnerability, if range shrinking due to climate change couples with other threats such as habitat fragmentation and degradation (Orsenigo et al. 2018), or land-use change (Miranda et al. 2014). Regardless of current and future climate change, the introduction of new actions in conservation *sensu* IUCN (2013) can compensate for species range loss due to threats other than climate change. Future studies, including climate projections would be of great value to elucidate potential responses of these gymnosperm species in this hotspot.

Surprisingly, three focal species have divergent suitability of habitats across the landscape. *Pilgerodendron uviferum* and *Lepidothamnus fonkii* displayed two ecological groups separating their populations into north and south. This result is less surprising when we consider that these species have the largest latitudinal range across the PTF (encompassing more than 15° of latitude), occurring in heterogeneous environments. Both *P. uviferum* and *L. fonkii*, have small isolated populations, and these two species niches overlapped within sectors, although, we found within species divergent suitability of habitats across the

landscape (Table 2). Moreover, both south sectors were classified as discontinuous species with wide range and an intermediate rarity score of 4, while both north sectors were classified as improbable species and have narrow range with a high rarity score of 7. Suggesting that overlapped north sectors of *P. uviferum* and *L. fonkii* are more threatened than southern sectors. Instead, *Saxegothaea conspicua* showed longitudinal divergence, between populations occurring along the Andes Cordillera (in the east), and populations occurring along the Coastal range (in the west).

Within-species niche differences can suggest new hypotheses on ecological, genetic and evolutionary divergences and support conservation decisions. High species diversity in these hotspots is often attributed to an accumulation of narrow-ranged species via high speciation rates and/or preservation of species over time, via low extinction rates (Jetz et al. 2004), usually hosting ancient and young species (Harrison and Noss 2017). In this way, niche divergences may favor genetic isolations that could lead to potential speciation. Therefore, the comparison between different geographic areas within the same species may be of interest to detect areas with divergent evolutionary potential. As ENMs are independent of genetic or phenotypic based adaptive responses, research of potential speciation mechanisms and the development of regional-scale conservation strategies might be of interest (Morente-López et al. 2020). From the evolutionary point of view, the observed disjunction between populations might indicate gene flow barriers, affecting between sectors connectivity, that in turn might encourage reproductive isolation through genetic divergence (Blanquart et al. 2013). PTF's gymnosperms were affected by Pleistocene/Holocene climatic conditions, so glacial/interglacial refugial areas are considered of great conservation relevance as core sources of genetic diversity (Souto et al. 2015b). Also, studies detecting characters under divergent natural selection could be useful to design conservation plans under predicted climate change conditions, to allow *in situ* adaptive divergence (Blanquart et al. 2013; Wang and Bradburd 2014).

Niche Overlap

We tested pairwise niche overlap to detect shared environmental constraints among gymnosperms, and compared between different geographic areas within the same species to detect evolutionary potential. Although, the number of statistically significant equivalent niche pairs represents only 17% of the total pairs compared, we found that eight out of nine of the studied species showed equivalent niches with at least one of the other gymnosperms of the PTF, and only *A. araucana* held a unique niche and occupies a set of environmental conditions not exploited by any of the other studied gymnosperms. It has been suggested that phylogenetically distant species will also be environmentally distant (Martínez-Méndez et al. 2016). Surprisingly, *F. cupressoides* and *P. andina* are parapatric and showed niche equivalency (Table 2). Conversely, we found that *P. uviferum* has multiple niche equivalences with phylogenetically distant species. We had considered here ancient lineages that had successfully surfed at least Pleistocene/Holocene climatic oscillations, so convergent and divergent niches can be explained by phylogenetic relationships, and other factors such as climatic conditions at the time of lineage diversification (Herrera 2020). Particularly in gymnosperms, climate adaptation has been shown to be genetically constrained, and plastic responses to climate appear to be relatively conserved and highly polygenic (Yeaman et al. 2016).

Rabinowitz's types of rarity

It has been suggested that magnitude of local abundance in combination with the extent of spatial distribution of a species may increase the risk of global extinction, with rare species being the most prone to it (Gaston 1994, Gaston et al. 2000). Thus, rare, endemic and improbable species, such as *P. andina*, *A. araucana*, *F. cupressoides*, and *L. fonkii* north and *P. uviferum* north, behold higher risk, compared with widespread species, with large populations. We classified our focal species according to *Rabinowitz's* types of rarity and tested niche volume hypothesis that widespread species with low habitat specificity, and continuous populations have larger niche volume compared to narrow species, with high habitat specificity and scattered populations. We showed that there is a significant relationship between geographic range, population size and niche volume. Niche volume tend to be smaller when the level of rarity is higher, as previously proposed (Slatyer et al. 2013). Traditionally, much effort has been devoted to conserve rare species (Broennimann et al. 2005) being the Rabinowitz's approach broadly accepted for assessing forms of rarity, but sometimes the data needed to perform this classification is not available. We calculated niche volume for nine emblematic species of the PTF, from open sources of occurrence data. Our results and the recent broad and public availability of georeferenced data has made niche volume relatively easy to estimate for any species, suggesting it as a handy tool as a proxy of rarity for conservation purposes.

Conservation gaps in a global biodiversity hotspot

We combined ENM, and forms of rarity, to detect conservation gaps in a global biodiversity hotspot, deploying patterns of habitat suitability, niche overlap and calculating prioritization scores for nine gymnosperm species, key elements of the PTF biodiversity hotspot, complementing traditional approaches of biodiversity conservation. We observed that there are conservation gaps in this biodiversity hotspot by overlaying areas of high suitability for gymnosperm species of the PTF and protected areas in Chile and Argentina. Particularly, we identify two areas with moderate to high suitability or hotspots shared by two or more gymnosperm species, one on the northern-central Coastal Range, and the other on the Andes Cordillera. These areas are in agreement with previous reports based on genetic diversity patterns (Souto et al. 2015b; Premoli et al. 2018). Thus, the areas that are currently suitable for the distribution of gymnosperm species are also areas of high genetic diversity and biodiversity, for these and other plant species (Durán et al. 2013; Moreira-Muñoz and Troncoso 2014; Scherson et al. 2014; Martínez-Telleria et al. 2017; Fuentes-Castillo et al. 2019). These represent relatively stable areas since Holocene and should be considered priority if we aim to preserve gymnosperms' niches in the PTF. These species are also threatened by land use change, so we plea for concrete actions in the design and management of conservation areas for their environments. Currently, both land use change studies (Miranda et al. 2014) and protected area surveys (Moreira-Muñoz and Troncoso 2014) indicate a strong deterioration and absence of conservation areas, particularly in the Coastal Range as in Nahuel Buta (Otano and Echeverría 2017; Premoli et al. 2018).

Protected areas have a core role in sustaining biodiversity, and native forests remnants are the key to preserve the entire ecosystem (Moreira-Muñoz and Troncoso 2014). Recently, in Patagonia, especially in Chile, a new strategy of public/private actions has been developed to create small biodiversity conservation areas, although with partial representation (Schutz 2018). Since such small areas, make insufficient representation of local biodiversity, and are biasedly distributed, and particularly missing in the Chilean central valley (Durán et al. 2013). Conservation planning requires setting priorities at the same spatial scale at which decision-making processes are undertaken considering all levels of biodiversity (Souto et al. 2015b).

Many studies highlight the importance and need to carry out concrete conservation actions in central Chile (Scherson et al. 2014; Martínez-Tellería et al. 2017; Fuentes-Castillo et al 2019) given its high number of endemism, a strong impact of land use change into exotic species plantations, a high frequency of fires, added to the forecasted impacts of climate change for the next 100 years.

The current availability of spatially explicit occurrence data from multiple species can help to identify biodiversity hotspots and aid the prioritization of conservation areas to establish science-based protected areas that might preserve the evolutionary potential of key habitats and species. In our study, we found large areas with high overlapping suitability, and our results allow the identification of species that require concrete conservation actions. Particularly, the area between -35° and -38.5° south latitude, both in Andes and Coastal ranges where *Araucaria*, *P. salignus*, and *P. andina* which are endemic, improbable and rare respectively have high overlapping suitability. The complete range of these species is within this area, with all their populations being highly threatened by anthropogenic disturbances. In addition, these species have high rarity scores, which increases their potential vulnerability, along with being paleoendemisms, making this area of high conservation value. Moreover, at this latitude *P. salignus* has low conservation scores, while *P. andina* has moderate scores, suggesting urgent conservation actions are needed. In Chilean central valley about -39.5° south latitude, *P. salignus* and *L. fonkii* north shared high overlapping suitability, both species have high rarity values and low conservation scores, again calling for conservation attention. Moving southward between -40 and -43° south latitude, along the coastal range, and including Chiloe Island, we found high overlapping suitability for *P. uviferum* north along with *F. cupressoides* and *S. conspicua*. These species are improbable, endemic or unlikely, respectively and all showed high conservation priority scores. In this region few, little and scattered conservations areas are settled, yet again claiming for conservation actions.

Our study supports the idea that conservation must contemplate large geographic areas and/or long-time scales so that evolutionary effects and events can progress (Lacher 2018). In such a process, the natural environment and ecosystem are protected and maintained so that all constituent species (known or unknown) are conserved and benefit (Jaisankar et al. 2018). Biodiversity protection and management through in situ conservation involves the creation of certain specific areas, be they national parks, sanctuaries, and biosphere reserves. Current conservation targets and goals have evolved over time from a more species-centric approach to one that considers a species' role in ecosystem functioning. We suggest that conservation efforts for the PTF, should consider such approaches, as they may be much more beneficial than specific actions for one or a few species in a small area. Although, Patagonian Temperate Forest is home of umbrella species, is a biodiversity and genetic hotspot, and represents a freshwater reservoir for the region, is also under many threats like highly invasive species' plantations, dump constructions and other anthropogenic disturbances. Thus, we appeal to make it a priority in the need for active conservation policies, supported by governmental agencies, the scientific sector and environmental groups. Our approach of overlapping habitat suitability of multiple species, and types of rarity highlights the relevance of integrative studies of species complexes aiming to aid conservation of key ecosystems, as global biodiversity hotspots.

Declarations

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Availability of data and material: All data is available on-line repositories as are expressed in main manuscript

Code availability: All software used in this study are referenced

Authors' contributions: P. Quiroga and C. Souto have the equal participation in the construction and design of the study, in writing, in development of the analyses performed, and in the interpretation results.

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Supplementary Information

Supplementary Information 1: Summary of statistically significant simplified model (S3ENM) obtained using KuENM and ENM or Suitability model obtained using MaxEnt for each one of the gymnosperm species from Patagonian Temperate Forest (PTF)

Supplementary Information 2: Correlation matrix including 19 bioclimatic variables clipped for nine gymnosperm species endemics of Patagonian Temperate Forest

Supplementary Information 3: ENM and KuENM analyses of *Lepidothamnus fonkii*, *Pilgerodendron uviferum* and *Saxegothaea conspicua* in divergent ecological conditions within each species' range

Supplementary Information 4: Lineal models testing the relationship of Rabinowitz's types of rarity and niche volume for nine gymnosperm species endemic of Patagonian Temperate Forest

Figure Legends

Figure 1: Statistically significant simplified ecological niche models (S3ENM) for a: *Araucaria araucana*; b: *Austrocedrus chilensis*; c: *Fitzroya cupressoides*; d: *Pilgerodendron uviferum* north and d' *Pilgerodendron uviferum* south; e: *Lepidothamnus fonkii* north; e' *Lepidothamnus fonkii* south; f: *Podocarpus nubigenus*; g: *Podocarpus salignus*; h: *Prumnopitys andina*; i: *Saxegothaea conspicua* east and i' *Saxegothaea conspicua* west. Grey line splits divergent ecological conditions.

Figure 2: Examples of pairwise niche equivalency tests and niche overlap results among sympatric and parapatric species.

a. *Austrocedrus chilensis* and *Prumnopitys andina* are sympatric and their niches are equivalent and overlapped; b. *Fitzroya cupressoides* and *Prumnopitys andina* are parapatric and their niches are equivalent and overlapped; c. *Araucaria araucana* and *Prumnopitys andina* are sympatric, and their niches are not equivalent nor overlapped; d. *Lepidothamnus fonkii* show divergent ecological condition between its north and south sector.

1 Represents the equivalency frequency test estimated by Schoener's D index and p value, for each comparison, respectively. The observed Schoener's D metric (D obs.) is indicated in red with a dot and vertical line.

2 Principal component analysis (multivariate space), showing the density occurrence of each pair of species (denser shading indicates higher density) and available environments (continuous line = 100%, dashed line = 75%) for each species (different colors for each species); overlapped area between niches in grey, for each comparison, respectively.

Figure 3: Areas of moderate to high overlapping suitability for Patagonian Temperate Forest gymnosperm species (yellow - red) and preserved areas (in blue). a: Detailed overlapping suitability for *Podocarpus salignus*, *Araucaria araucana* and *Prumnopitys andina* in the Costal Range from -35° to -40°S latitude; b: Details overlapping suitability for *Austrocedrus chilensis*, *Fitzroya cupressoides* and *Saxegothaea conspicua* west and east from -39° to -43°S latitude; C: Moderate to high overlapping suitability for nine gymnosperm species and preserved areas of PTF.

Table 1: Studied species, number of records included in niche model analyses; North and South Latitudinal boundaries; total range span in degrees of latitude.

Species	N° of records	Latitudinal boundaries		Latitudinal range
		North	South	
<i>Araucaria araucana</i>	343	-37.51°	-40.14°	2.63°
<i>Austrocedrus chilensis</i>	351	-34.95°	-43.73°	8.78°
<i>Fitzroya cupressoides</i>	171	-39.76°	-43.74°	3.98°
<i>Pilgerodendron uviferum</i>	277	-39.58°	-54.63°	15.05°
<i>P. uviferum</i> north	140	-39.60°	-44.43°	4.83°
<i>P. uviferum</i> south	131	-44.47°	-54.65°	10.18°
<i>Lepidothamnus fonkii</i>	37	-39.93°	-55.09°	15.56°
<i>L. fonkii</i> north	8	-39.95°	-44.41°	4.46°
<i>L. fonkii</i> south	29	-46.58°	-55.02°	8.44°
<i>Podocarpus nubigenus</i>	244	-38.31°	-51.01°	12.70°
<i>Podocarpus salignus</i>	483	-35.24°	-40.72°	5.48°
<i>Prumnopitys andina</i>	31	-35.80°	-39.13°	3.33°
<i>Saxegothaea conspicua</i>	1087	-35.40°	-46.57°	11.17°
<i>S. conspicua</i> east	648	-35.40°	-46.57°	11.17°
<i>S. conspicua</i> west	439	-37.55°	-43.47°	5.92°

Table 2: Pairwise niche overlap of nine gymnosperm species endemic of Patagonian Temperate Forest. Schoener's D index and p value in parenthesis for each comparison. In **bold** statistically significant tests of niche overlap (H0 = niches are equivalent). In **bold italics** pairwise niche comparisons tests for different sectors within a species' range.

	<i>A. araucana</i>	<i>A. chilensis</i>	<i>F. cupressoides</i>	<i>P. uviferum north</i>	<i>P. uviferum south</i>	<i>L. fonkii north</i>	<i>L. fonkii south</i>	<i>P. nubigenus</i>	<i>P. salignus</i>	<i>P. andina</i>	<i>S. conspicua east</i>
<i>A. chilensis</i>	0.506 (0.005)	-									
<i>F. cupressoides</i>	0.141 (0.002)	0.254 (0.005)	-								
<i>P. uviferum north</i>	0.133 (0.005)	0.119 (0.005)	0.457 (0.005)	-							
<i>P. uviferum south</i>	0.005 (0.005)	0.030 (0.005)	0.111 (0.005)	<i>0.199</i> (0.002)	-						
<i>L. fonkii north</i>	0.038 (0.005)	0.017 (0.005)	0.290 (0.009)	0.533 (0.154)	0.104 (0.005)	-					
<i>L. fonkii south</i>	0.004 (0.005)	0.016 (0.005)	0.098 (0.005)	0.084 (0.005)	0.586 (0.408)	<i>0.033</i> (0.002)	-				
<i>P. nubigenus</i>	0.075 (0.005)	0.119 (0.002)	0.541 (0.002)	0.485 (0.060)	0.498 (0.159)	0.248 (0.005)	0.419 (0.184)	-			
<i>P. salignus</i>	0.472 (0.005)	0.373 (0.005)	0.349 (0.009)	0.487 (0.095)	0.008 (0.005)	0.057 (0.002)	0.057 (0.002)	0.375 (0.005)	-		
<i>P. andina</i>	0.444 (0.002)	0.666 (0.113)	0.527 (0.469)	0.201 (0.010)	0.001 (0.005)	0.054 (0.002)	0.054 (0.002)	0.105 (0.002)	0.334 (0.005)	-	
<i>S. conspicua east</i>	0.267 (0.005)	0.322 (0.005)	0.694 (0.298)	0.482 (0.005)	0.098 (0.005)	0.015 (0.005)	0.138 (0.005)	0.423 (0.005)	0.471 (0.005)	0.525 (0.129)	-
<i>S. conspicua west</i>	0.067 (0.005)	0.052 (0.005)	0.553 (0.005)	0.733 (0.054)	0.076 (0.005)	0.349 (0.005)	0.078 (0.005)	0.338 (0.005)	0.290 (0.005)	0.012 (0.005)	<i>0.316</i> (0.005)

Table 3: Rarity classification of nine gymnosperm species from Patagonian Temperate Forest following Rabinowitz types of rarities (1981). Euclidian niche volume indicated in parenthesis, calculated with ten replicates. Arrow points assigned rarity scores.

Range		Wide ($\leq 8^\circ$)		Narrow ($\geq 8^\circ$)	
Habitat specificity		Broad	Restricted	Broad	Restricted
Local Population Size	Large dominant	<i>A. chilensis</i> (20483) ↓ 1 Common	<i>S. conspicua</i> east (45574) ↓ 2 Predictable	<i>S. conspicua</i> west (14631) <i>P. salignus</i> (16480) ↓ 5 Unlikely	<i>A. araucana</i> (1218) <i>F. cupressoides</i> (5129) ↓ 6 Endemic
	Small isolated	<i>P. nubigenus</i> (11979) ↓ 3 Scattered	<i>P. uviferum</i> south (3521) <i>L. fonkii</i> south (7386) ↓ 4 Discontinuous	<i>P. uviferum</i> north (13208) <i>L. fonkii</i> north (14858) ↓ 7 Improbable	<i>P. andina</i> (1679) ↓ 8 Rare

Table 4: Assessment of the degree of protection of gymnosperm species in conservation systems from Patagonian Temperate Forest. SRS: sampling representativeness score; GRS: geographical representativeness score; ERS ecological representativeness score; FCS: average score to provide a final conservation score. Class: HP: requires further action of high priority; MP: requires medium priority LP: requires low priority; SC: sufficiently conserved.

Species	SRS	GRS	ERS	FCS	FCS class
<i>Araucaria araucana</i>	62.75	59.55	100	60.61	LP
<i>Austrocedrus chilensis</i>	52.50	54.34	100	53.73	LP
<i>Fitzroya cupressoides</i>	23.40	25.00	100	24.47	HP
<i>Pilgerodendron uviferum</i> north	14.29	13.52	100	13.78	HP
<i>Pilgerodendron uviferum</i> south	70.00	55.01	50	60.01	LP
<i>Lepidothamnus fonkii</i> north	20.00	15.00	100	16.67	HP
<i>Lepidothamnus fonkii</i> south	100.00	88.53	100	92.35	SC
<i>Podocarpus nubigenus</i>	13.33	12.45	100	12.74	HP
<i>Podocarpus salignus</i>	2.00	3.04	100	2.69	HP
<i>Prumnopitys andina</i>	44.44	39.58	50	41.20	MP
<i>Saxegothaea conspicua</i> west	0	0.69	100	0.46	HP
<i>Saxegothaea conspicua</i> east	100.00	95.46	100	96.98	SC

Figure 1: Statistically significant simplified ecological niche models (S3ENM) for a: *Araucaria araucana*; b: *Austrocedrus chilensis*; c: *Fitzroya cupressoides*; d: *Pilgerodendron uviferum* north and d' *Pilgerodendron uviferum* south; e: *Lepidothamnus fonkii* north; e' *Lepidothamnus fonkii* south; f: *Podocarpus nubigenus*; g: *Podocarpus salignus*; h: *Prumnopitys andina*; i: *Saxegothaea conspicua* east and i' *Saxegothaea conspicua* west. Grey line splits divergent ecological conditions.

Figure 2: Examples of pairwise niche equivalency tests and niche overlap results among sympatric and parapatric species.

a. *Austrocedrus chilensis* and *Prumnopitys andina* are sympatric and their niches are equivalent and overlapped; b. *Fitzroya cupressoides* and *Prumnopitys andina* are parapatric and their niches are equivalent and overlapped; c. *Araucaria araucana* and *Prumnopitys andina* are sympatric, and their niches are not equivalent nor overlapped; d. *Lepidothamnus fonkii* show divergent ecological condition between its north and south sector.

1 Represents the equivalency frequency test estimated by Schoener's D index and p value, for each comparison, respectively. The observed Schoener's D metric (D obs.) is indicated in red with a dot and vertical line.

2 Principal component analysis (multivariate space), showing the density occurrence of each pair of species (denser shading indicates higher density) and available environments (continuous line = 100%, dashed line = 75%) for each species (different colors for each species); overlapped area between niches in grey, for each comparison, respectively.

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