Mating system and niche breadth in sister species of *Erythronium* in the Pacific Northwest: a study using Ecological Niche Modelling

by

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Abstract

Ecological niche models were used to compare the climatic niche breadths of *Erythronium oregonum* & *Erythronium revolutum*, sister species in the family Liliaceae native to western North America. The former is more outcrossing, while the latter is more inclined to self-pollinate. Herbarium records and iNaturalist data were compiled and fed into the niche modelling software Maxent. Analysis of the output reveals that the selfer, *E. revolutum*, occupies a broader niche than the outcrosser, *E. oregonum*. Further niche characterization demonstrates that the two sisters are divided in their climatic preferences and constraints, with *E. revolutum* favouring cooler, wetter, and less seasonal conditions. Possible reasons for this difference in niche breadth are discussed, although much historical, genetic, and biotic context remains open to further research.

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Acknowledgements

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Thanks to the generations of herbarium collectors who have picked hundreds of lilies and faithfully recorded where. Finally, thanks to the nameless masses on iNat: all of your casual weekend iPhone photos have added up into something bordering on science!

Introduction

The ecological niche breadth of a given taxon refers to the range of conditions that it can successfully occupy (Sexton *et al.*, 2017). Species zhave a set of optimal conditions under which their fitness is maximized, and as the conditions diverge from the ideal in either direction their fitness decreases (Lynch & Gabriel, 1987). Barring other limitations, a species distribution would be expected to mirror its niche breadth, surrounded on all sides by conditions that are inhospitable to it (Proulx, 1999). In the real world, while distribution size and niche breadth are correlated (Slatyer et al., 2013), species can be adapted to a narrow but widespread niche or have broad tolerances but be confined by geographic barriers (Peterson et al., 2011; Saupe et al., 2015).

As climate envelopes shift, habitats are fragmented, and alien species expand, the study of how niche breadth changes over time and how it can contribute to a species' expansion or extinction could help model future range shifts or select refugia for assisted migration (Sexton *et al.*, 2017). This is especially relevant to sessile organisms such as plants. Over large time scales the niche breadths of taxa are in flux and they can diverge rapidly between plant species within a single genus (Grossenbacher et al., 2014; Suarez-Mota & Villasenor, 2020). This suggests that the pressures upon individuals to maintain a broad tolerance to environmental conditions are subject to change, perhaps based on traits of the lineages involved, or on the stability of the environments the organisms inhabit.

Mutations that affect colonization ability, whether by changing the capacity of individual genotypes to disperse, adapt, or maintain genetic diversity, should impact the niche breadth of a taxon (Gaston, 2003). In flowering plants, mating system is thought to affect colonization ability (Pannell, 2015). Plant mating systems can determine the relative importance of inter- and intrapopulation genetic diversity within a species as well as its reliance on third-party pollination (St. Onge et al., 2011; Pettengill et al., 2016).

Taxa with a greater capacity to reproduce through self-fertilization (selfers), have been shown to have larger distributions than their more outcrossing counterparts in many cases (Randle et al., 2009). A broad analysis of hundreds of species from 15 different plant families found species with higher selfing ability consistently had larger ranges than related species with more reliance on outcrossing (Grossenbacher et al., 2015). The theoretical basis for this has been referred to as “Baker’s Law” (Stebbins, 1957). Baker (1955) suggested that plants with built-in reproductive assurance should be better equipped to expand from range peripheries with lower densities of mates and pollinators. Added complexity comes from the potential for outcrossing species to sabotage their own localized adaptation at range margins through homogenizing gene flow (gene swamping; Polechová & Barton, 2015; Polechová, 2018). This could slow or prevent diversifying evolution needed for niche expansion, although this concept has yet to find strong empirical support (Moerman et al., 2020).

Despite the diversity of flowering plant mating systems, there are very few species that are true obligate selfers, exclusively producing seeds from gametes originating in the same parent. It has been estimated that only 10-20% of flowering plants are >50% selfing (Wright *et al.*, 2013). The sheer prevalence of outcrossing suggests that selfing is disadvantageous in at least some cases. This has been attributed in part to reversed diversification associated with selfing's lack of recombination and higher vulnerability to genetic drift (Holt & Gaines, 1992). It could also come from low diversity associated with a recent origin. The transition from outcrosser to selfer is thought to be the most common change in mating system (Stebbins, 1974; Grant, 1981) and selfing lineages often emerge from outcrossing parents in their clade, so can be expected to be younger. In some cases outcrossers occupy broader niches than their selfing relatives within the same genus (Lowry & Lester, 2006).

Selfing plant taxa have been shown to have lower genetic diversity relative to outcrossers on average (Abbott & Gomes, 1989; Honnay & Jacquemyn, 2007; Lopez-Villalobos & Eckert, 2018), although their diversity between populations is the same or higher (Schoen & Brown, 1991; Pannell & Charlesworth, 2000). Populations with greater genetic diversity should tend to be more capable of adapting to novel environments (Fisher, 1930), and this would appear to predispose selfers to slower niche expansion over the long-term (David et al., 1993; Gamisch et al., 2015).

Self-pollination has been considered a homogenizing evolutionary dead-end (Stebbins, 1957; Takebayashi et al., 2001), although this perspective has been challenged (Igic & Busch, 2013; Hughes & Simons, 2015). It is important to make a distinction between obligate self-pollination, and mixed-mating systems in which unpollinated flowers have selfing as a backup. This type of mixed-mating system is common in flowering plants (Wright et al., 2013). Around 20% of flowering plants are predominantly selfing (Barrett 2002, 2010). Occasional outcrossing is thought to be important to the persistence of highly-selfing taxa, only a small amount of outcrossing can contribute significantly to genetic diversity (Ruane et al., 2020)

If autogamy increases fitness when mates or pollination are less available then we would expect to see localized selection for high selfing rates along range margins (García-Ramos & Kirkpatrick, 1997). Conversely, the vulnerability of geographically-peripheral populations to genetic drift may make gene flow from the range core advantageous (Polechová, 2018). Both of these statements make the assumption that peripheral populations will be smaller than central ones, known as the Abundant-center Hypothesis (ACH), an idea that has received lukewarm support theoretically (Dallas & Santini, 2020) and empirically (Herlihy & Eckert, 2015; Sexton et al., 2016). In at least some cases, however, the ACM premise has been demonstrated in the wild (Koski et al., 2019; Kennedy et al., 2021). Due to the heterogeneous nature of ranges, marginal habitat will not necessarily be geographically peripheral. Additionally, the assertion that a lack of pollen availability is a common limiting factor for peripheral populations has been recently challenged (Dawson-Glass & Hargreaves, 2022), although this has been supported by studies of some systems (Grindeland *et al*., 2005; Shao *et al*., 2008).

The prevalence and proximity of selfing-outcrossing sister species pairs suggests a budding speciation model in which selfing populations at range edges effectively speciate as their reproductive isolation increases (Stebbins, 1974; Grant, 1981; Anacker & Strauss, 2014). There is evidence that many distributions do follow a tolerance curve where peripheral populations struggle to reproduce through outcrossing under borderline abiotic conditions (Hargreaves et al., 2014). In some cases, selfing rates increase with distance from a proposed area of origin (Randle et al., 2009). The putative tendency of selfing lineages to bud from the periphery of an outcrossing sister/parent, partly preadapted to constraining conditions, would seem to put them in a position to rapidly expand in distribution. This could potentially lead to larger range sizes. If multiple highly-selfing lineages were to emerge from different points along a range margin with adaptations for slightly different abiotic conditions, rapid expansion and gradual genetic exchange between lineages through limited outcrossing could encourage an expansion in niche breadth over time.

Capacity to self-pollinate has been associated with high colonization ability in flowering plants (Pannell, 2015). It has been suggested that the limits placed by low heterozygosity on selfing lineages' adaptability may be offset by a rapid purging of deleterious alleles upon occupying novel conditions (Peterson & Kay, 2015). Inbreeding depression has been found to negatively correlate with distance from core range in some cases (Pujol et al., 2009). Whether this reduction is consistently associated with an increase in self-pollination is unknown. Self-pollination increases in prevalence on islands relative to adjacent mainland (Barrett, 1985; Martén-Rodriguez et al., 2015; Grossenbacher et al., 2017) and is also common among invasive species (van Kleunen & Johnson, 2007), implying a dispersal advantage. More highly-selfing plant species are known to have generally larger distributions than more outcrossing species (Grossenbacher, 2015) and species with larger ranges are generally better invaders (Randle et al., 2009; Grossenbacher, 2015). The extent to which observed elevated selfing rates in marginal populations are generally a result of demographic limitation (Moeller & Gaeber, 2005), protection of locally-optimized genotypes from recombination (Guo et al., 2009), or historical factors (Koski et al., 2019) is also not established.

It is uncertain whether the putative increased colonization ability of highly-selfing flowering plant species leads to them having a higher mean niche breadth. Some group-specific studies have found no correlation between niche breadth and mating system (Johnson et al., 2014; Evans & Jacquemyn, 2020). Other results favor selfers (Grant & Kalisz, 2020) or outcrossers (Lowry & Lester, 2006).

Ecological niche modelling (ENM), also referred to as species distribution modelling (SDM) in the literature, can be used to turn presence-only location data into a heat map of niche suitability for a given taxon. ENM has been used in other studies comparing niche breadth and mating system within groups (Grant & Kalisz 2020; Evans & Jacquemyn, 2020), and these models are common in the literature as a means of determining niche requirements. Here, I use the ENM program Maxent Version 3.4.4 (Phillips et al., 2022) to look specifically at the climatic component of niche breadth in comparing a selfing-outcrossing sister species pair: *Erythronium revolutum* (more selfing) and *Erythronium oregonum* (more outcrossing).

The assumption that there is a difference in selfing ability between the two species is based on two observations. First, that the herkogamy (distance between the stamens and gynoecium) is greater in *E. oregonum* than in *E. revolutum*. Herkogamy is related to mating system in related plant species (e.g. de Vos et al., 2018; Jimenez-Lobato, 2021), with a shorter distance increasing the chance that pollen will be incidentally transported from stamen to stigma. Secondly, observation of cultivated plants by Dr. Allen, has shown that *E. revolutum* reliably sets seed while *E. oregonum* does not do so.

E. oregonum and *E. revolutum* occupy distributions that are similar in latitudinal extent. Each follows a thin band of suitable habitat stretching from north-central California north to southern British Columbia (BC). They are generally allopatric but interfertile, and their differing habitat requirements are thought to be behind their continued separation as species (Allen & Antos, 1988). *E. revolutum* is found within 100km of the open Pacific coast (but less so inlets like Puget Sound), often much closer. It concentrates in moist forests, particularly in riparian areas (Washington: Camp & Gamon, 2011; California: Calflora, 2022; BC: Douglas et al., 1998). *E. oregonum* only approaches the open Pacific coast south of southern Oregon, preferring to roughly follow the lowlands comprising Willamette Valley, Puget Trough, and Georgia Depression to their northern terminus. It prefers mesic meadows and open woodland (Washington: Legler &

Giblin, 2022; California: Allen & Wetherwax, 2018; BC: Douglas et al., 1998). The difference in *Erythronium* species' tendency to self-pollinate is thought to be related to herkogamy (Allen, personal communication, February 28, 2022). Within *E. grandiflorum*, individuals with a greater distance between the anthers and stigma have a higher ratio of nonself- to self-origin pollen grains (Thomson & Stratton, 1985). These two Erythronium species have been shown to be each other's closest extant relative (sister species) through genetic analysis (Allen et al., 2003).

Figure 1. *Erythronium oregonum*, photo taken by Geraldine Allen.

Figure 2. *Erythronium revolutum*, photo taken by Dr. Geraldine Allen.

Methods

The Consortium of Pacific Northwest Herbaria, The Consortium of California Herbaria (I & II), and the Global Biodiversity Information Facility (GBIF) websites were consulted for location records of both target species. Records were removed that had latitudes and longitudes specified to two or fewer decimal places, which provides a minimum precision of <78 meters at the southern extent of the species distribution.

The bulk of the records used came from GBIF, which collects observations from the citizen science platform iNaturalist, as well as from more formal herbarium sources. iNaturalist data has been the basis for other biogeographical modelling efforts (e.g. Chapman et al., 2019). Even community-verified iNaturalist observations have the potential to be simultaneously inaccurate and within quality-controlled bounds for precision, making further culling necessary: observations were removed from locations that did not approximate the known range of the subject species. Only particularly egregious coordinates were removed to avoid confirmation bias: those in the ocean, east of the Cascades, south of the Bay Area, and North of Johnstone Strait (Figure 1.). While *E. revolutum* has been recorded from north of Johnstone Strait, these sites are at the heads of inlets on the southern BC coast, and the only points in the location data in the region were in alpine areas.

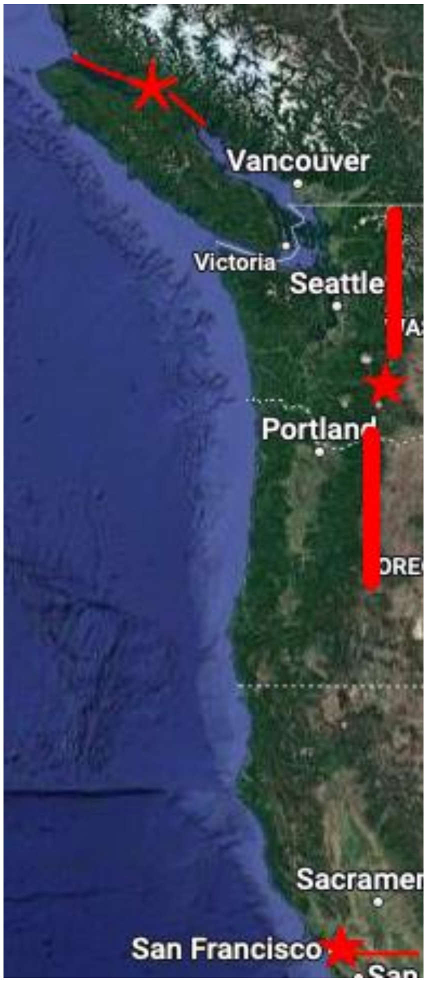


Figure 3. A satellite map of the study area Features used to define acceptable boundaries for location records are indicated.

The coastal distribution of these lilies and the inherent inaccuracy of coordinates, many predating GPS, led to many observations being placed a short distance into the ocean. These observations within ~60m of the shore (the largest distance in our data that could be accounted for by a lack of coordinate precision) were manually moved to the nearest land using the Vertex Editor Tool in QGIS 3.1.6 Hannover (QGIS.org, 2022).

From the location records, 2081 records for *E. oregonum* and 325 for *E. revolutum* were found to be acceptable for constructing the ENM. Both of these quantities are sufficient, occurrence numbers in the 100-200 range can be found in the literature (Stone & Wolfe, 2021), and elevation values are necessary at each point in order to characterize its climate. These were not provided for the majority of records, so the QGIS Point Sampling Tool was used to evaluate each vertex relative to a Digital Elevation Model downloaded from the United States Geographic Survey website.

ClimateNA (climatena.ca, Wang et al., 2016), a software that models the climate of North America gridwise from weather station data, was used to derive values for 265 climatic variables for each presence point, at a resolution of one kilometer. ClimateNA variables are, themselves, metrics derived from the same temperature and precipitation values, leading to high levels of correlation in some cases. It is thought that Maxent possesses some level of robustness with respect to this collinearity (Elith et al., 2010). There is support for using repeated runs of Maxent to isolate and progressively remove variables that do not contribute significantly to the model (Zeng et al., 2016). Despite this, expert pre-selection of ecologically relevant variables is recommended (Elith & Leathwick, 2009b) and outperforms the practice of leaving all variable thinning to the program itself (Zeng et al., 2016). Some sources also use a components analysis to aid in thinning (Grant & Kalisz, 2020).

Following Stone & Wolfe (2021), a Pearson's correlation matrix was used (one table for each species) to narrow the number of variables. This was done in Microsoft Excel 2011. Those variable combinations with *r* > 0.85 were grouped and the least derived of the set was retained. Ecological considerations informed further thinning, with input from Dr. Allen of the University of Victoria. A representative subset of 10 variables was isolated, with 2 having been thinned for making a less than 0.5% contribution to the final Maxent models.

Variable Code	Variable definition
CMD	Hargreaves' Climatic Moisture Deficit (Hargreaves, 1975)
CMI	Climatic Moisture Index
MAP	Mean annual precipitation
MSP	Mean summer precipitation
MAT	Mean annual temperature
NFFD	Number of frost-free days per year
PAS	Precipitation as snow
PPT04	Precipitation in April (used to represent general spring precipitation)

TD	Continentality (temperature difference between hottest and coldest quarter)
TMAX04	Maximum temperature in April
TMAX07	Maximum temperature in July

Table 1. Definition of the 11 bioclimatic variables kept from the ClimateNA analysis and used in the final model. All are derived from precipitation and/or temperature.

Background environmental surfaces for Maxent were sourced from Hamann *et a*l. (2013). A bias file was added to this set that was designed to account for the well-known sampling bias within iNaturalist, generally towards urban centres and roads (Di Cecco et al., 2021). The file randomly removes occurrences from areas of high density, but does not supplement areas of low density. Herbarium records are thought to have similar biases, particularly toward areas near roads (Daru et al., 2018), so the bias file may partly correct for this as well. Laboratory technician Tristan Zaborniak at the University of Victoria wrote the file using data sourced from iNaturalist. It was designed to counteract bias in sampling of vascular plants in western North America.

Five background raster extents were run through Maxent for each species with differing buffer sizes around known populations and differing inclusivity of outliers. These comparisons were made on the basis of the area under the receiving operator curve (AUC) value. AUC describes the likelihood that the model will assign a higher probability of occurrence to a random presence point than a random background point. It has been criticized as a metric because it treats all background points as absences, which is potentially not always the case due to imperfect surveying. This gives it a tendency to assign lower accuracy to models that predict suitability outside of known presence localities as well as to assume higher accuracy when lots of unsuitable background is included in the sample space (Lobo et al., 2008). Despite this, it is the most popular accuracy metric in species distribution modelling literature (Merow et al., 2013) with few alternatives. I settled on a rectangular sample space that extended somewhat (<150km) beyond the bounds of the predicted range edges that had been used to filter location coordinates earlier. One *E. oregonum* outlier was removed from central California, it had been questionable to begin with, and negatively impacted the AUC.

The bias file and environmental rasters were clipped to the dimensions mentioned above. To ensure that all were clipped to an identical extent (necessary for Maxent to function) the align rasters tool in QGIS was used. The climatic breadth present in the background given to Maxent affects the breadth of the output (Elith *et al.*, 2010), significantly the representation of extreme climates must be similar in both directions from the expected optimum conditions. This makes it less likely that Maxent will generate “pseudo-absence” background points disproportionately at one extreme of the represented climate conditions, biasing their comparison to presence points. Aligned rasters were reprojected and reconverted to ASCII. Notably, the line specifying the null value in the ASCII text was deleted during the conversion and had to be manually replaced before the files were acceptable to Maxent.

The trimmed background layers were then run in Maxent along with the herbarium data and the bias file for 100 bootstrap replicates with 75% of the occurrences in order to train the model, and again with 25% of the occurrences to test it. The response curve & jacknife settings were turned on. A random seed was used. Output was requested in cloglog format. Although logistic output types make more assumptions (Merow et al., 2013), for example that the average pixel value is 0.5, they also provide a more meaningful and interpretable metric: probability of presence rather than relative abundance (Phillips et al., 2017). Cloglog is thought to have little effect on results compared to regular logistic output except that it is better at predicting areas of moderately high probability and that it has improved model performance (according to the COR statistic) when samples are preselected to counteract bias (Phillips et al., 2017). The regularization and convergence thresholds were left at their default values. Much of the procedure followed Evans & Jacquemyn (2020) and Grant & Kalisz (2020).

Maxent output ASCII files were loaded directly into ENM Tools V1.3 (Warren et al., 2010) to calculate niche metrics. Niche breadth was determined using the Levins' B Index, both B1 and B2. Both values range from zero to one, with higher values indicating a broader niche. Sampling was carried out using the bootstrap method, with no other alterations to the default settings. Each of the 100 replicate maxent models was run through the Levins' B index and the distributions were compared between the two species for each B metric. This was done using two-tailed Mann-Whitney U tests in R Studio v2021.09.0+351 to determine whether there was a significant difference in niche breadth distributions. The distributions were also graphed in R Studio.

Maxent produces ENM maps as part of its output, but these maps are difficult to edit and show occurrence points at an excessive size. To produce interpretable maps, the ASCII file output was modified in QGIS. The average ENM output ASCII was recoloured and the occurrence points were added separately and resized. The print layout function was used to add the legend and to make everything easily exportable.

To better understand the separation in climatic niche between *E. oregonum* and *E. revolutum*, the two species were compared by the range of conditions that they inhabit. The climate data for each species was compared according to the 11 variables used in the earlier niche breadth analysis. A Shapiro-Wilk test was used to confirm whether the distributions could be considered normal. A Welch's t-test was then used to compare the means for each species for each variable. Box plots were made from the climate data using RStudio. The Schoener's D index for niche overlap was then calculated between the mean output of the two species. Like the Levins' B this is a value between 0 and 1 and was found using ENMTools.

Maxent Jackknife output was used to determine which variables were most important in the niche modelling process. To produce its Jackknife output, Maxent runs the model twice for every variable. The first time it omits the variable from the analysis and the second time it runs the analysis, but exclusively using that same variable. This allows it to see which variable contains the most relevant information that explains the target species' niche, while also assessing how much of that information is uniquely contributed by that variable. This is an important consideration because climate variables are so heavily correlated. Variables with a large overall contribution or unique contribution are more significant niche breadth and range constraints. This analysis does not say anything specific about the difference in climatic niches occupied by the two species, but instead gives the variables weights according to their importance in determining niche breadth.

Results:

The AUC values for the two niche models were both >0.9, a level of accuracy in line with what similar studies have considered acceptable (Grant & Kalisz, 2020; Evans & Jacquemyn, 2020). The mean AUC values for *E. revolutum* models was 0.945, and for *E. oregonum* models 0.949. The Maxent ENMs did show a significant difference in niche breadth between the two *Erythronium* species. The more highly selfing species, *E. revolutum*, was modelled to have a significantly broader niche than its more outcrossing sister, *E. oregonum*, according to both B1 and B2 metrics of the Levins' B index. With respect to the B1 metric, *E. revolutum* and *E. oregonum* had an average modelled niche breadth of 0.37, and 0.28, respectively (Fig. 4). For the B2 metric, *E. revolutum* and *E. oregonum* were modelled to have mean values of 0.94 and 0.92, respectively (Fig. 5). The Mann-Whitney U-test confirmed that the difference between the two species' niche breadths was significant. When B1 was used to compare the two species, the Z-score was –9.26 with a p-value of under 0.00001. When B2 was used for comparison the Z-score dropped to -7.62 with a p-value of less than 0.00001.

Figs. 4 & 5: Frequency distribution of B1 niche breadth output values from 100 replicate ENMs. Red indicates data from *Erythronium oregonum* models and blue is *Erythronium revolutum*. The Levins' B1 values (top graph) describes niche breadth in terms of its geographic availability in the model, and the Levins' B2 value (bottom graph) describes niche breadth in terms of the breadth of habitable conditions

The maps output by Maxent show a visible difference in the projected range size of the two species. From a qualitative assessment *Erythronium oregonum* would certainly appear to cover more ground and thus likely inhabit a greater variety of climatic niches than E. revolutum. This is not borne out by the quantitative analysis (Figs. 4 & 5).

Both maps show projected distributions of high-quality niche space that accurately match the distribution of location coordinates. Large areas of suitable habitat without records are few, with an exception of the northern Sierra Nevada, which is modelled as having low-moderate suitability for *E. oregonum*. Both maps show a latitudinal gap in Washington. *Erythronium oregonum* apparently has no formal records between Olympia, Washington and Portland, Oregon in any of the databases consulted. This is despite the high climatic suitability of the area. For *Erythronium revolutum*, a similar gap exists along the West side of the Olympic Penninsula.

The mapped niche of *E. revolutum* becomes noticeably patchy toward the extremes of its range on Vancouver lsland and in central California. In the former, patches of suitable habitat are present without records. In the latter, records are present outside of “suitable habitat”. Both ecological niche models approximate the actual range of both species (Allen, personal communication, March 28, 2022; range maps at Calflora, EfloraBC, University of Washington Herbarium websites).

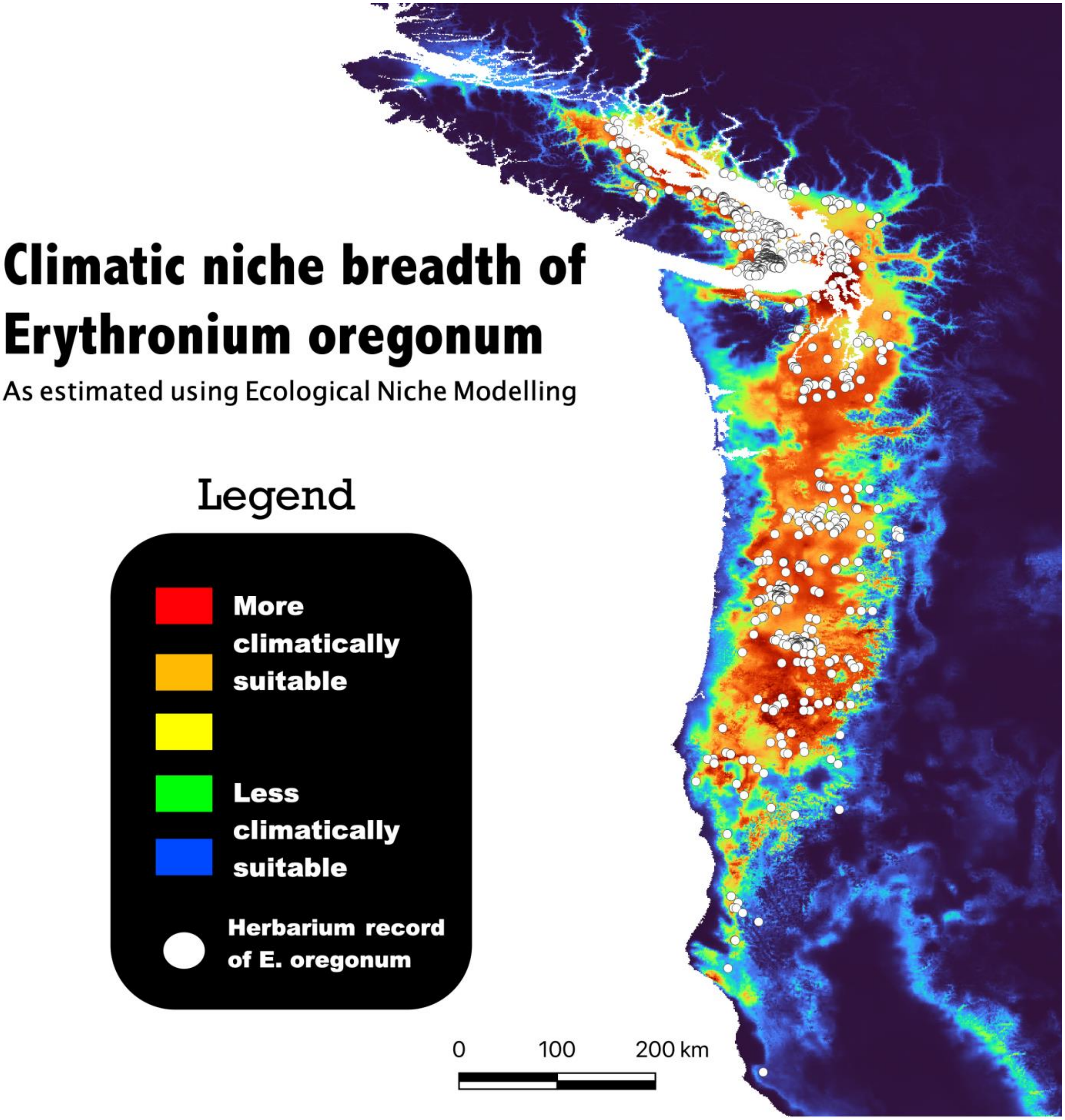


Fig. 6: The cropped and recoloured mean ENM output for the *Erythronium oregonum* data.

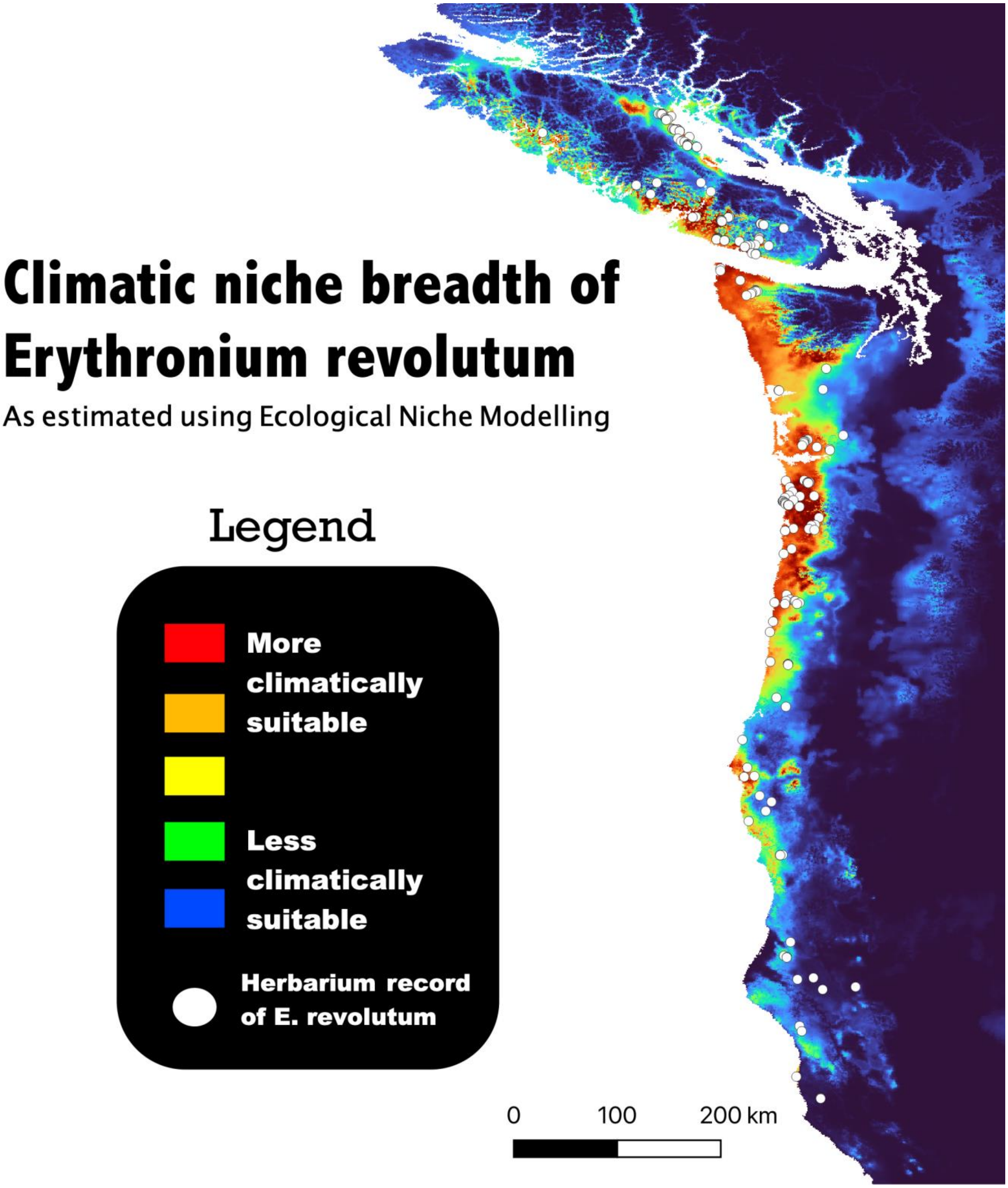
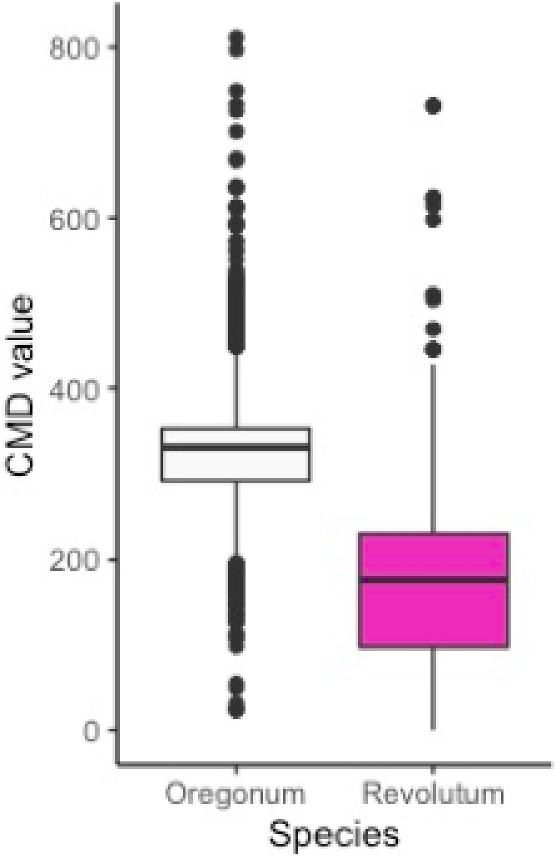


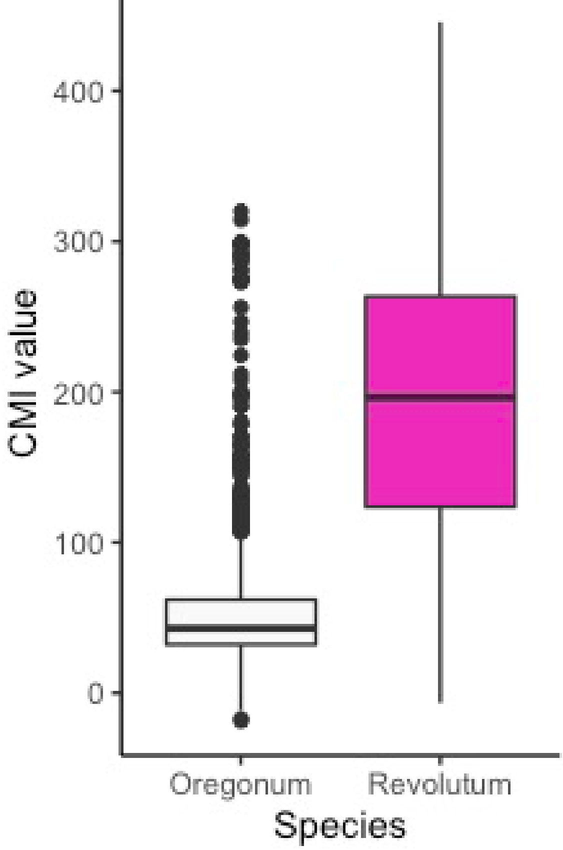
Fig. 7: The cropped and recoloured mean ENM output for the *Erythronium revolutum* data.

We also compared the climatic niche requirements for *Erythronium oregonum* and *Erythronium revolutum* on a variable-by-variable basis (Figures 8-18). A clear difference in precipitation conditions emerged between the two species, with *E. revolutum* occupying sites with higher precipitation values across every relevant metric: MAP, MSP, PAS, PPT04. *Erythronium revolutum* also occupied sites with a higher ratio of precipitation to evapotranspiration, represented by the variables CMD & CMI. Temperature was less clear-cut, with *E. oregonum* clearly occupying sites with higher MAT and a greater NFFD, but this distinction becomes less obvious when looking at monthly maximums (TMAX04, TMAX07), although it is still significant with *E. oregonum* growing in warmer sites. Continentality shows the least niche divergence, and was the only variable where the p-value of the Welch's t-test reached within a factor of one hundred of 0.05 (0.04). *E. oregonum* occupied more continental sites overall. There were a number of outliers in the data for both species. The niche overlap, as calculated as Schoener's D comparing the mean output for each species, was 0.438. This value is the sum of the difference in resource use between the two species for each of the twelve variables, divided by 2 to average for the two niches being compared and subtracted from 1 (so that it expresses similarity rather than difference).

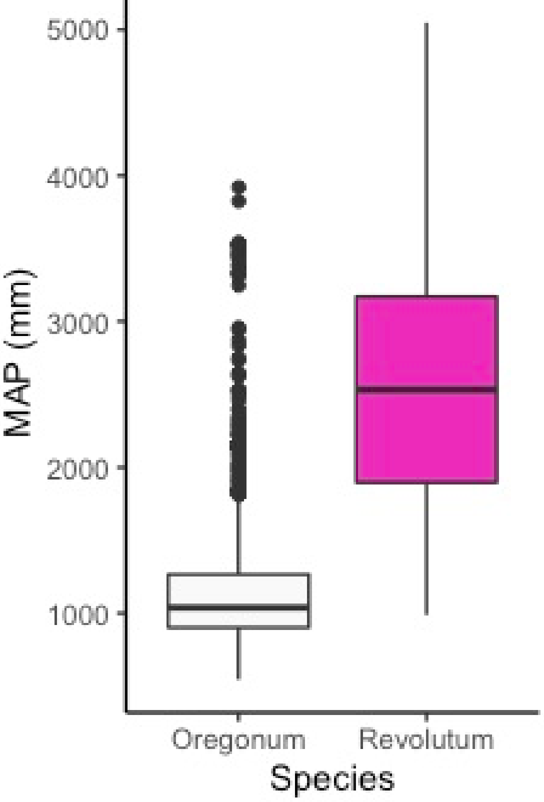
CMD



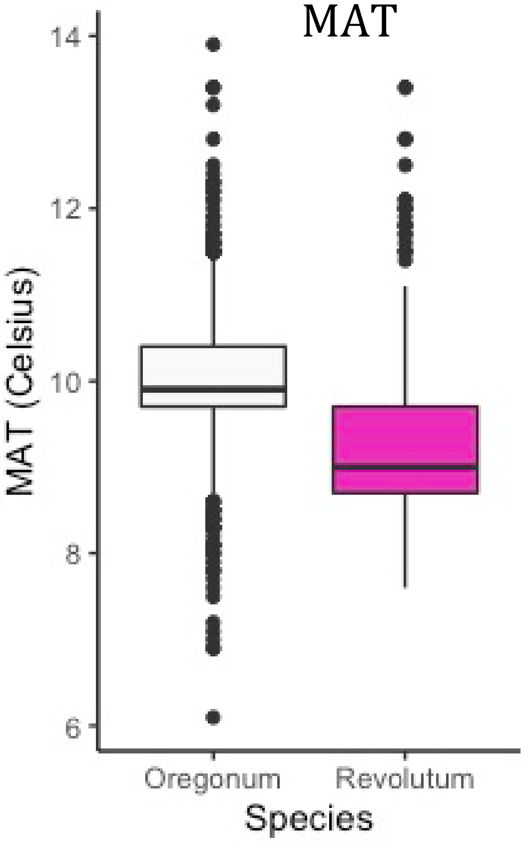
CMI

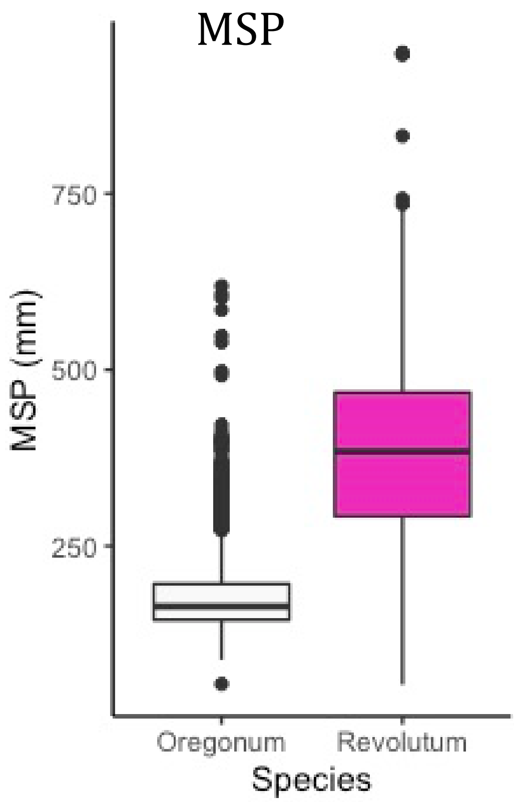


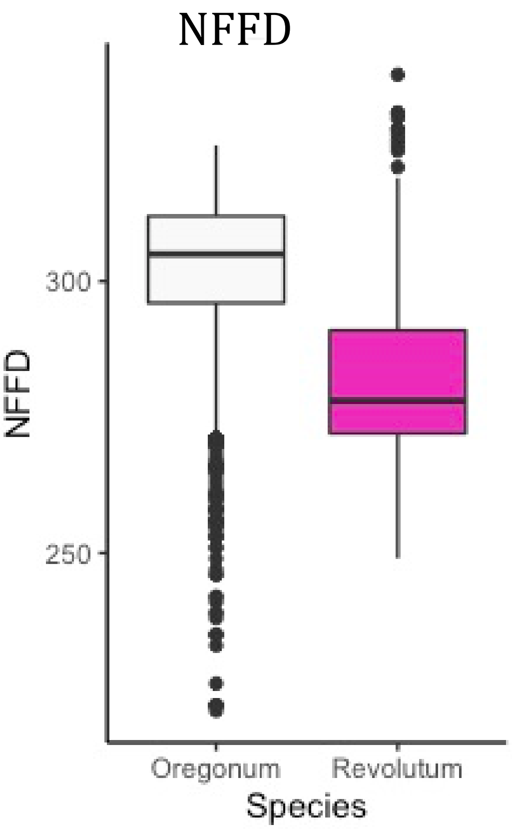
MAP

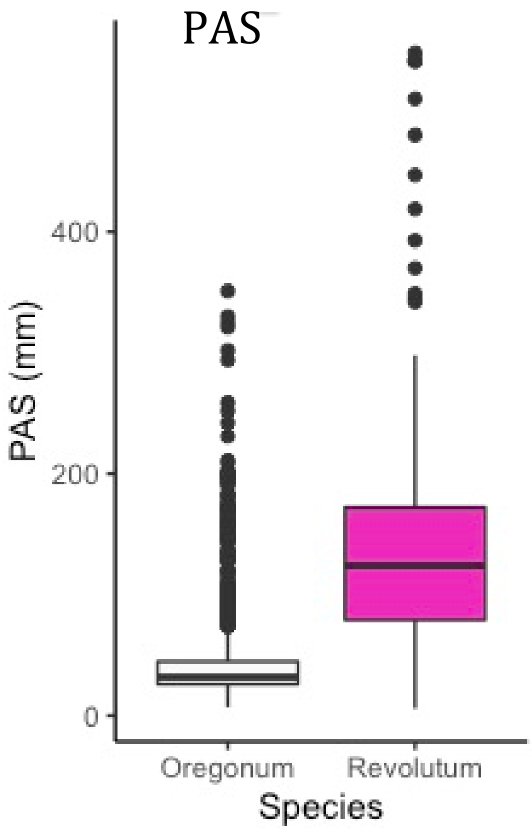


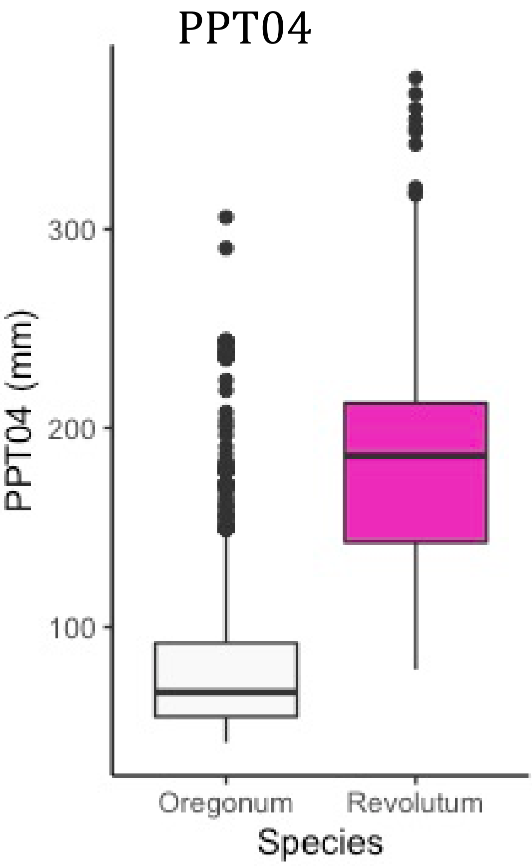
MAT

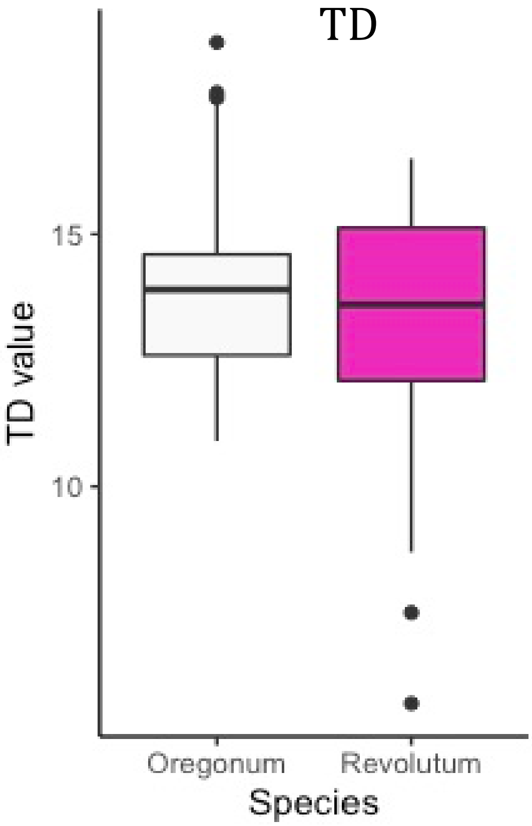


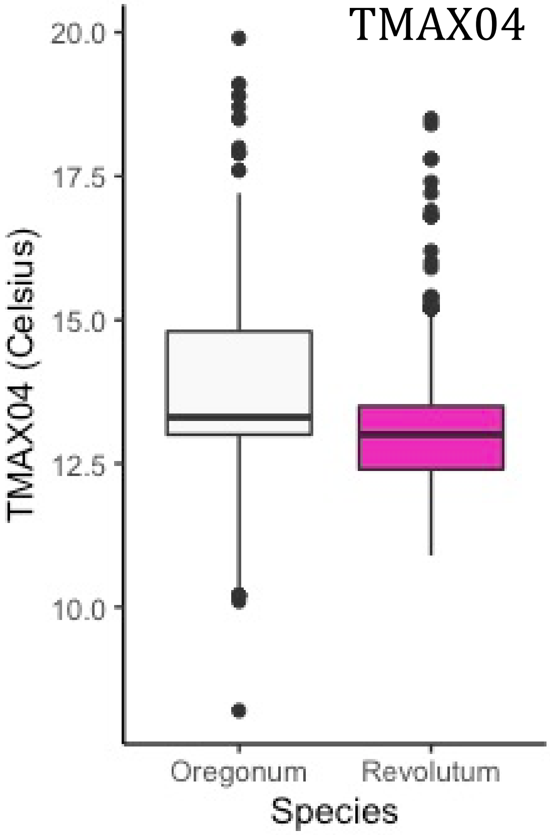

MSP
MSP (mm)
750
500
250
Oregonum
Revolutum
Species

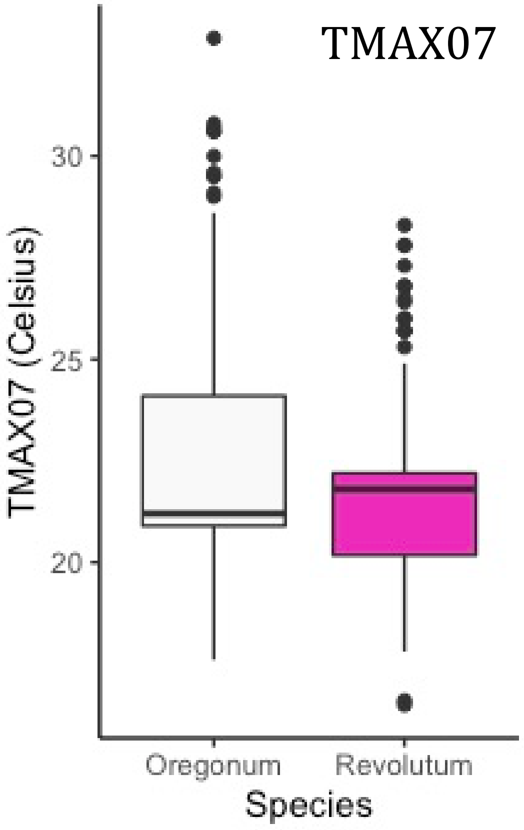

NFFD
NFFD
300
250
Oregonum
Revolutum
Species


PAS
PAS (mm)
400
200
0
Oregonum
Revolutum
Species


PPT04
PPT04 (mm)
300
200
100
Oregonum
Revolutum
Species







Figures 8-18: Comparing the two *Erythronium* species according to each of the 12 variables form the niche breadth analysis

The importance of individual variables to the analysis was then assessed (Tables 2 & 3). For *Erythronium oregonum*, the variables contributing the most to the final AUC were NFFD and TD. Of these two, the variable that would most successfully model the target niche on its own would be NFFD. The variable providing the largest amount of unique information was TD. MAT and CMI are also ranked high. The monthly temperature variables TMAX04 and TMAX07 meanwhile tended to rank as poor predictors. For *Erythronium revolutum*, the variable contributing the largest amount of unique information to the final AUC were CMD and PPT04, while the variables providing the most total information were MAT, TMAX04, and TMAX07. MSP, MAP, and PAS were poorer predictors. For both *E. oregonum*, and *E. revolutum*. The variables with higher relevance to niche breadth were generally not shared between the two species.

Tables 2 & 3. Contributions of modelled climate variables to AUC. A low value (green) in the “Variable omitted” column corresponds to a larger difference between total and “variable omitted” AUC values. A high value (green) in the “Variable only” column indicate variables with a high total contribution, even though that may overlap with other variables.

Erythronium oregonum

Total AUC value : 0.949

	Variable omitted	Variable only
CMD	0.942274	0.826088
CMI	0.941585	0.847849
MAP	0.941811	0.830714
MAT	0.941274	0.840557
MSP	0.942708	0.824517
NFFD	0.941431	0.872523
PAS	0.941712	0.826165
PPT04	0.941302	0.819985
TD	0.940424	0.853847
TMAX04	0.941914	0.792263
TMAX07	0.941783	0.772826

Erythronium Revolutum

Total AUC value: 0.945

	Variable omitted	Variable only
CMD	0.930731	0.833451
CMI	0.9386	0.722399
MAP	0.939043	0.722936
MAT	0.937632	0.869994
MSP	0.941001	0.742259
NFFD	0.939572	0.799705
PAS	0.941114	0.799702
PPT04	0.936156	0.724736
TD	0.941587	0.829933
TMAX04	0.937564	0.891039
TMAX07	0.939859	0.87715

Discussion:

This study is one of a small number in the literature looking for a connection between plant mating system and niche breadth by using sister species pairs as model systems. Our findings have been that the more highly selfing sister, *E. revolutum*, occupies a broader niche than its more outcrossing counterpart *E. oregonum*. When individual variables were selected to compare the two species, there was a clear difference in climatic niche. *Erythronium revolutum* tends to grow in areas with higher precipitation, lower temperatures, and a lower annual temperature differential than *E. oregonum*.

While experimental and theoretical studies have found a link between increased selfing ability and larger range size (Grossenbacher et al., 2015; Johnson et al., 2010) as well as improved colonization ability (Pannell, 2015; Van Kleunen et al., 2007), the connection to niche breadth has been less investigated and appears less consistent. Many authors (Park et al., 2018; Johnson, 2014; Randle et al., 2009), have not found a significant relationship between niche breadth and mating system, although it is also the case that most do not use ENM techniques. ENMs use predictive modelling to generate niche spaces that can extend beyond the known range of a species, they also synthesize multivariate differences using machine learning, making them particularly effective for niche mapping and comparisons.

The relationship modelled here between selfing ability and niche breadth does have some support in the literature. Notably, Grant & Kaliz (2020) also used ENMs to test the connection between mating system and niche breadth. Their system of study comprised eight selfing-outcrossing sister species pairs from the genera *Collinsia* & *Tonella*. In all but one of these pairs the selfing sister was found to occupy the broader niche. It is worth noting that *Collinsia* and *Tonella* are made up of annuals and are centred around California. It is possible that the higher stakes associated with seed set when there is only one season of opportunity, particularly the inherently time-limited reproduction of ephemeral winter species in xeric environments may make the effect of selfing on niche breadth easier to detect (Grant & Kalisz, 2020). It could also be speculated that winter ephemerals, especially in a heterogeneous and dry environment such as western North America may be distributed patchily or flowering after occasional high-precipitation events, perhaps making it more challenging to secure pollination services and providing an expansion advantage to genotypes with high selfing proficiency.

Evans & Jacquemyn (2020) also employ ENMs to look for a relationship between niche breadth and mating system. Their taxa of interest, *Epipactis* in Europe, is a group of long-lived perennials like our Erythronium species. No statistically significant association between selfing and niche breadth was found. The authors did, however, find extensive variation in niche breadths among outcrossers and facultative selfers, with primarily-selfing species being more consistently moderate in this regard. The authors suggest that biotic conditions, specifically the presence of mycorrhizal symbionts be incorporated into future modelling. While *Erythronium* are not likely to be as dependent upon mycorrhizal partners as orchids, biotic variables are rarely seen in ENM studies and the presence of predators, pathogens, symbionts, and competitors quite possibly (probably) does constrain Erythronium niche breadth to some extent.

Fumia et al. (2022) examined section *Petot*a of the genus *Solanum* for evidence of interactive effects of ploidy and mating system on niche breadth. They found the broadest niches belonged to self-incompatible diploid species. This was thought by the authors to be associated with these species' tendency to cross with other related species. *Erythronium revolutum*, despite being labelled a selfer, is in fact a facultative selfer. Like the diploid *Solanum* selfers it is possible that E. revolutum retains genetic diversity and expands into new niche space through occasional, key outcrosses while maintaining constant seed crops through selfing.

The results of this analysis are surprising, especially after looking at figures 6 & 7. Clearly the visibly smaller modelled area of habitat for *E. revolutum* is modelled as a more diverse set of climatic conditions than the much larger suitable area for *E. oregonum*. This is not unprecedented: Evans & Jacquemyn (2020) found that many *Epipactis* species with broad niches did not have large ranges, while some other species with large ranges were inhabiting widespread but narrow niches.

Erythronium revolutum occurrence data clusters near the exposed Pacific coastline, in a highly maritime-influenced climate. It is possible that a steeper gradient of temperature and precipitation exists near the immediate coast than 100-200km further inland (where we find *E. oregonum*) leading to a wider variety of climatic niches, although published information on such a difference, if it exists, is lacking. Something else that stands out in figs. 6 & 7 is the switch that occurs at the south of the two species' ranges. South of the Willamette Valley in Oregon, we see occurrence records move from a somewhat inland distribution to a coastal one. Simultaneously, *E. revolutum*, which otherwise hugs the coast, juts inland into the Northern California Siskiyou region. This relatively small number of occurrence records could be expanding the estimated niche breadth of *E. revolutum* significantly, given the high climatic & topographic diversity in the region and in California in general. Further analysis will begin with quantifying the effect these occurrences are having on results.

The two species' niches are characterized and constrained by different variables as shown by Maxent's Jackknife measure of variable importance. The variables are generally very similar to one another in terms of their contribution to the final model. Despite this, monthly temperature maximums (at least in April and July) were clearly more niche-characterizing for *E. revolutum* than *E. oregonum*, and the same goes for Hargreaves' Climatic Moisture Index values. *E. oregonum* meanwhile was characterized more strongly by growing season length and annual temperature differential. *E. revolutum*, being often localized to riparian areas, matches the description of a plant for which a low moisture deficit may be niche-characterizing. Similarly, its confinement largely to maritime climates aligns with its modelled preference for cooler monthly maximum temperatures. We also see this continental-maritime divide in climate preference in the importance of a relatively high annual temperature differential to *E. oregonum.*

Erythronium species are also known to hybridize (Allen, 2008; Roccaforte et al., 2015) and it cannot be ruled out that the seemingly anomalous dogleg into inland California is the result of intergrading between *E. revolutum* and one or more of the multitude of other *Erythonium* species present in that region. This would be the case especially if collectors diagnosed species affiliations based on obvious morphology. This risk would be especially present with iNaturalist identifiers making diagnoses using the characters visible in photos. The identifying features of such hybrids can be subtle and gradated (Allen, 2008). A genetic analysis of California *E. revolutum* samples may be an interesting taxonomic avenue.

The increased niche breadth of *E. revolutum* relative to *E. oregonum* could be considered in terms of historical factors. The Cordilleran ice sheet, which would have significantly altered the latitudinal position of climatic niches, was present in the northern part of both species' ranges until 19-20 thousand years ago (Clark *et al*., 2009). During this time the two *Erythronium* species, or their common ancestor, may have persisted in the south of their current range (Winkler *et al*., 2012; Allen *et al.,* 2015). Effective colonizing species often have a high capacity for self-fertilization (Panell, 2015; Martén-Rodriguez, 2015; Van Kleunen & Johnson, 2007), so it could be speculated that the selfing ability of *E. revolutum* could be related to a postglacial "land grab". If this were the case, however, why would we not see a similar pattern in *E. oregonum* or most other plants in the region? We would expect to see a gradient of selfing ability associated with past proximity to glaciation, which to my knowledge has been uninvestigated.

It is also possible that a genetically-diverse founder population with a relatively broad niche breadth persisted in Northern California while a post glacial coastal expansion facilitated by self-fertilization, occurred due to a lack of competition. An improved understanding of the timeline of separation between *E. oregonum* and *E. revolutum*, particularly the increase in selfing rates in *E. revolutum*, may provide insight into this. Investigating the potential for differential selfing rates in different subregions of both species' ranges could also yield findings of interest. Newly established plant populations can see rapid changes in mating system, especially in cases of pollen limitation (Brys et al., 2013; Kalisz & Vogler, 2003).

It could be that environmental differences between the two species' niches contributed to a divergence in mating system after specialization for their respective niches had partially occurred. *Erythronium revolutum* populations are quite localized in abundance for much of their range (Allen, personal comment March 5, 2022). The extent to which pollen transfer would be limited by the localized patchiness of their distribution is unknown, but this could favour an increase in selfing after a broad niche has already been attained. Study of *Sericocarpus rigidus*, a plant from the same region, but more aligned with *E. oregonum* in climatic niche, showed that small, isolated patches exposed to ambient pollinator activity did not have lower viable seed production than hand-pollinated patches (Bigger, 1997).

E. oregonum is also a plant of mesic meadow environments (Douglas, 1998), which may expose it to extra-genus competition to a greater degree than *E. revolutum* experiences in more forested, maritime, rainier climes. The historically large extent of contiguous oak savannah over the range of *E. oregonum* could be speculated to have produced a high density and diversity of flowering perennial forbs, potentially leading to a co-abundance of herbivory and seed predation. This, alongside the increased competition of a heavily-flowered open habitat, may have favoured *E. oregonum* to maintain higher rates of outcrossing to cope with these pressures. It is possible that bulb rot could be a concern of long-lived geophytes in wet climates, five bulb rot pathogens have been isolated from a wetland *Camassia* population in the Pacific Northwest (Freed, 2018). in that case we would expect *E. revolutum* to need the extra recombination to maintain resistance in its wetter environment, but this is not supported by our analysis.

It is also possible, of course, that any hypothetical postglacial expansion happened after *E. revolutum* had already diverged into a more selfing mating system. Being highly proficient at selfing should increase additive genetic variance for tolerance to new environments (Levin, 2010), and occasional outcrossing can be sufficient to maintain genetic diversity (Ruane *et al*., 2020). It may be the sheer (theoretical) colonization ability of selfers that is responsible for *E. revolutum*'s relatively broader niche. Even selfers with low genetic variation may be quite capable of local adaptation (Hereford, 2010). Consideration of epigenetic adaptation and phenotypic plasticity may also be important to niche expansion in selfers.

Selfers often occupy more stressful environments, with Grant & Kalisz (2020) finding them more abundant at higher elevations and in drier areas, reinforcing Randle et al. (2009) and Arroyo et al., (2006)’s findings around elevation and mating system. Ricote et al. (2019) also found an association between time limitation by drought risk and predominantly selfing mating systems. This variation is generally attributed to a lack of biotic pollination. Any effects relating to a lack of competition or disease at such sites have not been tested. In our case, analysis of individual variables has shown that the more-selfing *E. revolutum* occupies wetter, colder environments with less seasonal temperature change. Whether these environments are more or less stressful for members of this genus is unknown.

Celis et al. (2019) found an association between conifer-driven succession and a decline in flower and pollinator diversity and density, thought to be at least partly the result of declining light levels. *E. revolutum*, outside of California, is generally confined to the Coast Range Ecoregion as the maritime Pacific Northwest is known in US sources and to the Coastal Western Hemlock (CWH) zone within British Columbia. Such environments are historically more heavily-forested and less fire-prone than the Puget Trough, Willamette Valley, or Georgia Depression, where *E. oregonum* is abundant. In fact, the gap in *E. oregonum*’s range mentioned earlier is where the Willamette Valley and Puget Trough ecoregions shrink and meet, squeezed by the Coast Range & Cascade regions.

Indigenous burning in the region was long used in the cultivation of other long-lived geophytes for food purposes (Stucki et al., 2021). Fire-based succession may be part of what ties *E. oregonum* to its niche and provides improved access to pollinators. This may also increase population density, heightening the potential for competition, disease, and abundant herbivores. *Erythronium montanum*, which occurs locally within the CWH zone on the San Juan Ridge on Vancouver Island, has been observed to flower *en masse* in response to clearcutting (Allen, personal comment, March 5, 2022). This may be an indication of light-limitation in a related species occupying high-precipitation, heavily-forested niche within 5km of *E. revolutum* habitat. Further investigation could assess whether light limitation plays a role in pollination success and competition dynamics in different *Erythronium* species, potentially tying this to differences in mating system.

Flowers with *Erythronium*-like morphology are thought to be most effectively pollinated by bumblebees (Thomson, 1986; Thomson & Thomson, 1989), with visits from Syrphid flies and other small pollinators believed to contribute minimally to seed set (Theobald et al., 2016). A study on pollen limitation in another Erythronium from the same region (*E. montanum*) revealed little pollen limitation at low elevations with the authors predicting that late frosts or light limitation from dense canopy may be the primary constraints (Theobald et al., 2016). Higher elevations, however, did show some level of pollen limitation, although the large differences in pollinator populations between years, and other confounding factors make this conclusion a challenge to generalize.

It is important to consider the limitations of this small and specific study. The location points used to model the niches of *E. oregonum* and *E. revolutum* came mostly from iNaturalist, a website where two incorrect opinions can send an observation to a research grade status. The map of *Erythronium* records on iNaturalist is continually changing and has already visibly expanded on Vancouver Island and contracted in northern California since the records were taken for this project. It also misses interesting location records, such as the ones on Valdez Island and at Kingcome Inlet in British Columbia (Douglas et al., 1998). There is also an inherent circularity to the practice of using the known and mapped parts of a distribution as input for the generation of a complete, ecological distribution: a model based on the known distribution of a species will, of course, support the known distribution.

Further limitations arise from the climate-focused nature of this analysis. Other studies (e.g. Evans & Jacquemyn, 2020) have used bedrock type, soil type, or forest cover as environmental variables. Even more exciting would be the possibility to look at biotic factors, which is rarely done, probably because of the difficulty around making a consistent map. Another possibility would be to look at the phylogenetic relationship between *E. oregonum* & *E. revolutum*, particularly the time depth at which their mating systems diverged.

Conclusion:

Ecological niche modelling of a selfing-outcrossing sister species pair in the genus Erythronium has revealed that the sister with the greater capacity to self-fertilize also occupies a broader climatic niche. This may be a result of improved colonization ability intrinsic to self-pollination, or to historical factors. Further research on selfing-outcrossing sister species pairs ideally incorporating biotic impacts on niche breadth, has the potential to improve understanding of niche dynamics and partitioning in times of widespread climatic change.

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