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Impact of Climate Change on the Distribution of Four Closely Related *Orchis* (Orchidaceae) Species

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Abstract: Long-term monitoring programs and population demographic models have shown that the population dynamics of orchids are to a large extent dependent on prevailing weather conditions, suggesting that the changes in climatic conditions can have far reaching effects on the population dynamics and hence the distribution of orchids. Although a better understanding of the effects of climate change on the distribution of plants has become increasingly important during the final years, only a few studies have investigated the effects of changing temperature and precipitation on the distribution of orchids. In this study, we investigated the impact of climate change on the distribution of four terrestrial orchid species (*Orchis anthropophora*, *Orchis militaris*, *Orchis purpurea* and *Orchis simia*). Using bioclimatic data for current and future climate scenarios, habitat suitability, range shifts and the impact of different abiotic factors on the range of each species were modelled using Maxent. The results revealed an increase in suitable habitat area for *O. anthropophora*, *O. purpurea* and *O. simia* under each RCP (Representative Concentration Pathway) scenario, while a decrease was observed for *O. militaris*. Furthermore, all four of the orchids showed a shift to higher latitudes under the three RCPs leading to a significant range extension under mild climate change. Under severe climate change, a significant decline in the distribution area at the warm edge of their distributions was observed. Overall, these results show that mild climate change may be beneficial for the studied orchid species and lead to range expansion. However, continued warming may yet prove detrimental, as all species also showed pronounced declines at lower latitudes when temperature increases were larger than 4 °C.

Keywords: dispersal; Maxent; mycorrhiza; orchids; range expansion; species distribution modeling

1. Introduction

Understanding the various factors that limit the distribution of plant and animal species is a central theme in ecology and evolutionary biology [1,2]. The topic has gained momentum as predicted changes in climatic conditions will most likely shift species' distributions and ecology [3,4]. There is mounting evidence that species have already shifted their ranges over recent decades and will continue to do so throughout the 21st century. However, the shifts in distribution are not necessarily associated with range contractions, because not all species will immediately show declines at rear edges [5–8], suggesting that mild climate change may be favorable for many species. Better insights into the processes that drive species distributions are therefore important for applied ecology and species conservation [9].

In general, a species can only persist at a given location when the number of individuals recruiting and surviving in a population is larger than the number of individuals dying and emigrating, i.e., when the population has an intrinsic population growth rate $\lambda > 1$. Understanding the processes governing population demography can therefore help to forecast which species can resist range shifts, which will successfully shift their ranges and which will show rapid declines as a result of continued climate change [10,11]. One way to assess the current and future performance of plant and animal populations involves performing demographic analyses across the entire range of the species and comparing the population growth rates and vital rates between the edge and core populations [5]. Detailed investigations of range-wide variation in the demography of two North American tundra plants (*Silene acaulis* and *Polygonum viviparum*), for example, has shown that the population growth rates of southern populations were not lower than those of northern ones and that compensatory changes in demographic rates were buffering southern populations against the negative effects of a warming climate [6]. Similarly, about 50% of all monitored populations of plant species with an arctic-alpine and boreal distribution across western North America remained stable or even increased in abundance across the rear edge populations occurring in the northern Rocky Mountains [7].

Such methods are, however, generally labor intensive, are usually conducted across multiple years at a limited number of sites, and do not allow for the assessment of population growth parameters at sites where the species is currently absent. An alternative approach that is currently widely applied, is environmental niche modeling [12–15]. In this case, geographic biodiversity records, typically in the form of observed presences, are related to the abiotic and/or biotic characteristics at those locations and are subsequently used to forecast the impact of global environmental change on the distribution of the species [9,10,16]. While these models lack direct information about the ecological processes governing range distributions, they have the advantage of allowing for the identification of potentially suitable areas across large spatial scales and the use of different climate change scenarios.

Orchids represent an interesting study system to investigate the impact of climatic conditions on current and future distribution ranges. Despite the evolutionary success of the family [17], most of its members tend to have restricted distribution areas and many species are currently in decline, most likely as a result of severe habitat loss due to land conversion and urban development, the habitat degradation of the remaining patches, over-collection and a loss of critical ecological interactions [18–20]. Although there are very few studies that have directly investigated the impact of climate change on orchid decline, it has been suggested that climate extremes further contribute to threaten orchid populations [18].

There is ample evidence that the demography of orchid species is dependent on prevailing weather conditions. For example, warm winter conditions favored the population performance of the terrestrial orchid *Himantoglossum hircinum* in a nature reserve in Germany [21]. Similarly, demographic modeling showed that observed changes in climatic conditions were beneficial to the long-term survival of the same species in the UK and suggested that they may have even been the driving force behind the current range expansion of the species in England [22]. Detailed demographic analyses using integral projection models also showed that milder winters and wetter springs had a positive effect on the demography of populations of the lady orchid (*Orchis purpurea*) at the northern edge of its distribution [23]. Although it is hard to generalize from these case studies, these results suggest that climate warming may have beneficial effects on the population dynamics of orchids at the cold edge of their distribution ranges. However, to what extent climate change affects the demography of orchids at the warm edges of their distributions remains largely unclear [20].

Here, we used species distribution modeling to assess the effect of climate change on the European distribution of four species of the orchid genus *Orchis*. This genus consists of 21 terrestrial orchid species and several subspecies and varieties that are widely distributed across most of Europe and some parts of Asia Minor [24]. Specifically, we tested how the suitable habitat available to the species changed when the modelling species distributions under the current climate and climate scenarios projected for 2050 and compared the importance of environmental characteristics to each species to investigate how habitat selection contributes to distribution patterns. Because of the beneficial impacts of climate change on the demography of orchids at the northern edges of their distributions, we predict that potentially suitable areas will shift pole-wards or to higher elevations as the Earth's climate warms, possibly leading to range expansions under mild climate change. However, under severe climate change, orchid populations may no longer be buffered against changes in the climate at the warm edges of their distributions and therefore may be more susceptible to decline than more central populations, ultimately leading to range contractions.

2. Materials and Methods

2.1. Study Species

The four species studied here (*Orchis anthropophora*, *O. militaris*, *O. purpurea* and *O. simia*) belong to the so called 'anthropomorphic' group of the genus *Orchis* [25]. Although *O. anthropophora* displays pronounced differences in flower morphology (Figure 1), phylogenetic analyses based on DNA sequences have placed the four species within the same genus [25]. Before, *O. anthropophora* was assigned to the genus *Aceras*, of which it was the sole member [24]. In general, *O. anthropophora*, *O. purpurea* and *O. simia* prefer somewhat warmer conditions for growth and survival than *O. militaris*. As a result, *O. anthropophora*, *O. purpurea* and *O. simia* are species with a mainly Mediterranean distribution, whereas *O. militaris* has a more continental distribution, occurring from the Atlantic coast to Mongolia [24]. However, in grazed dry meadows and calcareous grasslands of Western Europe they can often be found growing together.

Figure 1. Overview of the four study species. From left to right: *Orchis anthropophora*, *Orchis militaris*, *Orchis purpurea*, and *Orchis simia*. All pictures courtesy of Daniel Tyteca.

All species except *O. anthropophora*, which is mainly pollinated by beetles, are visited by generalist pollinators such as bees and bumblebees and occasionally butterflies [26]. Fruit set in the four investigated *Orchis* species tends to be generally low (<20%) [26,27], but within a single fruit a substantial number of seeds can be found. The seeds require a mycorrhizal fungus for germination. The four *Orchis* species are mycorrhizal generalists that associate with a large number of mycorrhizal fungi, most often members of the Tulasnellaceae and Ceratobasidiaceae [28–32]. The four species also share a substantial proportion of their fungi, and as a result hybridization can be encountered in sympatric populations [24,33–35].

2.2. Occurrence Data and Predictor Variables

We acquired the GPS coordinates recorded for each species in Europe from the years 1999–2019 available from the GBIF online repository (Global Biodiversity Information Facility; www.GBIF.org). After removing the records with missing data or a spatial resolution lower than 100 m, we aggregated the locality points for each species into a 5 km grid squares to reduce the effects of spatial clustering and sampling bias using QGIS v3.4 [36]. After aggregation, we took the midpoint of each 5 km grid square, resulting in each species having between 1350 and 4315 occurrence records to be used in modelling.

The mean annual temperature and annual rainfall of the study area were downloaded as rasters from the WorldClim Bioclim database (http://worldclim.org/version1) [37]. One raster of dominant bedrock type (a categorical variable) [38] (https://esdac.jrc.ec.europa.eu/resource-type/european-soil-database-maps) and twelve of derived topsoil characteristics were obtained from the European Soil Data Centre (ESDAC) [39,40] (https://ec.europa.eu/eurostat/web/lucas/data/primary-data/2018; https://esdac.jrc.ec.europa.eu/content/european-soil-database-derived-data). A principal component analysis (PCA) was performed on each set of six physical (relating to texture and water availability) and six biochemical (biochemical levels and pH) soil rasters and the first two components of the two PCAs were used in the modelling. An elevation raster was acquired from the EarthEnv online repository [41] (https://www.earthenv.org/topography). Raster alignment and cropping was performed in R v3.6.2 [42] using the 'RStoolbox' [43] and 'raster' [37] packages.

2.3. Maxent Modelling

The ecological niche of each species was modelled in Maxent v3.4.1 [44] using the processed occurrence data and environmental rasters. Maxent uses the concept of maximum entropy to estimate the probability distribution of species occurrences given the environmental predictor variables of the occupied pixels, and then projects the probability of a species occurring in each pixel to the entire study site as a measure of habitat suitability [45]. Seventy five percent of the data were used to train the model and the remaining 25% to test, using a random seed, 100 bootstrap replicates and leaving the remaining settings as the default [45,46]. The output includes a map of the predicted distribution of each species, the contribution of each variable to the distribution of the species, response curves of each species' occurrence to the environmental variables, and measures of fit such as the area under the receiver operating curve (AUC).

The models were then projected onto the climatic conditions of 2050 predicted by RCP (Representative Concentration Pathway) 2.6, RCP 4.5 and RCP 8.5. In RCP 2.6, carbon dioxide (CO_2) emissions start declining by 2020 and reach zero by 2100. In this scenario, global temperature rise is expected to stay below 2 °C by 2100. In RCP 4.5, greenhouse gas emissions peak around 2040, then decline, while in RCP 8.5 greenhouse gas emissions continue to rise throughout the 21st century. Under RCP 4.5 and 8.5, the global temperature is expected to rise between 2 and 3 °C and between 2.6 and 4.8 °C, respectively. Therefore, these models represent moderate (RCP 2.6 and RCP 4.5) to more extreme (RCP 8.5) scenarios of the range of future climate scenarios.

2.4. Data Analysis

We used ENMTools v1.3 [47] to calculate Levins' *B* value for 100 replicate ecological niche maps for each species. The mean Levins' *B* value was calculated to represent the niche breadth of each species, with values closer to 0 indicating narrow niche and values closer to 1 indicating wide niche breadth. A value of Schoener's *D* was calculated for each species pair in ENMTools to investigate the niche overlap among the four *Orchis* species, with values closer to 1 indicating more similar habitat preferences and values closer to 0 indicating less similar habitat preferences.

To calculate the area of suitable habitat available to each species, we extracted all the pixels above the maximum training sensitivity plus the specificity threshold from each mean Maxent output map, to give binary presence/absence maps for each species at each climate scenario. We used these maps to investigate the change in available habitat from the current climate to the three RCPs in 2050, and calculated the area of current habitat that would be lost if the species was not able to track the habitat changes in the future, using QGIS v3.4. The contributions of environmental variables to each species' habitat were visualized as a heat map using the package 'pheatmap' [48] in R.

3. Results

The data for all four species fit the Maxent models well, with all having an AUC value of at least 0.87. The suitable habitat (in terms of climate and soil) available to the four *Orchis* species was predicted by Maxent to cover most of the western European mainland, extending to Romania in the east, southern Poland in the north and the Mediterranean in the south, as well as parts of Spain and the United Kingdom (Figure 2). The northern distribution of the *O. militaris* habitat extended into Sweden, and this species had the largest current suitable habitat (2,465,675 km^2) of the four species, as well as the widest niche breadth (Levins' $B = 0.4687 \pm 0.0012$) (Table 1 and Figure 3). *Orchis simia* had the smallest suitable habitat available (1,791,875 km^2) and the narrowest niche breadth (0.2797 ± 0.0011) (Table 1 and Figure 3). In terms of niche similarity, *O. purpurea* and *O. anthropophora* demonstrated the highest similarity with an 85.3% overlap, while *O. simia* and *O. militaris* demonstrated the lowest (but still considerable) overlap of 64.2% (Table 2).

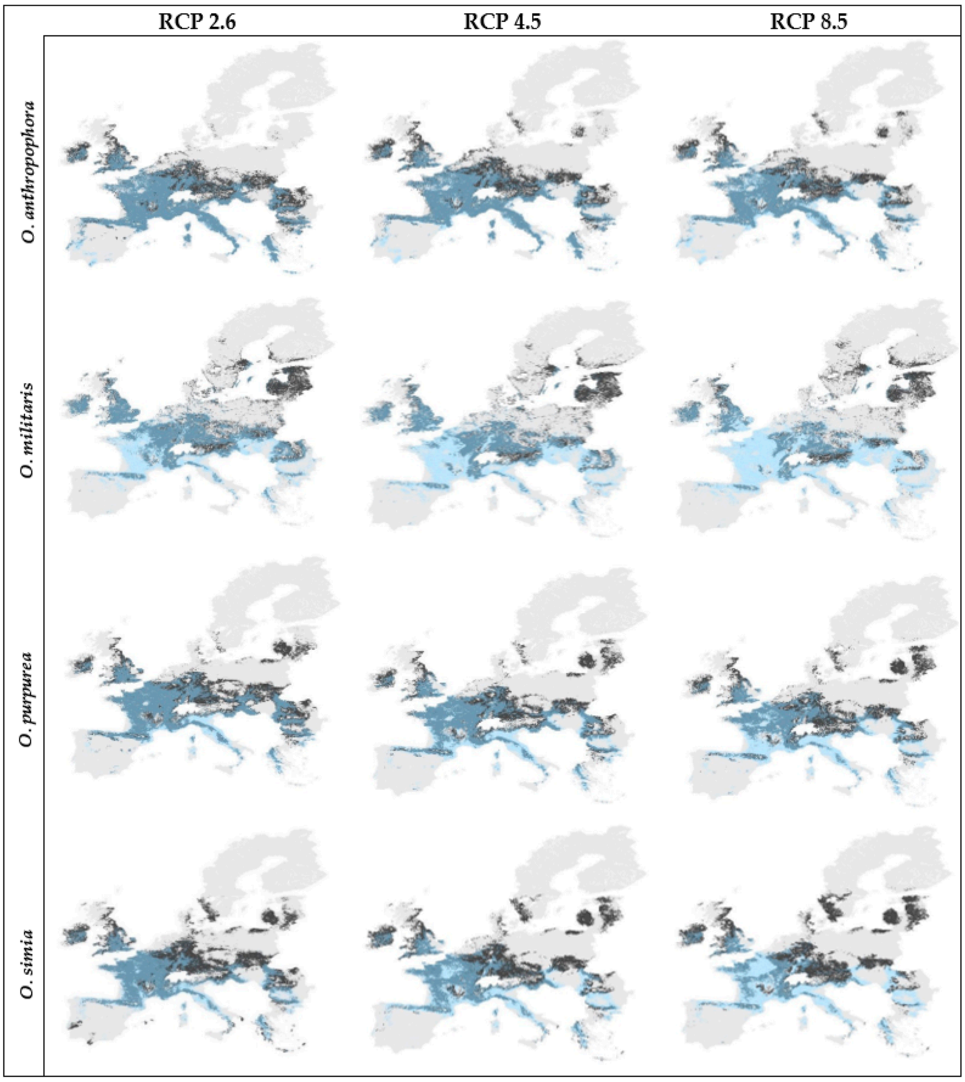

Figure 2. Habitat distributions for four *Orchis* species in Europe, predicted by Maxent based on abiotic environmental variables, for the current climate and three increasingly severe climate scenarios predicted for 2050 (RCP 2.6, 4.5 and 8.5). Light blue areas represent the current distributions, black areas represent the future distributions and the dark blue areas represent the habitat that is available in both current and future scenarios.

Table 1. Levins' *B* value (niche breadth) and current area of suitable habitat (km^2) predicted for four *Orchis* species, as well as the potential habitat loss expected for 2050 if the species are unable to disperse into new areas with the same habitat characteristics as are currently occupied.

Species	Levins' *B*	Potential Habitat Loss (%)		
		RCP 2.6	RCP 4.5	RCP 8.5
Orchis anthropophora	0.3748 ± 0.0011	8.6087	12.2136	22.5989
Orchis militaris	0.4687 ± 0.0012	29.5588	36.8489	45.2645
Orchis purpurea	0.3912 ± 0.0008	22.3596	27.5207	38.8076
Orchis simia	0.2797 ± 0.0011	24.4939	37.1175	51.4098

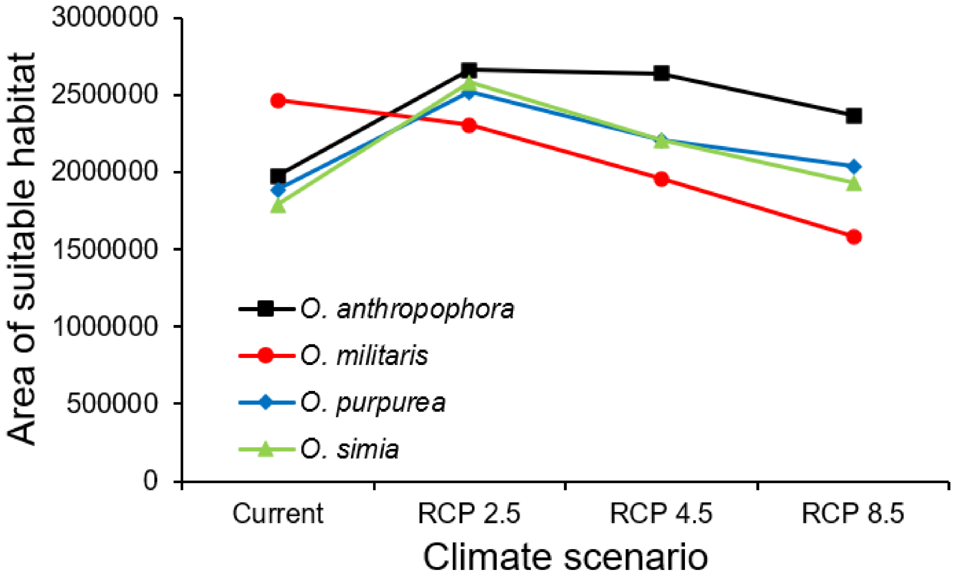

Figure 3. Current and predicted area of suitable habitat in 2050 for the four *Orchis* species under three different climate change scenarios (RCP (Representative Concentration Pathway) 2.6, RCP 4.5 and RCP 8.5).

Table 2. Overlap in the ecological niche between each *Orchis* species pair. Values closer to one indicate more similar habitat preferences.

Species	*Orchis anthropophora*	*Orchis militaris*	*Orchis purpurea*	*Orchis simia*
Orchis anthropophora	1	0.7073	0.8531	0.8032
Orchis militaris		1	0.7374	0.6423
Orchis purpurea			1	0.8331
Orchis simia				1

The high degree of niche similarity was reflected by the variable contributions output (Figure 4), with the four species reflecting similarly weak associations with bedrock, elevation and two of the soil components, while being more affected by the first two soil components (pH and potassium level, and soil texture), temperature and precipitation (Figure 4). *Orchis simia* had a notably strong association (36%) with temperature and *O. militaris* with the primary biochemical component (pH and potassium level, 32%). The mean annual temperatures and annual precipitation of the habitats predicted for the four species were similar to one another, with *O. militaris* occupying areas with the lowest temperature of 9.4 ± 0.04 °C and *O. anthropophora* the highest of 10.9 ± 0.06 °C (Table 3). Precipitation levels were also similar among the species, with *O. militaris* occupying areas with the highest precipitation of 800.7 ± 3.88 mm^3 and *O. purpurea* the lowest of 761.3 ± 2.04 mm^3.

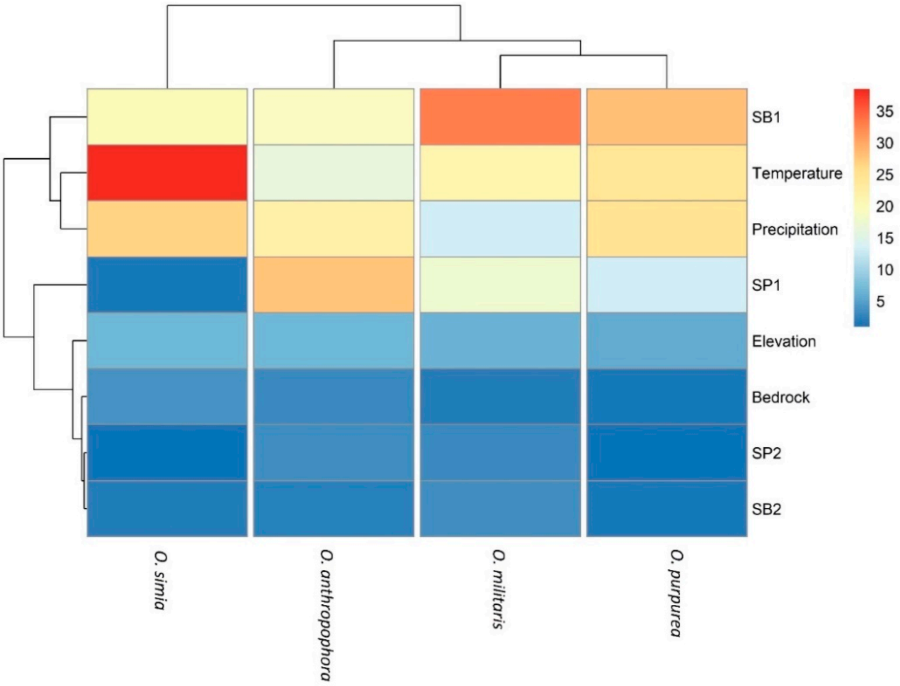

Figure 4. Heatmap of variable importance for the ecological niche model of each *Orchis* species. Red and orange cells indicate a higher dependence of the species' occurrence on the corresponding habitat variable and blue cells indicate low dependence. The environmental variables used are mean annual temperature, annual precipitation, elevation, bedrock type, and the first two axes of a principal component analysis of a dataset of physical soil characteristics (SP1, SP2) and of a biochemical soil dataset (SB1, SB2).

Table 3. Mean values of the climatic variables for each *Orchis* species habitat.

Species	Mean Annual Temperature (°C)	Annual Precipitation (mm^3)
Orchis anthropophora	10.89 ± 0.06	795.84 ± 3.41
Orchis militaris	9.42 ± 0.04	800.67 ± 3.88
Orchis purpurea	10.63 ± 0.03	761.29 ± 2.04
Orchis simia	10.79 ± 0.06	785.20 ± 5.24

The area of suitable habitat predicted for 2050 increased for *O. anthropophora*, *O. purpurea* and *O. simia* by an average of 703,216.7 ± 47,295.3 km^2 for RCP2.6, 468,183.3 ± 102,112.6 km^2 for RCP4.5 and 226,983.3 ± 82,144.5 km^2 for RCP8.5 (Figure 3). For these species, the distribution of habitat expanded into the north, reaching southern Sweden and the northern United Kingdom, and continued in the central latitudes of mainland Europe, and disappeared in parts of the Mediterranean region and western Europe (Figure 2). The habitat of *O. militaris* decreased by 15,890, 507,850 and 878,550 km^2 for the respective climate scenarios (Figure 3), with the northern limits of the distribution extending further into Estonia and Latvia, but diminishing considerably in western and eastern mainland Europe. If the species were not able to track the climate northwards, the area of current habitat would decrease in 2050 for the four *Orchis* species by 19.3 ± 4.5, 24.5 ± 5.7 and 36.7 ± 8.0% for each climate scenario, respectively (Table 1). *O. militaris* would be particularly negatively affected, with its available habitat decreasing by 33.6% in the most optimistic climate scenario (RCP2.6) and 61.3% in the worst-case scenario (RCP8.5).

4. Discussion

4.1. Changes in Distribution Area

The distribution ranges of the Mediterranean species *O. anthropophora*, *O. purpurea* and *O. simia* were predicted to increase under mild climate change, while that of the more continental *O. militaris* was predicted to decrease. These results are in line with demographic studies that have shown that milder winters and wetter springs have a positive impact on the population growth rate of orchids growing at the leading edge of their distributions [22,23]. Two populations of *Orchis purpurea* at the northern edge of their distributions showed population growth rates that were consistently above 1.0 between 2004 and 2015, indicating that the prevailing climatic conditions during that period were favorable for orchid growth [23] (Williams et al. 2015). Similarly, climate change was predicted to increase the future population growth rates of *Himantoglossum hircinum* at the northern edge of its distribution in the UK [22]. Here, the species benefits from the slightly warmer climate throughout the year and less precipitation in summer. The number of populations of this species has increased from 10 to 17 between 1988 and 2000 and has continued to rise to at least 26 populations by 2015 [22].

With the climate becoming more benign, novel habitats that were predicted to become suitable for growth included large areas of Estonia, Finland and Sweden. These areas currently already support a large number of orchid species that often co-occur with the investigated species in more southern areas (e.g., *Anacamptis morio*, *Orchis mascula*, *Gymnadenia conopsea*), suggesting that edaphic and habitat conditions are suitable to sustain orchid growth. Under severe climate change, suitable habitats were predicted to disappear at the rear edge of the distribution, most notably in Southern Italy, Croatia and Greece. In these areas, climatic conditions were predicted to no longer sustain the growth of these orchid species. Although the precise mechanisms leading to the disappearance of these species at southern edges is unknown, it is likely that increased drought has a strong negative effect on seed germination, survival and flowering. Previous research has indeed shown that drought negatively affects the probability of flowering and hence fecundity [23].

4.2. Role of Climatic vs. Abiotic Variables

Previous research has shown that the ecological niche of orchids is a function of precipitation and temperature, altitude, soil composition, bedrock and vegetation type [49–54]. Using eight different environmental and climatic variables, our results showed that soil biochemistry and climate were the most important variables determining the distribution of the four *Orchis* species, whereas the underlying bedrock and altitude only played a minor role, suggesting that the species can occur both in lowland and mountainous areas. This study modeled the habitat available to species in 2050 based on abiotic environmental factors, but did not cover whether the species would actually be able to expand north into these climatically suitable areas given that there are likely anthropogenic and biotic factors that will limit this. It is, therefore, also important to look at the habitat associations of species, because although *O. militaris* was the only species of the four which demonstrated a loss in total habitat, whilst for the more severe climate scenarios, *O. simia* and *O. purpurea* showed the greatest latitudinal shift in habitat, and the strong association of *O. simia* occurrence with temperature and precipitation likely means that in the long term or with severe changes in climate, this species could be very much affected by climate change.

4.3. Colonization Potential

For the species that have limited dispersal capabilities or those with habitats that have become largely fragmented, keeping track of optimal habitat conditions may be difficult or even impossible [55], and these species may ultimately go extinct if they do not adapt to changing climatic conditions. However, seed dispersal in orchids may occasionally occur over fairly large distances [56], and once populations have established, they can quickly expand. *Orchis simia*, for example, managed to colonize the Netherlands in 1972 and establish a viable population [57]. The nearest natural population was thought to be 50 km away. Similarly, a single flowering plant of *O. simia* and two non-flowering rosettes were found in 1974 in a dune area in east Yorkshire, England, more than 250 km north of the nearest site in the Thames valley [58]. A large population of *O. militaris* was found in a disused chalkpit near Mildenhall, Suffolk, England, in 1955, some 100 km from its previously known site. These and other examples [56] indicate that orchids are capable of sporadically crossing large distances and establishing novel populations at large distances from existing populations.

4.4. What about Crucial Interactions?

For orchid populations to colonize new habitats and to persist in the long term, partnerships with at least two different organisms need to be established. Interactions with mycorrhizal fungi are needed to facilitate germination and subsequent establishment as a seedling, and pollinators are required to pollinate the flowers and hence to produce seeds. Failure to pollinate the flowers will negatively affect fecundity and hence the recruitment of new individuals. A recent study has modeled the distributions of two sexually deceptive orchid species and their unique pollinator under climate change [59]. Results showed that including the interaction with the pollinator led to pronounced differences in the distribution range under climate change. However, in this case, both orchid species were pollinated by a single insect species, which is unlikely to be the case in the four studied *Orchis* species. The four studied orchid species are pollinated by generalist pollinators such as bees and bumblebees that are attracted to the flowers by their color or form, but quickly learn to avoid them as they do not provide any reward [27]. For example, the flowers of *O. militaris* have been shown to be visited by at least 49 different insect species, including hoverflies, bumblebees and bee flies [60]. However, most of these insects probably did not function as an effective pollinator, and pollinia were only observed in two species (*Apis mellifera* and *Bombus lapidarius*). Nonetheless, these insect species have very broad distribution ranges and therefore are probably not limiting their fruit set at potentially novel growth locations.

The germination of orchid seeds generally requires the establishment of a mycorrhiza [61,62]. Previous research has shown that the investigated *Orchis* species tend to be mycorrhizal generalists that associate with a large number of fungi [27–31]. Moreover, the seeds of *O. militaris* were able to germinate at mine tailing hills where the species did previously not occur, suggesting that the mycorrhizal fungi needed to facilitate seed germination are widespread and not necessarily limiting the distribution of the orchid [63]. Similar results have been observed for several species of the orchid genus *Epipactis*. Seed introduction experiments using seed packages showed that local growth conditions had little influence on germination patterns, and seedlings were found in more habitats than expected from the adults' ecology [64]. However, it should be noted that most seed introduction experiments using seed packages usually do not monitor the subsequent growth to the adult stage, so it remains unclear whether some habitat patches may be only temporarily suitable or whether introduced seeds germinating in seed packets would establish and form self-sustaining populations [62].

To unambiguously know whether orchid populations can establish and persist in habitats that have been predicted to become suitable in the future, species distribution models are ideally combined with seed introduction or transplant experiments. For example, a recent study that simultaneously applied an SDM (species distribution model) using high-resolution spatial predictors, and an integral projection (demographic) model, based on a transplant experiment, in central Sweden, showed that the predicted habitat suitability and population growth rate, yielded by the two approaches, were not correlated across the transplant sites at the cold range margin [65]. These results suggest that local microclimate, light and soil conditions may have a large effect on the distribution and performance of plant species and that mere extrapolation of suitable habitat from SDMs is likely to generate some spurious results [65]. However, orchids transplant experiments are not easy to conduct, and preferably, introduction experiments should start from seeds.

4.5. Implications for Conservation and Future Perspectives

Using environmental niche modeling, our results showed that orchid populations at the warm edge of their distribution range are bound to decline under severe climate change, and even if such extreme scenarios may be unlikely in the future [66], warrant for more detailed research on the demography, population genetics and adaptive potential of range edge populations. Only a few studies have compared demographic rates across the entire distribution range of species, and some of these have shown that populations may be buffered against climatic change. However, at present no such studies are available for orchids, and we currently do not know whether demographic buffering mitigates the negative impact of climatic variation and helps orchid populations at the warm edge of their distribution to persist in an increasingly variable environment. Second, orchids critically rely on mycorrhizal fungi for germination and seedling establishment, however, we virtually know nothing about the global distribution patterns of orchid mycorrhizal fungi and how they affect the ability of orchids to shift their distribution range under climate change. We also do not know how the distribution range of the fungi themselves will be affected by climate change. Previous research has already shown that orchid mycorrhizal communities vary across large geographic distances and generally decrease in species richness with increasing latitude [67]. More extensive datasets about the distribution of orchid mycorrhizal fungi need to be generated in order to define the environmental variables determining the distribution of fungi and orchids relying on these fungi.

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References

1. Gaston, K.J. *The Structure and Dynamics of Geographic Ranges*; Oxford University Press: Oxford, UK, 2003.
2. Sexton, J.P.; Montiel, J.; Shay, J.E.; Stephens, M.R.; Slatyer, R.A. Evolution of ecological niche breadth. *Annu. Rev. Ecol. Evol. Syst.* **2017**, *48*, 183–206. [CrossRef]
3. Chen, I.C.; Hill, J.K.; Ohlemüller, R.; Roy, D.B.; Thomas, C.D. Rapid range shifts of species associated with high levels of climate warming. *Science* **2011**, *333*, 1024–1026. [CrossRef] [PubMed]
4. Scheffers, B.R.; De Meester, L.; Bridge, T.C.L.; Hoffmann, A.A.; Pandolfi, J.M.; Corlett, R.T.; Butchart, S.H.M.; Pearce-Kelly, P.; Kovacs, K.M.; Dudgeon, D.; et al. The broad footprint of climate change from genes to biomes to people. *Science* **2016**, *354*, 719. [CrossRef]
5. Hampe, A.; Petit, R.J. Conserving biodiversity under climate change: The rear edge matters. *Ecol. Lett.* **2005**, *8*, 461–467. [CrossRef]
6. Doak, D.F.; Morris, W.F. Demographic compensation and tipping points in climate-induced range shifts. *Nature* **2010**, *467*, 959–962. [CrossRef] [PubMed]
7. Lesica, P.; Crone, E.E. Arctic and boreal plant species decline at their southern range limits in the Rocky Mountains. *Ecol. Lett.* **2017**, *20*, 166–174. [CrossRef] [PubMed]
8. Vilà-Cabrera, A.; Premoli, A.C.; Jump, A.S. Refining predictions of population decline at species' rear edges. *Glob. Chang. Biol.* **2019**, *25*, 1549–1560. [CrossRef] [PubMed]
9. Guisan, A.; Tingley, R.; Baumgartner, J.B.; Naujokaitis-Lewis, I.; Sutcliffe, P.R.; Tulloch, A.I.T.; Regan, T.J.; Brotons, L.; McDonald-Madden, E.; Mantyka-Pringle, C.; et al. Predicting species distributions for conservation decisions. *Ecol. Lett.* **2013**, *16*, 1424–1435. [CrossRef] [PubMed]
10. Ehrlén, J.; Morris, W.F. Predicting changes in the distribution and abundance of species under environmental change. *Ecol. Lett.* **2015**, *18*, 303–314. [CrossRef]

11. Merow, C.; Latimer, A.M.; Wilson, A.M.; McMahon, S.M.; Rebelo, A.G.; Silander, J.A. On using integral projection models to generate demographically driven predictions of species' distributions: Development and validation using sparse data. *Ecography* **2014**, *37*, 1167–1183. [CrossRef]
12. Franklin, J. Predictive vegetation mapping: Geographic modelling of biospatial patterns in relation to environmental gradients. *Prog. Phys. Geogr.* **1995**, *19*, 474–499. [CrossRef]
13. Guisan, A.; Zimmermann, N.E. Predictive habitat distribution models in ecology. *Ecol. Model.* **2000**, *135*, 147–186. [CrossRef]
14. Guisan, A.; Thuiller, W. Predicting species distribution: Offering more than simple habitat models. *Ecol. Lett.* **2005**, *8*, 993–1009. [CrossRef]
15. Elith, J.; Leathwick, J.R. Species distribution models: Ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* **2009**, *40*, 677–697. [CrossRef]
16. Bush, A.; Mokany, K.; Catullo, R.; Hoffmann, A.; Kellermann, V.; Sgro, C.; McEvey, S.; Ferrier, S. Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. *Ecol. Lett.* **2016**, *19*, 1468–1478. [CrossRef]
17. Christenhusz, M.J.M.; Byng, J.W. The number of known plants species in the world and its annual increase. *Phytotaxa* **2016**, *261*, 201–217. [CrossRef]
18. Swarts, N.D.; Dixon, K.W. Terrestrial orchid conservation in the age of extinction. *Ann. Bot.* **2009**, *104*, 543–556. [CrossRef]
19. Gale, S.W.; Fischer, G.A.; Cribb, P.J.; Fay, M.F. Orchid conservation: Bridging the gap between science and practice. *Bot. J. Linn. Soc.* **2018**, *186*, 425–434. [CrossRef]
20. Shefferson, R.P.; Jacquemyn, H.; Kull, T.; Hutchings, M.J. The demography of terrestrial orchids: Life history, population dynamics and conservation. *Bot. J. Linn. Soc.* **2020**, *192*, 315–332. [CrossRef]
21. Pfeifer, M.; Wiegand, K.; Heinrich, W.; Jetschke, G. Long-term demographic fluctuations in an orchid species driven by weather: Implications for conservation planning. *J. Appl. Ecol.* **2006**, *43*, 313–324. [CrossRef]
22. van der Meer, S.; Jacquemyn, H.; Carey, P.D.; Jongejans, E. Recent range expansion of a terrestrial orchid corresponds with climate-driven variation in its population dynamics. *Oecologia* **2016**, *181*, 435–448. [CrossRef] [PubMed]
23. Williams, J.L.; Jacquemyn, H.; Ochocki, B.M.; Brys, R.; Miller, T.E.X. Life history evolution under climate change and its influence on the population dynamics of a long-lived plant. *J. Ecol.* **2015**, *103*, 798–808. [CrossRef]
24. Kretzschmar, H.; Eccarius, W.; Dietrich, H. *The Orchid Genera Anacamptis, Orchis, Neotinea: Phylogeny, Taxonomy, Morphology, Biology, Distribution, Ecology and Hybridisation*; EchinoMedia: Bürgel, Germany, 2007.
25. Bateman, R.M.; Hollingsworth, P.M.; Preston, J.; Yi-Bo, L.; Pridgeon, A.M.; Chase, M.W. Molecular phylogenetics and evolution of Orchidinae and selected Habenariinae (Orchidaceae). *Bot. J. Linn. Soc.* **2003**, *142*, 1–40. [CrossRef]
26. Claessens, J.; Kleynen, J. *The Flower of the European Orchid: Form and Function*; Jean Claessens & Jacques Kleynen: Voerendaal, The Netherlands, 2011; pp. 137–144.
27. Jacquemyn, H.; Brys, R. Lack of strong selection pressures maintains wide variation in floral traits in a food-deceptive orchid. *Ann. Bot.* **2020**, in press. [CrossRef] [PubMed]
28. Jacquemyn, H.; Honnay, O.; Cammue, B.P.A.; Brys, R.; Lievens, B. Low specificity and nested subset structure characterize mycorrhizal associations in five closely-related species of the genus *Orchis*. *Mol. Ecol.* **2010**, *19*, 4086–4095. [CrossRef] [PubMed]
29. Jacquemyn, H.; Brys, R.; Hutchings, M.J. Biological flora of the British Isles: *Orchis anthropophora* (L.) All. (*Aceras anthropophorum* (L.) W.T. Aiton). *J. Ecol.* **2011**, *99*, 1551–1565. [CrossRef]
30. Jacquemyn, H.; Merckx, V.; Brys, R.; Tyteca, D.; Cammue, B.P.A.; Honnay, O.; Lievens, B. Analysis of network architecture reveals phylogenetic constraints on mycorrhizal specificity in the genus *Orchis* (Orchidaceae). *New Phytol.* **2011**, *192*, 518–528. [CrossRef]
31. Jacquemyn, H.; Brys, R.; Cammue, B.P.A.; Honnay, O.; Lievens, B. Mycorrhizal associations and reproductive isolation in three closely-related *Orchis* species. *Ann. Bot.* **2011**, *107*, 347–356. [CrossRef]
32. Oja, J.; Kohout, P.; Tedersoo, L.; Kull, T.; Kõljalg, U. Temporal patterns of orchid mycorrhizal fungi in meadows and forests as revealed by 454 pyrosequencing. *New Phytol.* **2015**, *205*, 1608–1618. [CrossRef]

33. Schatz, B.; Geoffroy, A.; Dainat, B.; Bessiere, J.M.; Buatois, B.; Hossaert-McKey, M.; Selosse, M.A. A case study of modified interactions with symbionts in a hybrid Mediterranean orchid. *Am. J. Bot.* **2010**, *97*, 1278–1288. [CrossRef]
34. Jacquemyn, H.; Brys, R.; Honnay, O.; Roldán-Ruiz, I.; Lievens, B.; Wiegand, T. Non-random spatial structuring of orchids in a hybrid zone of three *Orchis* species. *New Phytol.* **2012**, *193*, 454–464. [CrossRef] [PubMed]
35. Jacquemyn, H.; Brys, R.; Honnay, O.; Roldán-Ruiz, I. Asymmetric gene introgression in two closely related *Orchis* species: Evidence from morphometric and genetic analyses. *BMC Evol. Biol.* **2012**, *12*, 178. [CrossRef] [PubMed]
36. QGIS Development Team. *QGIS Geographic Information System*; Open Source Geospatial Foundation Project: Chicago, IL, USA, 2019.
37. Hijmans, R.J.; Cameron, S.E.; Parra, J.L.; Jones, P.G.; Jarvis, A.; Richardson, K. *WorldClim Version 1.3*; University of California: Berkeley, CA, USA, 2005.
38. Van Liedekerke, M.; Jones, A.; Panagos, P. *ESDBv2 Raster Library—A Set of Rasters Derived from the European Soil Database Distribution v2. 0*; CD-ROM, EUR 19945 EN; European Commission and the European Soil Bureau Network: Ispra, Italy, 2006.
39. Ballabio, C.; Lugato, E.; Fernandez-Ugalde, O.; Orgiazzi, A.; Jones, A.; Borrelli, P.; Montanarella, L.; Panagos, P. Mapping LUCAS topsoil chemical properties at European scale using Gaussian process regression. *Geoderma* **2019**, *355*, 113912. [CrossRef] [PubMed]
40. Hiederer, R. *Mapping Soil Properties for Europe—Spatial Representation of Soil Database Attributes*; EUR26082EN Scientific and Technical Research series; Publications Office of the European Union: Luxembourg, 2013.
41. Amatulli, G.; Domisch, S.; Tuanmu, M.N.; Parmentier, B.; Ranipeta, A.; Malczyk, J.; Jetz, W. A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Sci. Data* **2018**, *5*, 180040. [CrossRef]
42. R Core Development Team. *R: A Language and Environment for Statistical Computing (Version 3.6.2)*; R Foundation for Statistical Computing: Vienna, Austria, 2019. Available online: http://www.R-project.org (accessed on 15 January 2020).
43. Leutner, B.; Horning, N.; Schwalb-Willmann, J.; Hijmans, R. *RStoolbox: Tools for Remote Sensing Data Analysis*, R package version 0.1 7; R Foundation for Statistical Computing: Vienna, Austria, 2017.
44. Phillips, S.J.; Anderson, R.P.; Dudík, M.; Schapire, R.E.; Blair, M.E. Opening the black box: An open-source release of Maxent. *Ecography* **2017**, *40*, 887–893. [CrossRef]
45. Merow, C.; Smith, M.J.; Silander, J.A. A practical guide to MaxEnt for modeling species ′ distributions: What it does, and why inputs and settings matter. *Ecography* **2013**, *36*, 1058–1069. [CrossRef]
46. Barbet-Massin, M.; Jiguet, F.; Albert, C.H.; Thuiller, W. Selecting pseudo-absences for species distribution models: How, where and how many? *Methods Ecol. Evol.* **2012**, *3*, 327–338. [CrossRef]
47. Warren, D.L.; Glor, R.E.; Turelli, M. ENMTools: A toolbox for comparative studies of environmental niche models. *Ecography* **2010**, *33*, 607–611. [CrossRef]
48. Kolde, R. *Pheatmap: Pretty Heatmaps*, R package version 1.0.8; R Foundation for Statistical Computing: Vienna, Austria, 2015.
49. Djordjević, V.; Tsiftsis, S.; Lakušić, D.; Jovanović, S.; Stevanović, V. Factors affecting the distribution and abundance of orchids in grasslands and herbaceous wetlands. *Syst. Biodivers.* **2016**, *14*, 355–370. [CrossRef]
50. McCormick, M.K.; Whigham, D.F.; O'Neill, J.P.; Becker, J.J.; Werner, S.; Rasmussen, H.N.; Bruns, T.D.; Taylor, D.L. Abundance and distribution of *Corallorhiza odontorhiza* reflect variations in climate and ectomycorrhizae. *Ecol. Monogr.* **2009**, *79*, 619–635. [CrossRef]
51. Acharya, K.P.; Vetaas, O.R.; Birks, H.J.B. Orchid species richness along Himalayan elevational gradients. *J. Biogeogr.* **2011**, *38*, 1821–1833. [CrossRef]
52. Tsiftsis, S.; Tsiripidis, I.; Karagiannakidou, V.; Alifragis, D. Niche analysis and conservation of the orchids of east Macedonia (NE Greece). *Acta Oecol.* **2008**, *33*, 27–35. [CrossRef]
53. Bowles, M.; Zettler, L.; Bell, T.; Kelsey, P. Relationships between soil characteristics, distribution and restoration potential of the federal threatened eastern prairie fringed orchid, *Platanthera leucophaea* (Nutt.) Lindl. *Am. Midl. Nat.* **2005**, *154*, 273–286. [CrossRef]
54. Štípková, Z.; Romportl, D.; Černocká, V.; Kindlmann, P. Factors associated with the distributions of orchids in the Jeseníky Mountains, Czech Republic. *Eur. J. Environ. Sci.* **2017**, *7*, 135–145. [CrossRef]

55. Honnay, O.; Verheyen, K.; Butaye, J.; Jacquemyn, H.; Bossuyt, B.; Hermy, M. Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecol. Lett.* **2002**, *5*, 525–530. [CrossRef]
56. Arditti, J.; Ghani, A.K.A. Tansley Review No. 110. Numerical and physical properties of orchid seeds and their biological implications. *New Phytol.* **2000**, *145*, 367–421. [CrossRef]
57. Willems, J.H. Establishment and development of a population of *Orchis simia* Lamk. in The Netherlands, 1972 to 1981. *New Phytol.* **1982**, *91*, 757–765. [CrossRef]
58. Crackles, E. The Monkey Orchid in Yorkshire. *Naturalist* **1975**, *932*, 25–26.
59. Tsiftsis, S.; Djordjević, D. Modelling sexually deceptive orchid species distributions under future climates: The importance of plant-pollinator interactions. *Sci. Rep.* **2020**, *10*, 10623. [CrossRef]
60. Henneresse, T.; Tyteca, D. Insect visitors and potential pollinators of *Orchis militaris* (Orchidaceae) in Southern Belgium. *J. Insect Sci.* **2016**, *16*, 104. [CrossRef]
61. Rasmussen, H.N. *Terrestrial Orchids: From Seed to Mycotrophic Plant*; Cambridge University Press: Cambridge, UK, 1995.
62. McCormick, M.K.; Jacquemyn, H. What constrains the distribution of orchid populations? *New Phytol.* **2014**, *202*, 392–400. [CrossRef]
63. Shefferson, R.P.; Kull, T.; Tali, K. Mycorrhizal interactions of orchids colonizing Estonian mine tailing hills. *Am. J. Bot.* **2008**, *95*, 156–164. [CrossRef] [PubMed]
64. Těšitelová, T.; Těšitel, J.; Jersáková, J.; Říhová, G.; Selosse, M.A. Symbiotic germination capability of four *Epipactis* species (Orchidaceae) is broader than expected from adult ecology. *Am. J. Bot.* **2012**, *99*, 1020–1032. [CrossRef] [PubMed]
65. Greiser, C.; Hylander, K.; Meineri, E.; Luoto, M.; Ehrlén, J. Climate limitation at the cold edge: Contrasting perspectives from species distribution modelling and a transplant experiment. *Ecography* **2019**, *43*, 637–647. [CrossRef]
66. Hausfather, Z.; Peters, G.P. Emissions—The 'business as usual' story is misleading. *Nature* **2020**, *577*, 618–620. [CrossRef]
67. Duffy, K.J.; Waud, M.; Schatz, B.; Petanidou, T.; Jacquemyn, H. Latitudinal variation in mycorrhizal diversity associated with a European orchid. *J. Biogeogr.* **2019**, *46*, 968–980. [CrossRef]