

SPECIES DISTRIBUTION MODELLING PREDICTS
THE EXTINCTION OF THE EAST-PYRENEAN LOCAL
ENDEMIC FORM OF *PEDICULARIS COMOSA*:
P. C. ASPARAGOIDES IN A NEAR FUTURE

PASCALINE SALVADO^{1*}, NOÉMIE COLLETTE¹, ANAIS GIBERT¹, MARIA
MARTIN², CÉLINE QUÉLENNEC², JEAN-MARC LEWIN³, JOSEPH GARRIGUE²,
JEAN-ANDRÉ MAGDALOU², CHRISTOPHE HURSON², DIANE SOREL²,
VALÉRIE DELORME-HINOUX^{1,3}, JORIS A. M. BERTRAND¹

¹Laboratoire Génome et Développement des Plantes (LGDP, UMR 5096 UPVD/CNRS), Université de
Perpignan Via Domitia, Perpignan, France

²Fédération des Réserves Naturelles Catalanes, Prades, France

³Association Charles Flahault, Toulouges, France

*Corresponding author: pascaline.salvado@univ-perp.fr

ABSTRACT.-.Anthropogenic climate change is rapidly driving species towards extinction, especially in vulnerable habitats like mountain regions such as the Pyrenees. With each degree of temperature rise, the threat accelerates, endangering diverse plant species. Due to their patrimonial importance and the susceptibility of mountainous species to climate and land-use changes, the conservation of endemic species in the Pyrenees is a crucial issue. Local populations of *Pedicularis comosa* in the Eastern Pyrenees provide an interesting biological model for studying climate change effects on mountain plant biodiversity. Here, an endemic pink-flowered morphotype described as *Pedicularis comosa* subsp. *asparagoides* coexists with the widely distributed, yellow-flowered *Pedicularis comosa* subsp. *comosa*. Because of its local-endemism, *P. c.* subsp. *asparagoides* is threatened as it is known to occur sporadically from a restricted number of sites in the Albères, the Salines Massif and the Canigó Massif. Our study highlights that climate change is a serious threat to *P. c.* subsp. *asparagoides*. Using Ecological Niche Modelling (ENM), we found that its current habitat could become unsuitable within less than two decades, outpacing the species' natural dispersal ability to newly suitable areas. Therefore, our findings suggest that conservation measures, such as assisted migration, are necessary to protect this unique morphotype.

KEYWORDS: ECOLOGICAL NICHE MODELLING, PYRENEES, ENDEMISM,
PEDICULARIS, GLOBAL CHANGE, BIODIVERSITY LOSS, CONSERVATION,
OROBANCHACEAE

INTRODUCTION

Anthropogenic climate change is unequivocally causing shifts in species distribution and abundance, which will inevitably lead to extinctions in the near future. This poses an unprecedented threat to vulnerable species that are often experiencing reduced population sizes as well as habitat degradation and fragmentation. The risk of extinction due to climate change is expected not only to increase but to accelerate with every degree rise in global temperatures (Urban 2015). Global change affects species differently depending on their habitat, bioregion, or elevation zone (Leidner & Neel 2011, Pauli *et al.* 2012). Recent studies have shown an accelerated turnover in plant species richness in European mountains over the last decade, making mountain regions particularly sensitive to climate change (Gottfried *et al.* 2012, Steinbauer *et al.* 2018). Mountain biodiversity is especially vulnerable to two main factors. Firstly, temperatures in mountains are rising faster than the global average (Bravo *et al.* 2008). Secondly, habitats are especially prone to be altered by changes in land-use (Mottet *et al.* 2006, García-Vega & Newbold 2020).

The Pyrenees are home to one of the most diverse plant species assemblages in Europe, with 3652 identified species, 3.4 % of which are endemic to these mountains (Gómez *et al.* 2017, Pomeda-Gutiérrez *et al.* 2023). This richness is the result of a combination of historical factors, complex topography, and a unique geographical position at the intersection of two biomes. These include Mediterranean forests, woodlands and scrub, and temperate broadleaf and mixed forests (Dinerstein *et al.* 2017, Pironon *et al.* 2022). Furthermore, the Pyrenees can be divided into three main altitudinal categories. The high mountain zone is characterized by Boreo-Alpine flora and vegetation, while the mid-altitude zone displays a predominantly Medio-European landscape, despite the discernible differentiation between the Atlantic and Mediterranean sides. The low-altitude zone exhibits a greater contrast between the typical Atlantic territory on one side and the Mediterranean territory on the other (Ninot *et al.* 2007). However, all this floristic diversity in the Pyrenees is also one of the most affected by ongoing climate and land-use changes (Lasanta-Martínez *et al.* 2005, Engler *et al.* 2011). It is therefore important that we conserve the endemic species in the Pyrenees both for their heritage value and in order to ensure their continued viability in the face of ongoing environmental changes.

Local populations of *Pedicularis comosa* L., 1753 provide an interesting biological model to assess the impact of climate change on mountain plant biodiversity. Noticeably, a particular endemic morphotype with pink flowers is especially at risk as it is known to occur sporadically from a restricted number of sites in the Eastern Pyrenees in the Albères, the Salines Massif and the Canigó Massif. In contrast, the yellowish/ivory white flower morphotype has a wide but fragmented distribution area across several European mountain ranges. The two forms have been classified either as distinct species or as two subspecies of *Pedicularis comosa* (subsp. *comosa* for the yellow-flowered one and subsp. *asparagoides* for the pink-flowered one). Both morphotypes are likely to be affected by climate change and habitat loss due to the decline of extensive pasture that maintains open grasslands favorable to their perennity. Yet, because of its local-endemism, *P. c.* subsp. *asparagoides* is considered as Near Threatened (NT) on the French and Pyrenean Red Lists, but Endangered (EN) on the Catalan Red List, while *P. c.* subsp. *comosa* has Least Concern (LC) status. In the present study, we used an Ecological Niche Modelling approach to i) characterize the climatic niche of the endemic pink-flowered form, ii) evaluate the extent of its suitable habitat and iii) predict the spatio-temporal dynamics of this suitable habitat in the future following different scenarios of climate evolution.

MATERIALS & METHODS

Plant system

Pedicularis comosa is a perennial herbaceous, allogamous and hemiparasite plant that can grow up to 60 cm in height. Its lifespan is not well documented, but it is believed to be over 10 years. The plant flowers between May and July depending on elevation, and is cross-pollinated by bumblebees (*Bombus* sp.). However, knowledge of the biology and ecology of this species of Orobanchaceae, including its biotic partners, remains incomplete. In absence of current genetic studies to further support the existence of two distinct species, the parapatric distribution of the two color forms seems rather consistent with a subspecies status rather than species. Indeed, out of flower color variation, the two morphotypes only display very few and subtle morphological differences. These differences may be restricted to the maximum width of foliar segments, which were found to be narrower for *P. c.* subsp. *asparagoides*, and the stamen threads' hairiness (Floralab EFA294/19). However, these traits may be strongly influenced by very local environmental conditions. Additionally, *P. c.* subsp. *asparagoides* is typically found at lower elevations (from 800 to 1,800 m above sea level) compared to *P. c.* subsp. *comosa* which generally occurs at higher elevations in the Pyrenees (from 1,250 and 2,500 m a.s.l.).

Ecological Niche Modelling

In order to assess the future trends of spatial dynamics of *P. c.* subsp. *asparagoides* distribution in a context of global change, we first conducted Ecological Niche Modelling (ENM) analyses based on approaches similar to the ones implemented in (Salvado *et al.* 2022, Gibert *et al.* 2024)). In this study, ENM relies on occurrences data as well as current and predicted interpolated bioclimatic data for future projections.

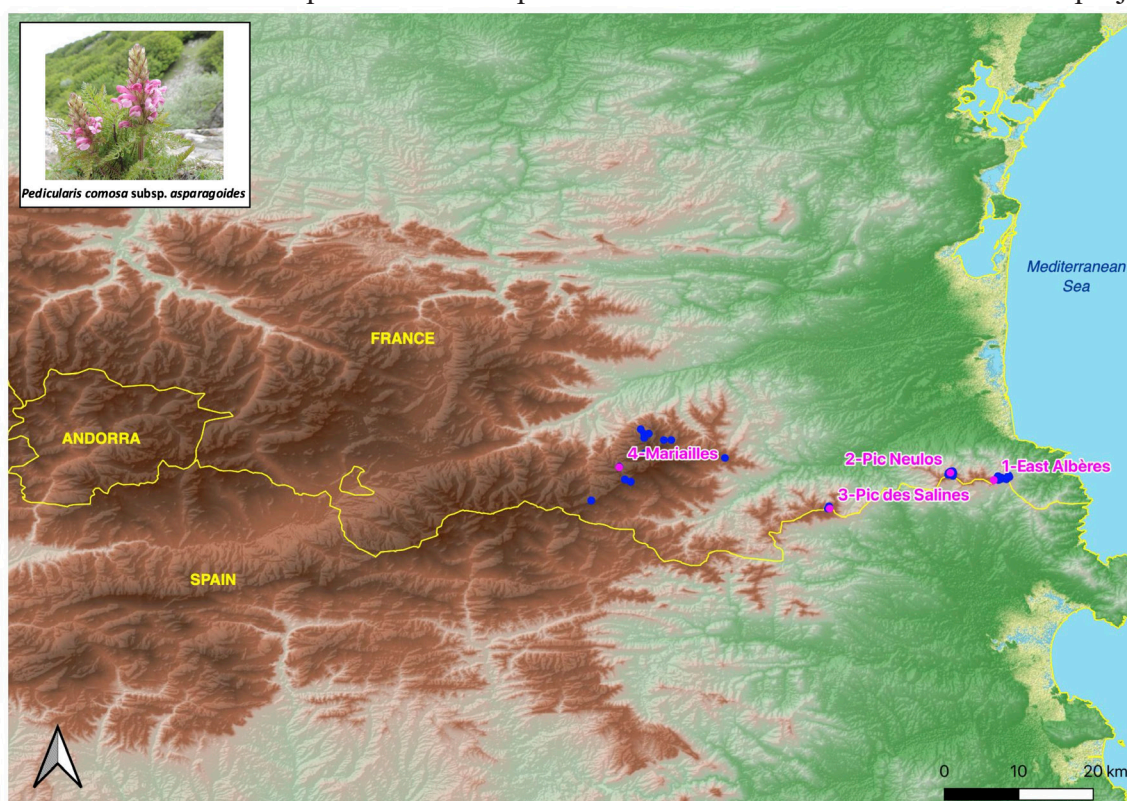


Fig. 1: Map representing the different occurrences of *Pedicularis comosa* subsp. *asparagoides*. Pink dots represent the sites surveyed for this study while the blue dots correspond to the occurrence data provided by the Mediterranean National Conservatory from 1992 to today in the Simethis database.

Occurrences data acquisition

To conduct this study, we directly recorded the presence of the pink-flowered *P. c.* subsp. *asparagoides* in the field at four documented sites in the Eastern-Pyrenees (within the framework of the Interreg-POCTEFA research project Floralab). To complete our survey, we also used the occurrences data compiled by the National Mediterranean Botanical Conservatory (CBNMed) in the Simethis database (Fig. 1). Pink-flowered *P. c.* subsp. *asparagoides* occurs mainly in the Albères with 1-East-Albères, 2-Pic Neulos and 3-Pic des Salines, but also in the Canigó massif at 4-Mariailles (Supplementary Appendix SII).

Current bioclimatic data

We downloaded the 19 bioclimatic layers from CHELSA v.2.1 (Karger *et al.* 2017). These layers available in CHELSA are similar to those available in WORLDCLIM (Fick and Hijmans 2017) in a way that they consist of a global downscaled climate dataset that outputs temperature and precipitation estimates at a maximal resolution of 30 arc seconds (approximately 1 km). In the current study, we used the most recent version of CHELSA as the methodology and bias correction it implements have been shown to outperform WORLDCLIM in mountainous environments (Karger *et al.* 2017, Bobrowski *et al.* 2021). Current climate data correspond to time averaged variables over the period 1981-2010.

Future bioclimatic data at different time periods and based on different scenarios

Future climates correspond to estimates from phase 3b of the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP3b) based on output of phase 6 of the Coupled Model Intercomparison Project (CMIP6). They consist of the output of five GCMs (GFDL-ESM4, UKESM1-0-LL, MPI-ESM1-2-HR, IPSL-CM6A-LR and MRI-ESM2-0) and three climate scenario specifiers (SSP126, SSP370, SSP585). Climate scenarios specifiers reflect different Shared Socioeconomic Pathways (SSPs) associated with different levels of radiative forcing: +2.6, +7.0 and +8.5 W/m², which can be considered as a plausible range of greenhouse gas concentrations that appear to be optimistic, rather likely and pessimistic, respectively, in terms of climate change. Annually averaged data were downloaded for three future time periods: 2011-2040 (“2035”), 2041-2070 (“2055”) and 2071-2100 (“2085”).

Ecological Niche Modelling procedure

The ENM analyses were conducted thanks to the R-package ENMwizard v.0.3.7 (Heming *et al.* 2018, Gutiérrez *et al.* 2019, Bagley *et al.* 2020). We first spatially filtered occurrences to keep only those that were at least 1 km away from each other using the R-package ‘spThin’ (Aiello-Lammens *et al.* 2015). Due to the relatively small spatial scale of the area under study, we only considered a total of 10 out of the 107 occurrences initially available. We then examined raw values for the 19 bioclimatic variables extracted at each occurrence point (bio1 to bio19) and we selected the less correlated ones (Person correlation coefficient < 0.75) thanks to the R-package ‘caret’ (Kuhn 2019) and kept two variables: bio12 (“Annual precipitation”), and bio18 (“Precipitation of Warmest Quarter”) for model fitting.

The calibration area for the models was created as a buffer of 0.5° around the minimum convex polygon encompassing all occurrences. We used the maximum entropy method (implemented in MaxEnt ver. 3.4.1, (Phillips *et al.* 2006, Phillips *et al.* 2017) to calibrate model and evaluated model performance thanks to the package ENMeval (Muscarella *et al.* 2014) as implemented in ENMwizard. We evaluated models using a geographic partition scheme of type “block” and optimized two parameters of MaxEnt: the Regularization Multipliers (RM) and the Feature Classes (FC). RM was varied from 0.5 to 4.5, incremented by 0.5 whereas a suite of 15

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FCs (L, for Linear, P, for Product, Q, for Quadratic and H for Hinge) or combination of them were evaluated: L, P, Q, H, LP, LQ, LH, PQ, PH, QH, LPQ, LPH, LQH, PQH, LPQH, resulting in a total of 135 models. Model selection was done by computing the corrected Akaike Information

Model selection criterion	Threshold methods	Current	2011-2040			2041-2070			2071-2100		
			SSP			SSP			SSP		
			126	370	585	126	370	585	126	370	585
Low AIC	x10ptp	10806	7945	8090	7837	6428	6118	6449	8194	6425	3535
	mtss	9961	6898	6718	6667	5263	4512	4722	6773	4848	1140
AUC	x10ptp	6012	3716	3662	3377	1335	1632	1616	2396	604	0
	mtss	5194	2603	2402	2342	534	560	410	642	150	0

Table I: Current and future *P.c. asparagoides* suitable area (in km²) as modeled and predicted from ENM under different model selection criteria (LowAIC and AUC) and thresholding methods (10th percentile of training presence, x10ptp, and Maximum training sensitivity plus specificity, mtss).

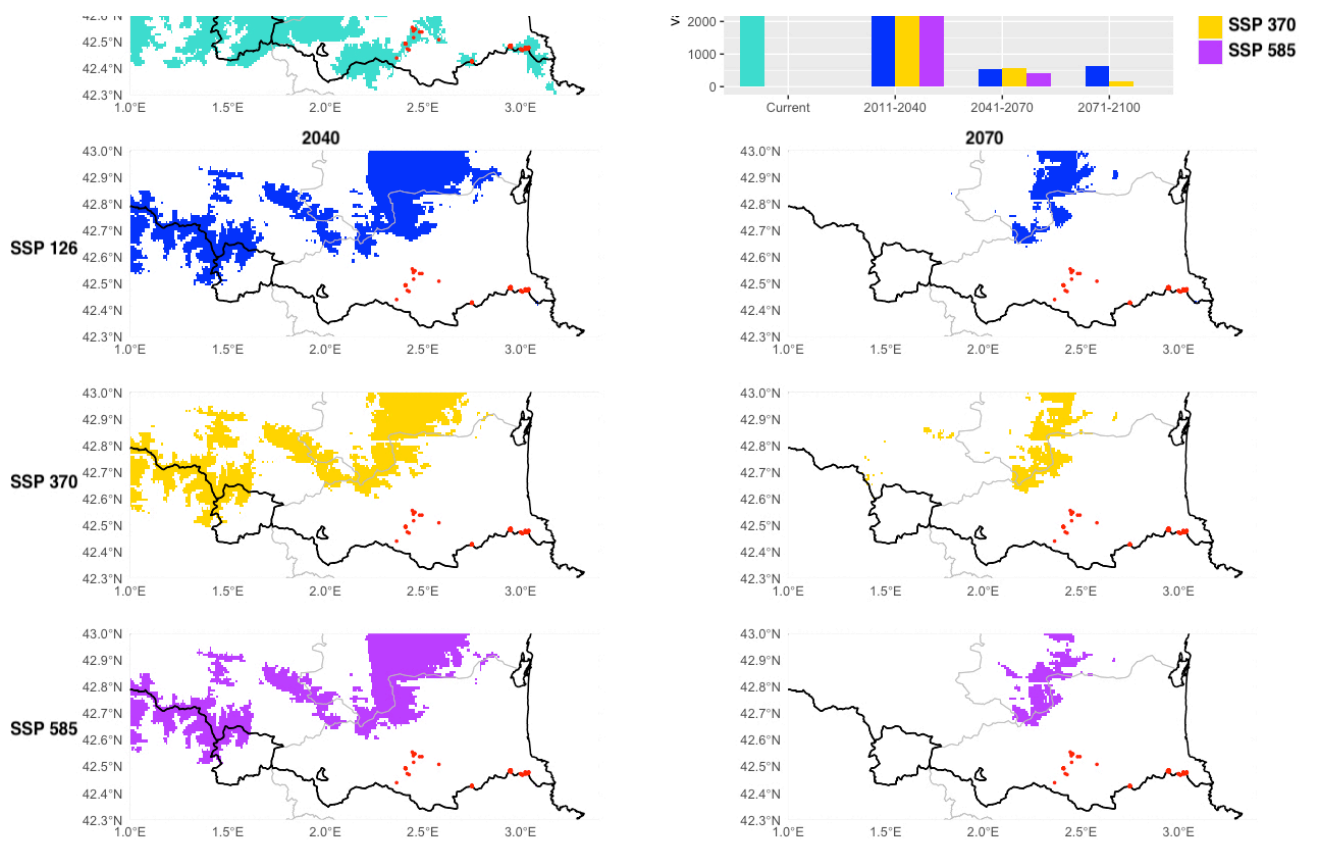


Fig. 2: Geographic areas holding suitable climatic conditions for *P.c. asparagoides* with projection under present climatic conditions (average for 1981-2010) and consensus projection (from 5 Global Climate Models (GCMs): GFDL-ESM4, UKESM1-0-LL, MPA-ESM1-2-HR, IPSL-CM6A-LR, and MRI-ESM2-0), for various plausible climatic scenarios for years 2035 (average for 2011-2040), 2055 (average for 2041-2070) and three Shared Socioeconomic Pathways (SSPs): SSP 126, SSP 370, and SSP 585. The barplot displays current and future area values under various plausible climatic scenarios. These values correspond to the model selected with “AUC” criteria.

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Criterion (“LowAIC”) and the Area Under the receiver operating characteristic Curve (“AUC”) in the function ENMWizard::calib_md_b(). The best selected model was then spatially projected as current niche. For future predictions, a spatial projection of the consensus of the five GCMs was performed for each time period and each SSPs. Area calculations were carried out after applying a 10-percentile (x 10 ptp) and Maximum training sensitivity plus specificity (mtss) threshold rules.

RESULTS

Suitable habitats for *P. c. asparagoides* and prediction of its spatial dynamics

ENMeval analyses identified RM = 0.5 and a combination of Linear and Quadratic feature (LQ) classes as the best-performing parameters for calibrating the final ENM following the “LowAIC” and M = 0.5 and a combination of Product (P) and Hinge feature (H) classes following the “AUC” optimality criteria. The first model had the best AICc score (153.6) and an AICc weight of 0.12 whereas the second one had an AICc score of 210.6 and an AICc weight of $4.87 \cdot 10^{-14}$. These two models had mean omission rates of 0.190 and 0.115 for the 10th percentile and the lowest presence training thresholds, respectively, as well as a mean test AUC of 0.82. Values of these diagnostic metrics are provided for all candidate models in Supplementary Appendix SIII. Current suitable area for *P. c. asparagoides* was found to be 9,961 and 5,194 km² following “LowAIC” and “AUC” selection model criteria, respectively (the values were similar whatever the threshold method used). All future consensus spatial projections predict a

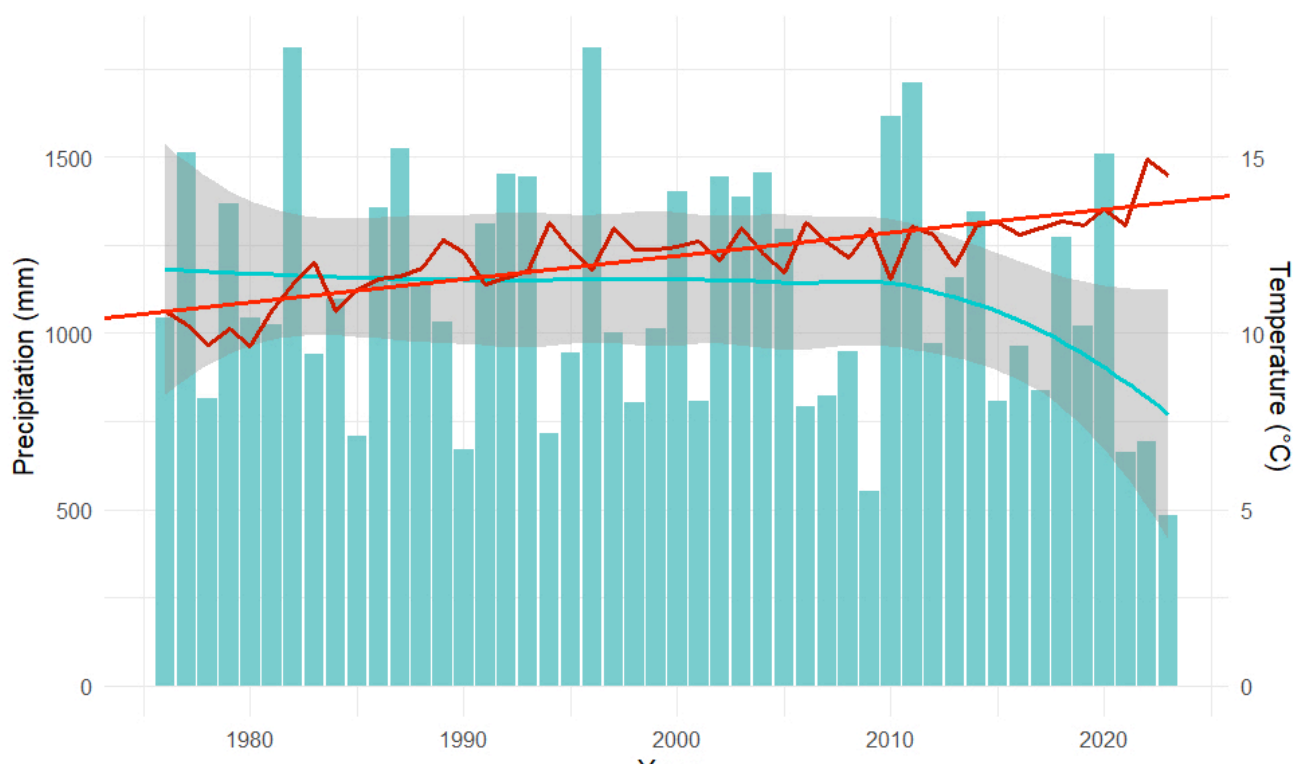


Fig. 3: Barplot representing the mean amount of precipitations (in mm) and temperatures (°C) for each year from 1976 to 2023 in the Natural Reserve of The Massane Forest.

dramatic decrease of the suitable area (Table I and Fig. 2). For SSP585, the suitable area would have completely disappeared for the time period 2071-2100. We also notice some slightly different outcomes depending on the selection model criteria with SSP370 scenarios giving sometimes higher values than SSP585, and even SSP126 (e.g. time period 2041-2070, “AUC” criterion).

Bioclimatic variables description from extreme models to local data

Across various climate models, regardless of the SSP considered, it is obvious that the Mean Annual Air Temperature (bio1) is projected to rise significantly, ranging from +3.85 to +7.38°C, during the period 2071-2100 over the study area, as indicated by MRI_ESM2_0 and UKESM1_0_LL respectively, which are among the models with the most extreme outcomes available in CHELSA (Supplementary Appendix SI). Additionally, all models predict a decrease in Annual Precipitation (bio12) ranging from -97.85 to -149.08 mm, also for the period 2071-2100, with MRI_ESM2_0 and UKESM1_0_LL showing the most pronounced decreases. Similar trends are observed for Mean Monthly Precipitation during the warmest quarter (bio18), with projected decreases ranging from -28.83 to -49.41 mm for the same time period. Similar forecasts are predicted among other time periods (i.e. 2011-2040 and 2041-2070).

Turning to local meteorological observation data from the Natural Reserve of the Massane Forest (Fig. 3), where *P. c. asparagoides* is found, we observe a gradual increase in temperatures over the years since 1976 to reach an average of +3.08°C in 2023, with a peak in 2022, coinciding with a severe heatwave in the region. Precipitation levels exhibit fluctuations over the years, with a notable occurrence of three consecutive years (2021, 2022, and 2023) marked by low precipitation levels (i.e., 662.8 mm, 693.7 mm and 482.4 mm respectively). These three consecutive values are the lowest ever recorded since 1960.

DISCUSSION

Climate change as a major threat for *P. c. asparagoides*

P. c. asparagoides is facing a number of threats that are likely to contribute to the decline of its populations. One of the most obvious threats is habitat loss due to reduced cattle grazing which leads to the closure of open habitats and subsequently reduces the species' reproductive capacity by increasing shaded areas. In addition, trampling can be a significant threat, particularly in populations close to footpaths. Nevertheless, our findings highlight that climate change poses the most significant threat to this species. The current suitable habitat for *P. c. asparagoides* is estimated to cover an area of approximately 5,194 km². All the different climatic scenarios considered systematically a dramatic decrease of the spatial extent of the ecological niche of *P. c. asparagoides*. For instance, an SSP with a radiative forcing value of +2.6 W/m² (i.e. SSP126) is considered as a rather optimistic trajectory, with CO₂ emissions starting to decline by 2020 and stopping completely by 2100, limiting the global temperature increase to below 2°C by 2100. SSP370 is usually considered as a baseline rather than a mitigation target. Under SSP585, emissions are projected to continue to increase throughout the 21st century and can be considered as a pessimistic scenario where the average temperature could rise by about 4°C by 2100. The different outcomes of these scenarios are likely to account for the complete disappearance of *P. c. asparagoides*' bioclimatic niche by 2100 when considering its theoretical ecological niche, with some slight differences depending on the climatic scenario considered (i.e. SSP). However, when considering the bioclimatic conditions of its realised (actual) niche, the endemic morphotype is predicted to disappear by 2040, if

not earlier, irrespective of the SSP scenario. These results suggest that the threat category of this plant in Red Lists may be upgraded following a taxonomic assessment of this species on the basis of genetic data.

Our direct field observations combined with local meteorological data provided by the Natural Reserve of the Massane Forest corroborate these alarming findings. In 2023, we observed a significant decrease in the number of flowering individuals. Since we started monitoring nearby populations in 2021, we have noticed a decline in flowering individuals at several sites following three consecutive years of drought in the Eastern Pyrenees region. Specifically affected areas include 1- East-Albères, 3-Pic des Salines and 4-Mariailles. The situation is particularly concerning in the Albères massif where we only observed three individuals at the rosette stage in 2023, none of which produced flowers. Situated 5 km away from the Mediterranean Sea and 30 km away from the highest peaks of the Pyrenees chain, the Albères represent a biogeographical crossroads or a continental islet (Trave 2000) characterised by unique climatic conditions. While these unique conditions have historically fostered the emergence of numerous subspecies or species, the ongoing effects of climate change pose a serious threat to biodiversity of this mountain subrange. Consequently, there are many reasons to be concerned about the survival of this endemic morphotype. The region has experienced a severe precipitation deficit since 2020, in addition to a series of exceptionally warm years. Precipitation has fluctuated from year to year, with three consecutive years (2021, 2022, and 2023) characterized by low precipitation levels, an unprecedented event over the last six decades.

Projections from different climate models show an expected increase in mean annual temperature, ranging from +1.06 to +2.9°C by 2040 for the most optimistic and pessimistic scenarios, respectively. By 2070, these temperatures are expected to increase further, ranging from +2.94 to +5.99°C for the most optimistic and pessimistic scenarios, and by 2100, the projections range from +3.85 to +7.38°C for the same scenarios. Annual precipitation is projected to a decrease over the years, with estimates ranging from -97.85 mm to -149.08 mm by 2100, for the most optimistic and pessimistic scenarios, respectively. A study focusing on Mediterranean mountain regions predict even more profound changes (Bravo *et al.* 2008), with projected warming ranging from +1.4 to +5.1°C by 2055 and +1.6 to +8.3°C by 2085. In addition, this study predicts a reduction in precipitation, especially in spring, ranging from -17% to -4.8% according to different models by 2085. These climatic alterations are expected to accelerate species ranges shifts and contribute to extinctions. Indeed, another study (Thuiller *et al.* 2005), which modelled the distribution of European plants in relation to climate reported that mountain species close to the Mediterranean basin will be disproportionately sensitive to climate change, with an expected loss of around 60 % of species by 2085.

It is important to note that while these results provide valuable insights, they should not be interpreted as precise predictions, given the uncertainties in climate change scenarios and modelling techniques.

Additional threats and reflection on conservation strategies

Taken together, the multiple threats posed by both climate and land-use changes are undoubtedly accelerating population decline, fragmentation, and habitat loss of the endemic *P. c. asparagoides*. However, a lack of understanding regarding many facets of this morphotype poses an additional form of threat, as effective management and monitoring efforts are hampered by insufficient awareness of its specific characteristics. In particular, there is limited knowledge of the pollination mechanisms of *P.c. asparagoides*, yet climate change could also negatively impact the survival of its pollinators (described as *Bombus sp.*), thereby exerting further pressure on this endemic plant.

Furthermore, *P. c. asparagoides* is a hemi-parasitic species, relying on host plants for nutrition. Still, the host plants of this endemic plant are poorly characterized and exhibit considerable variability across different sites. This inherent dependence makes *P. c. asparagoides* even more vulnerable to climate change as it relies on other species that may also struggle to adapt to future climatic conditions.

There is therefore a growing need to gather additional information about this threatened morphotype, which may disappear more quickly than expected. Genomic data could provide valuable insights into its biodiversity patterns and differentiation, enabling recommendations for conservation strategies. Currently only the endemic, pink-flowered *P. c. subsp. asparagoides* benefits from local protection measures, a strategy that may prove suboptimal for conserving the species' overall genetic diversity. Waiting for such complementary studies, our results show that current habitat of *P. c. asparagoides* may become climatically unsuitable too soon for the endemic form to reach through natural dispersal areas that are predicted to remain favourable to its establishment in the future. Among others, our findings therefore suggest that practical conservation actions such as assisted migration could be envisaged on this particular morphotype.

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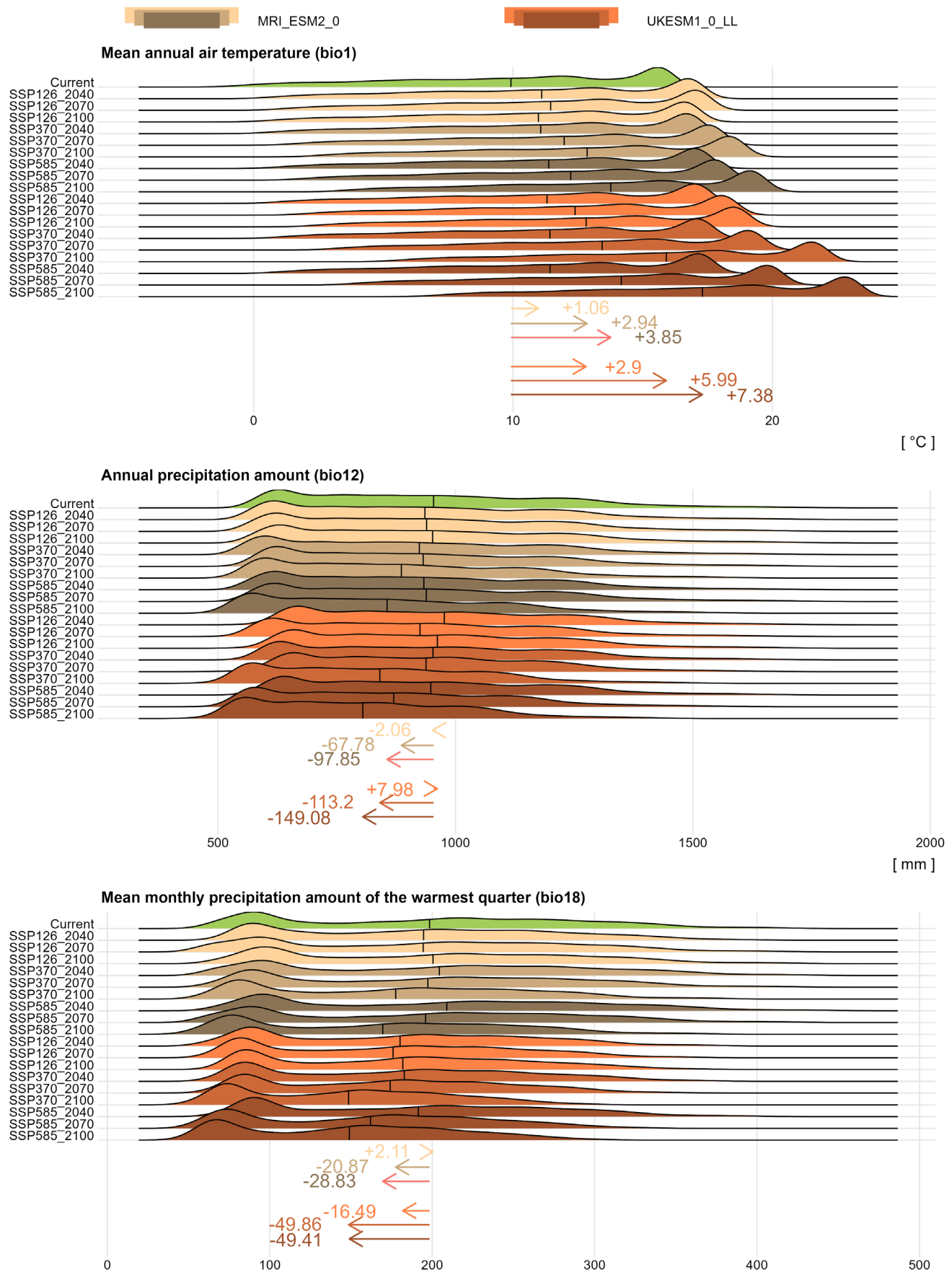
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Supplementary Appendix SI: Bioclimatic variables predicted by the most optimistic and pessimistic models from CHELSA (MRI_ESM2_0 in beige and UKESM1_0_LL in orange). The arrows represent the variation delta with current data (1981-2010). Bio 12 and Bio 18 are the least correlated variables which were kept for modelling, and Bio 1 is an important variable to consider for interpretation.



Supplementary Appendix SII: Geographic coordinates of all the individuals used for the Ecological Niche Modelling.

Origin of the data	Site	Longitude	Latitude
Current Project	1-East Albères	3.0094533	42.4676933
Current Project	1-East Albères	3.0091301	42.4676567
Current Project	1-East Albères	3.0306533	42.4744367
Current Project	1-East Albères	3.0327667	42.4733983
Current Project	1-East Albères	3.0341299	42.4735616
Current Project	1-East Albères	3.0342334	42.4733650
Current Project	1-East Albères	3.0379066	42.4736317
Current Project	1-East Albères	3.0376901	42.4734067
Current Project	1-East Albères	3.0264033	42.4718316
Current Project	1-East Albères	3.0045150	42.4696766
Current Project	1-East Albères	3.0028500	42.4710201
Current Project	1-East Albères	3.0015934	42.4720383
Current Project	1-East Albères	3.0004783	42.4726884
Current Project	1-East Albères	2.9988884	42.4722834
Current Project	2-Pic Neulos	2.9469367	42.4821717
Current Project	2-Pic Neulos	2.9469617	42.4822367
Current Project	2-Pic Neulos	2.9470601	42.4822267
Current Project	2-Pic Neulos	2.9491601	42.4824267
Current Project	2-Pic Neulos	2.9490367	42.4824401
Current Project	2-Pic Neulos	2.9466700	42.4821234
Current Project	2-Pic Neulos	2.9454667	42.4826483
Current Project	2-Pic Neulos	2.9453067	42.4828384
Current Project	2-Pic Neulos	2.9449867	42.4829234
Current Project	2-Pic Neulos	2.9449716	42.4830300
Current Project	2-Pic Neulos	2.9448866	42.4832550
Current Project	2-Pic Neulos	2.9480550	42.4858867
Current Project	2-Pic Neulos	2.9480951	42.4860367
Current Project	2-Pic Neulos	2.9482516	42.4857883
Current Project	2-Pic Neulos	2.9484550	42.4857900
Current Project	2-Pic Neulos	2.9483467	42.4859484
Current Project	2-Pic Neulos	2.9483033	42.4859950
Current Project	2-Pic Neulos	2.9448266	42.4852601
Current Project	3-Pic des Salines	2.75129008	42.425822

Current Project	3-Pic des Salines	2.7512698	42.4257481
Current Project	3-Pic des Salines	2.751554	42.4258129
Current Project	3-Pic des Salines	2.75129008	42.425822
Current Project	3-Pic des Salines	2.7511663	42.4256084
Current Project	3-Pic des Salines	2.75129008	42.425822
Current Project	3-Pic des Salines	2.75129008	42.425822
Current Project	3-Pic des Salines	2.75129008	42.425822
Current Project	3-Pic des Salines	2.75129008	42.425822
Current Project	3-Pic des Salines	2.75129008	42.425822
Current Project	3-Pic des Salines	2.7510827	42.4259754
Current Project	3-Pic des Salines	2.7513776	42.4259652
Current Project	3-Pic des Salines	2.75129008	42.425822
Current Project	3-Pic des Salines	2.75129008	42.425822
Current Project	3-Pic des Salines	2.75129008	42.425822
Current Project	3-Pic des Salines	2.75129008	42.425822
Current Project	4-Mariailles	2.410365	42.493818
Current Project	4-Mariailles	2.410058	42.492972
Current Project	4-Mariailles	2.410070	42.492973
Current Project	4-Mariailles	2.409742	42.493352
Current Project	4-Mariailles	2.409815	42.493317
Current Project	4-Mariailles	2.409688	42.493462
Current Project	4-Mariailles	2.409255	42.492977
Current Project	4-Mariailles	2.409432	42.492798
Current Project	4-Mariailles	2.409403	42.492777
Current Project	4-Mariailles	2.410170	42.492995
Current Project	4-Mariailles	2.411377	42.491872
Current Project	4-Mariailles	2.411452	42.491690
Current Project	4-Mariailles	2.411470	42.491765
Simethis		3.037751155303667	42.47370842497783
Simethis		2.748394684405623	42.42559769965901
Simethis		3.024092633365992	42.4781619598532
Simethis		2.428841174816695	42.46927335780286
Simethis		3.030599764999641	42.47478939940824
Simethis		2.458011344744675	42.54728403084814
Simethis		2.750306179425731	42.4297189937229

Simethis		3.024092633365992	42.4781619598532
Simethis		2.94941640062159	42.485173169975866
Simethis		2.482457723721556	42.536716398944186
Simethis		2.944489047391093	42.48150316303968
Simethis		2.949514903301299	42.48361809901637
Simethis		2.364795297194514	42.43882452813665
Simethis		3.037702585153056	42.473708442157026
Simethis		3.026130348235697	42.472821992195264
Simethis		2.419370073987095	42.47297971951335
Simethis		3.039719810015859	42.47600890220826
Simethis		3.029471181467996	42.47616503985768
Simethis		3.041507341809779	42.479540921589994
Simethis		2.94921417066564	42.480300979445985
Simethis		3.030551043609525	42.47450176443133
Simethis		2.946355270671749	42.48583687021818
Simethis		2.951761794448117	42.483448345547416
Simethis		2.948508137345314	42.48221531731918
Simethis		2.458011344744675	42.54728403084814
Simethis		2.949514903301299	42.48361809901637
Simethis		2.452071904592277	42.51556482662973
Simethis		2.450540753123123	42.540116888289184
Simethis		2.943964745912053	42.483696230132615
Simethis		2.494625271190652	42.53677468444805
Simethis		3.024092633365992	42.4781619598532
Simethis		3.024697371929783	42.47239985011868
Simethis		3.026908493359582	42.4750690544605
Simethis		2.581479665603023	42.507835416417926
Simethis		2.450342556377736	42.54696614697758
Simethis		2.445081852351362	42.554247756137435
Simethis		2.946551638545184	42.48359867731852
Simethis		2.410418007514649	42.49373198633484
Simethis		2.943336328684332	42.480495779029745
Simethis		3.040097334918682	42.4775998227363
Simethis		3.04258612480521	42.47678085432683
Simethis		2.951000741612207	42.47861186907505

Simethis		2.946638218248845	42.48188180172431
Simethis		2.950666576048302	42.48606367930499
Simethis		2.948334787706038	42.48598167334945
Simethis		2.950423262207637	42.48654897988215

Supplementary Appendix SIII: Summary of the 135 models of Maxent ENMs generated by ENMeval. The two best models are indicated in bold.

	settings	features	rm	trainAUC	avgtestAUC	vartestAUC	avgdltAUC	validdltAUC	avgtestAOTF	vartestAOTF	avgtestdTP	vartestdTP	AUC	dltAUC	v-AUC	parameters	select	models	rankAUC
1	L_0.5	L	0.5	0.844	0.80783	0.00367	0.04686	0.00619	0.08333	0.02778	0.14583	0.02951	153.939	0.37857	0.09628	2		Mod_0.5_L	5
2	P_0.5	P	0.5	0.7313	0.73188	0.06962	0.08346	0.01355	0.0625	0.01563	0.14583	0.02951	162.272	8.71129	0.00149	1		Mod_0.5_P	20
3	Q_0.5	Q	0.5	0.8442	0.81471	0.00637	0.0477	0.00627	0.08333	0.02778	0.14583	0.02951	153.629	0.06839	0.11243	2		Mod_0.5_Q	2
4	H_0.5	H	0.5	0.9148	0.82027	0.00621	0.08957	0.00936	0.14583	0.02951	0.22917	0.02488	210.565	57.0041	4.87E-14	9	AUCmp, AUC10	Mod_0.5_H	113
5	LP_0.5	LP	0.5	0.8439	0.79526	0.00168	0.05009	0.00553	0.08333	0.02778	0.14583	0.02951	154.512	0.95126	0.0723	2		Mod_0.5_LP	8
6	LQ_0.5	LQ	0.5	0.8447	0.81624	0.00617	0.0466	0.00613	0.08333	0.02778	0.14583	0.02951	153.561	0	0.11634	2	LowAIC	Mod_0.5_LQ	1
7	LH_0.5	LH	0.5	0.9148	0.82027	0.00621	0.08957	0.00936	0.14583	0.02951	0.22917	0.02488	210.565	57.0041	4.87E-14	9		Mod_0.5_LH	114
8	PQ_0.5	PQ	0.5	0.8439	0.79648	0.00171	0.04946	0.0055	0.08333	0.02778	0.14583	0.02951	154.446	0.88494	0.07474	2		Mod_0.5_PQ	6
9	PH_0.5	PH	0.5	0.9148	0.82027	0.00621	0.08957	0.00936	0.14583	0.02951	0.22917	0.02488	210.565	57.0041	4.87E-14	9		Mod_0.5_PH	115
10	QH_0.5	QH	0.5	0.9148	0.82027	0.00621	0.08957	0.00936	0.14583	0.02951	0.22917	0.02488	210.565	57.0041	4.87E-14	9		Mod_0.5_QH	116
11	LPQ_0.5	LPQ	0.5	0.8439	0.79648	0.00171	0.04946	0.0055	0.08333	0.02778	0.14583	0.02951	154.446	0.88494	0.07474	2		Mod_0.5_LPQ	7
12	LPH_0.5	LPH	0.5	0.9148	0.82027	0.00621	0.08957	0.00936	0.14583	0.02951	0.22917	0.02488	210.565	57.0041	4.87E-14	9		Mod_0.5_LPH	117
13	LQH_0.5	LQH	0.5	0.9148	0.82027	0.00621	0.08957	0.00936	0.14583	0.02951	0.22917	0.02488	210.565	57.0041	4.87E-14	9		Mod_0.5_LQH	118
14	PQH_0.5	PQH	0.5	0.9148	0.82027	0.00621	0.08957	0.00936	0.14583	0.02951	0.22917	0.02488	210.565	57.0041	4.87E-14	9		Mod_0.5_PQH	119
15	LPQH_0.5	LPQH	0.5	0.9148	0.82027	0.00621	0.08957	0.00936	0.14583	0.02951	0.22917	0.02488	210.565	57.0041	4.87E-14	9		Mod_0.5_LPQH	120
16	L_1	L	1	0.8465	0.74595	0.01847	0.09977	0.01545	0.08333	0.02778	0.39583	0.18229	156.091	2.52986	0.02384	2		Mod_1.0_L	11
17	P_1	P	1	0.7313	0.60994	0.01623	0.08346	0.01355	0.0625	0.01563	0.14583	0.02951	164.451	10.8095	0.0005	1		Mod_1.0_P	27
18	Q_1	Q	1	0.845	0.76823	0.00585	0.07963	0.00583	0.08333	0.02778	0.39583	0.18229	154.802	1.33124	0.05979	2		Mod_1.0_Q	10
19	H_1	H	1	0.915	0.81258	0.00436	0.09108	0.00914	0.14583	0.02951	0.22917	0.02488	172.676	19.1149	8.22E-06	7		Mod_1.0_H	63
20	LP_1	LP	1	0.8456	0.71915	0.01357	0.1055	0.01224	0.14583	0.02951	0.39583	0.18229	158.264	4.70306	0.01108	2		Mod_1.0_LP	16
21	LQ_1	LQ	1	0.8449	0.7693	0.00994	0.07834	0.00587	0.08333	0.02778	0.39583	0.18229	154.799	1.23796	0.06265	2		Mod_1.0_LQ	9
22	LH_1	LH	1	0.915	0.81258	0.00436	0.09108	0.00914	0.14583	0.02951	0.22917	0.02488	172.676	19.1149	8.22E-06	7		Mod_1.0_LH	64
23	LP_1	PQ	1	0.8466	0.71915	0.01357	0.10574	0.01222	0.14583	0.02951	0.39583	0.18229	158.199	4.63799	0.01144	2		Mod_1.0_PQ	15
24	PH_1	PH	1	0.915	0.81258	0.00436	0.09108	0.00914	0.14583	0.02951	0.22917	0.02488	172.676	19.1149	8.22E-06	7		Mod_1.0_PH	65
25	QH_1	QH	1	0.915	0.81734	0.00418	0.08649	0.00806	0.14583	0.02951	0.22917	0.02488	188.286	34.7252	3.35E-09	8		Mod_1.0_QH	111
26	LQ_1	LPQ	1	0.8466	0.71915	0.01357	0.10574	0.01222	0.14583	0.02951	0.39583	0.18229	158.199	4.63799	0.01144	2		Mod_1.0_LQ	14
27	LPH_1	LPH	1	0.915	0.81258	0.00436	0.09108	0.00914	0.14583	0.02951	0.22917	0.02488	172.676	19.1149	8.22E-06	7		Mod_1.0_LPH	66
28	LQH_1	LQH	1	0.915	0.81734	0.00418	0.08649	0.00806	0.14583	0.02951	0.22917	0.02488	188.286	34.7252	3.35E-09	8		Mod_1.0_LQH	112
29	PQH_1	PQH	1	0.915	0.81258	0.00436	0.09108	0.00914	0.14583	0.02951	0.22917	0.02488	172.676	19.1149	8.22E-06	7		Mod_1.0_PQH	67
30	LPQH_1	LPQH	1	0.915	0.81258	0.00436	0.09108	0.00914	0.14583	0.02951	0.22917	0.02488	172.676	19.1149	8.22E-06	7		Mod_1.0_LPQH	68
31	L_1.5	L	1.5	0.8478	0.69329	0.0264	0.10512	0.01112	0.08333	0.02778	0.33333	0.22222	160.128	6.56717	0.00436	2		Mod_1.5_L	17
32	P_1.5	P	1.5	0.7313	0.5	0	0	0	0	0	0	0	170.055	16.4945	3.05E-05	1		Mod_1.5_P	58
33	Q_1.5	Q	1.5	0.8468	0.74219	0.01682	0.10059	0.01486	0.08333	0.02778	0.39583	0.18229	157.06	3.49941	0.02022	2		Mod_1.5_Q	13
34	H_1.5	H	1.5	0.9121	0.80653	0.00474	0.09373	0.00841	0.14583	0.02951	0.3125	0.07581	177.09	23.5295	9.04E-07	7		Mod_1.5_H	87
35	LP_1.5	LP	1.5	0.8365	0.68824	0.05662	0.0523	0.02462	0	0	0.33333	0.22222	166.151	12.5901	0.00021	2		Mod_1.5_LP	32
36	LQ_1.5	LQ	1.5	0.8468	0.74233	0.01689	0.10088	0.01488	0.08333	0.02778	0.39583	0.18229	156.941	3.38062	0.02146	2		Mod_1.5_LQ	12
37	LH_1.5	LH	1.5	0.9121	0.80653	0.00474	0.09373	0.00841	0.14583	0.02951	0.3125	0.07581	177.09	23.5295	9.04E-07	7		Mod_1.5_LH	88
38	PQ_1.5	PQ	1.5	0.8362	0.68824	0.05662	0.0523	0.02462	0	0	0.33333	0.22222	166.087	12.5262	0.00022	2		Mod_1.5_PQ	30
39	PH_1.5	PH	1.5	0.9121	0.80653	0.00474	0.09373	0.00841	0.14583	0.02951	0.3125	0.07581	177.09	23.5295	9.04E-07	7		Mod_1.5_PH	89
40	QH_1.5	QH	1.5	0.9103	0.81513	0.0044	0.08469	0.00648	0.14583	0.02951	0.22917	0.02488	153.869	0.30837	0.09772	4		Mod_1.5_QH	113
41	LPQ_1.5	LPQ	1.5	0.8362	0.68824	0.05662	0.0523	0.02462	0	0	0.33333	0.22222	166.087	12.5262	0.00022	2		Mod_1.5_LPQ	31
42	LPH_1.5	LPH	1.5	0.9121	0.80653	0.00474	0.09373	0.00841	0.14583	0.02951	0.3125	0.07581	177.09	23.5295	9.04E-07	7		Mod_1.5_LPH	90
43	LQH_1.5	LQH	1.5	0.9103	0.81513	0.0044	0.08469	0.00648	0.14583	0.02951	0.22917	0.02488	153.869	0.30837	0.09772	4		Mod_1.5_LQH	4
44	PQH_1.5	PQH	1.5	0.9121	0.80653	0.00474	0.09373	0.00841	0.14583	0.02951	0.3125	0.07581	177.09	23.5295	9.04E-07	7		Mod_1.5_PQH	91
45	LPQH_1.5	LPQH	1.5	0.9121	0.80653	0.00474	0.09373	0.00841	0.14583	0.02951	0.3125	0.07581	177.09	23.5295	9.04E-07	7		Mod_1.5_LPQH	92
46	L_2	L	2	0.8111	0.68824	0.05662	0.0523	0.02462	0.08333	0.02778	0.33333	0.22222	167.842	14.2813	9.22E-05	2		Mod_2.0_L	40
47	Q_2	Q	2	0.8473	0.67538	0.04698	0.08571	0.01763	0.08333	0.02778	0.33333	0.22222	160.441	6.88041	0.00373	2		Mod_2.0_Q	19
48	LH_2	H	2	0.906	0.80112	0.00803	0.0934	0.01095	0.08333	0.02778	0.3125	0.07581	181.403	27.8424	1.05E-07	7		Mod_2.0_H	105
49	LP_2	LP	2	0.7748	0.68824	0.05662	0.0523	0.02462	0	0	0.33333	0.22222	168.371	14.8105	7.07E-05	1		Mod_2.0_LP	49
51	LQ_2	LQ	2	0.8474	0.67425	0.04615	0.08694	0.01743	0.08333	0.02778	0.33333	0.22222	160.324	6.76377	0.00395	2		Mod_2.0_LQ	18
52	LH_2	LH	2	0.906	0.80112	0.00803	0.0934	0.01095	0.08333	0.02778	0.3125	0.07581	181.403	27.8424	1.05E-07	7		Mod_2.0_LH	106
53	PQ_2	PQ	2	0.7748	0.68824	0.05662	0.0523	0.02462	0	0	0.33333	0.22222	168.282	14.7216	7.40E-05	1		Mod_2.0_PQ	47
54	PH_2	PH	2	0.906	0.80112	0.00803	0.0934	0.01095	0.08333	0.02778	0.3125	0.07581	181.403	27.8424	1.05E-07	7		Mod_2.0_PH	107
55	QH_2	QH	2	0.9023	0.81256	0.00795	0.07644	0.00806	0.08333	0.02778	0.3125	0.07581	163.93	10.3691	0.00665	5		Mod_2.0_QH	25
56	LPQ_2	LPQ	2	0.7748	0.68824	0.05662	0.0523	0.02462	0	0	0.33333	0.22222	168.282	14.7216	7.40E-05	1		Mod_2.0_LPQ	48
57	LPH_2	LPH	2	0.906	0.80112	0.00803	0.0934	0.01095	0.08333	0.02778	0.3125	0.07581	181.403	27.8424	1.05E-07	7		Mod_2.0_LPH	108
58	LQH_2	LQH	2	0.9023	0.81256	0.00795	0.07644	0.00806	0.08333	0.02778	0.3125	0.07581	163.93	10.3691	0.00665	5		Mod_2.0_LQH	26
59	PQH_2	PQH	2	0.906	0.80112	0.00803	0.0934	0.01095	0.08333	0.02778	0.3125	0.07581	181.403	27.8424	1.05E-07	7		Mod_2.0_PQH	109
60	LPQH_2	LPQH	2	0.906	0.80112	0.00803	0.0934	0.01095	0.08333	0.02778	0.3125	0.07581	181.403	27.8424	1.05E-07	7			

104	PQH_3.5	PQH	3.5	0,8428	0,68042	0,04744	0,10292	0,02059	0,08333	0,02778	0,33333	0,22222	180,782	27,2218	1,43E-07	5		Mod_3.5_PQH	103
105	LPQH_3.5	LPQH	3.5	0,8428	0,68042	0,04744	0,10292	0,02059	0,08333	0,02778	0,33333	0,22222	180,782	27,2218	1,43E-07	5		Mod_3.5_LPQH	104
106	L_4	L	4	0,7748	0,60688	0,04923	0,0523	0,02462	0	0	0,33333	0,22222	171,417	17,8564	1,54E-05	1		Mod_4.0_L	62
108	Q_4	Q	4	0,7748	0,68824	0,05662	0,0523	0,02462	0	0	0,33333	0,22222	168,516	14,9557	6,58E-05	1		Mod_4.0_Q	51
109	H_4	H	4	0,8201	0,68744	0,0578	0,0523	0,02462	0	0	0,33333	0,22222	178,206	24,6455	5,18E-07	4		Mod_4.0_H	93
111	LQ_4	LQ	4	0,7748	0,68824	0,05662	0,0523	0,02462	0	0	0,33333	0,22222	168,516	14,9557	6,58E-05	1		Mod_4.0_LQ	52
112	LH_4	LH	4	0,8201	0,69514	0,06274	0,0523	0,02462	0	0	0,33333	0,22222	178,206	24,6455	5,18E-07	4		Mod_4.0_LH	94
114	PH_4	PH	4	0,8201	0,68744	0,0578	0,0523	0,02462	0	0	0,33333	0,22222	178,206	24,6455	5,18E-07	4		Mod_4.0_PH	95
115	QH_4	QH	4	0,8201	0,69673	0,06389	0,0523	0,02462	0,08333	0,02778	0,33333	0,22222	169,405	15,8446	4,22E-05	2		Mod_4.0_QH	53
117	LPH_4	LPH	4	0,8201	0,68744	0,0578	0,0523	0,02462	0	0	0,33333	0,22222	178,206	24,6455	5,18E-07	4		Mod_4.0_LPH	96
118	LQH_4	LQH	4	0,8201	0,69673	0,06389	0,0523	0,02462	0,08333	0,02778	0,33333	0,22222	169,405	15,8446	4,22E-05	2		Mod_4.0_LQH	54
119	PQH_4	PQH	4	0,8201	0,68744	0,0578	0,0523	0,02462	0	0	0,33333	0,22222	178,206	24,6455	5,18E-07	4		Mod_4.0_PQH	97
120	LPQH_4	LPQH	4	0,8201	0,68744	0,0578	0,0523	0,02462	0	0	0,33333	0,22222	178,206	24,6455	5,18E-07	4		Mod_4.0_LPQH	98
121	L_4.5	L	4.5	0,7748	0,52848	0,0073	0,0523	0,02462	0	0	0,25	0,25	173,286	19,7251	6,06E-06	1		Mod_4.5_L	78
123	Q_4.5	Q	4.5	0,7748	0,60688	0,04923	0,0523	0,02462	0	0	0,33333	0,22222	169,521	15,9603	3,98E-05	1		Mod_4.5_Q	55
124	H_4.5	H	4.5	0,7785	0,60983	0,05296	0,0523	0,02462	0	0	0,25	0,25	176,793	23,2327	1,05E-06	3		Mod_4.5_H	81
126	LQ_4.5	LQ	4.5	0,7748	0,60688	0,04923	0,0523	0,02462	0	0	0,33333	0,22222	169,521	15,9603	3,98E-05	1		Mod_4.5_LQ	56
127	LH_4.5	LH	4.5	0,7785	0,60983	0,05296	0,0523	0,02462	0	0	0,25	0,25	176,793	23,2327	1,05E-06	3		Mod_4.5_LH	82
129	PH_4.5	PH	4.5	0,7785	0,60983	0,05296	0,0523	0,02462	0	0	0,25	0,25	176,793	23,2327	1,05E-06	3		Mod_4.5_PH	83
130	QH_4.5	QH	4.5	0,786	0,68824	0,05662	0,0523	0,02462	0	0	0,33333	0,22222	175,494	21,9333	2,01E-06	3		Mod_4.5_QH	79
132	LPH_4.5	LPH	4.5	0,7785	0,60983	0,05296	0,0523	0,02462	0	0	0,25	0,25	176,793	23,2327	1,05E-06	3		Mod_4.5_LPH	84
133	LQH_4.5	LQH	4.5	0,786	0,68824	0,05662	0,0523	0,02462	0	0	0,33333	0,22222	175,494	21,9333	2,01E-06	3		Mod_4.5_LQH	80
134	PQH_4.5	PQH	4.5	0,7785	0,60983	0,05296	0,0523	0,02462	0	0	0,25	0,25	176,793	23,2327	1,05E-06	3		Mod_4.5_PQH	85
135	LPQH_4.5	LPQH	4.5	0,7785	0,60983	0,05296	0,0523	0,02462	0	0	0,25	0,25	176,793	23,2327	1,05E-06	3		Mod_4.5_LPQH	86