Assessing the impact of climate change on habitat for at-risk amphibians in the Pacific Northwest: which species are suitable for species distribution modeling?

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Introduction

The Pacific Northwest is a hotspot for temperate amphibian biodiversity and is home to many species of salamanders and frogs found nowhere else on earth. Changing climatic conditions threaten habitat for many of these species, primarily through increased air and water temperature and the drying of habitats. Among the most commonly used tools for evaluating the potential impacts of climate change on habitat suitability are species distribution models (SDMs). This approach develops models that describe suitable habitat for a focal species (or set of species) based on relationships between environmental variables and contemporary species occurrences. These models can then be used to predict changes in the availability of suitable habitat for these species using anticipated values of environmental variables derived from climate projections. However, this approach is only likely to yield robust predictions about the impacts of climate change when certain criteria are met. More specifically, the environmental variables used to develop the SDMs should be closely linked to the species' habitat requirements and should be available at a spatial resolution consistent with the species' habitat use, in addition there must be sufficient contemporary species occurrence data from throughout the range of the target organisms to develop a robust model. As a first step towards assessing climate impacts on at-risk amphibians in the Pacific Northwest, we evaluated whether these criteria were met for 17 amphibian species of greatest conservation need in the region (Tables 1 and 2). We found that overall feasibility for SDMs was high for 7 of these species. Efforts to model habitat suitability are already being conducted by other research groups for 3 of these 7 species. For the remaining 4 species, we provide a review of scientific literature relevant to the development of SDMs for these species. Developing these SDMs and using climate projections to predict changes in habitat suitability will comprise the next phase of our project.

Table 1: Species distribution model criteria for sensitive Pacific Northwest amphibians (abridged)

Species	Ideal model resolution ¹	Utility of ESU- specific models ²	Locality data quality ³	Representativeness of occurrence points ⁴	Predictor variable quality	Overall SDM feasibility ⁵
Van Dyke's salamander (<i>Plethodon vandykei</i>)	30m	High	High	Medium	High	High
Rocky Mountain tailed frog (Ascaphus montanus)	100-200m	Medium	High	Medium	High	High
Cope's giant salamander (Dicamptodon copei)	30m	Low	High	Medium	High	High
Coeur d'Alene salamander (Plethodon idahoensis)	30m	Medium	High	Medium	High	High
Foothill yellow-legged frog (<i>Rana boylii</i>)	50-100m	High	High	High	Medium	High (√)
Cascade torrent salamander (Rhyacotriton cascadae)	30m	Medium	High	High	High	High (√)
Columbia torrent salamander (Rhyacotriton kezeri)	30m	Low	High	High	Medium	High (√)
Western toad (Anaxyrus boreas)	100-200m	High	High	Medium	Medium	Medium
Cascades frog (Rana cascadae)	100-200m	High	High	High	Low	Medium
Oregon slender salamander (Batrachoseps wrighti)	50-100m	Medium	High	Medium	Medium	Medium
Olympic torrent salamander (Rhyacotriton olympicus)	30m	Low	High	Low	High	Medium
Southern torrent salamander (Rhyacotriton variegatus)	30m	Medium	High	High	Low	Medium
Northern leopard frog (Rana pipiens)	100-200m	Medium	Low	Medium	Low	Low
Oregon spotted frog (Rana pretiosa)	50-100m	Medium	Medium	Medium	Low	Low
Idaho giant salamander (Dicamptodon aterrimus)	30m	Medium	Medium	Low	High	Low
Larch Mountain salamander (Plethodon larselli)	30m	Medium	High	Medium	Low	Low
Siskiyou Mountains salamander (Plethodon stormi)	30m	Medium	High	High	Low	Low

¹See full version of table for a justification of ideal model resolutions for each species.

²Likelihood of multiple, ecologically different ESUs inferred from past/ongoing studies on each species and its qualitative variety of occupied habitats relative to suspected dispersal/connectivity.

³Locality data were considered "high quality" if locational accuracy was high relative to the spatial scale of an optimal SDM for many (~200+) occurrence points, and if the data were qualitatively recent enough to reflect contemporary occupancy patterns.

⁴Occurrence points were considered representative if they captured the full diversity of major climates/regions occupied by the species.

⁵Overall feasibility of SDMs based on the preceding columns, as well as the redundancy or novelty of constructing new SDMs for each species. See full version of table for a formal justification for each species. Check marks represent species that are currently being modeled by others.

Table 2: Species distribution model criteria for sensitive Pacific Northwest amphibians (full)

Species	Ideal model resolution, and justification	Important predictor variables	Likelihood of multiple clades with different niches ¹	Sufficiency of high- quality locality data ²	Availability of unbiased environ. data at occurrence points ³	most	Overall current feasibility of SDMs ⁴	Justification for feasibility rating	Tasks to increase appropriateness of SDMs in future
Western toad (Anaxyrus boreas)	100-200m grid cells; this species is often observed moving hundreds of meters between core breeding habitats and likely tends to have moderate-to- large home ranges relative to other amphibians on this list.	Microclimate variables (mean and variation of water temperature, air temperature, humidity, and precipitation), wetland vegetation type, wetland size, wetland hydroperiod, fish presence/absence, elevation, and availability of stream backwaters (northern Idaho populations only?)	High	High	Medium	Medium	Medium	This species has lots of available occurrence data, but exceptions exist across lots of large wilderness areas within the species' range, some of which contain relatively unique climatic conditions. Additionally, this species appears to use different habitat types in different portions of its range (e.g., ponds/lakes in most places, but often river backwaters in northern Idaho), but boundaries of ESUs translating into regional niche differences are currently unclear. In ponds/lakes, this species may be impacted by the presence/absence of fish, but such data are currently lacking for most regions within its range.	(1) Additional sampling effort is needed for this species for most major wilderness areas within the PNW, especially those representing unique climates relative to other portions of the species' range (e.g., the semi-arid Salmon River Drainage). (2) Lab-based research is needed to confirm and assess the geographic boundaries of apparent niche differences present in different regions within this species range (e.g., use of river backwaters in northern Idaho versus exclusive use of ponds/lakes elsewhere).

Foothill yellow- legged frog (Rana boylii)	50-100m grid cells overlapping watercourses; the core habitat of this species (slow-to-moderate gradient streams with areas of backwater) occurs at relatively fine spatial scales and the species is generally restricted to these habitats and immediately adjacent areas.	Microclimate variables (mean and variation of water temperature, air temperature, stream discharge, humidity, and precipitation), forest stand class, fire history, Strahler stream order, stream gradient, streamflow permanence, topographical variables (elevation, slope, aspect, and exposure), and geology	High	High	High	Medium		This is a well-studied species with lots of high-quality locality data. However, this also means that reasonable SDMs are already in development for this species and are likely to be frequently updated/improved by other groups, which would limit the utility of creating new SDMs. Also, this species contains multiple ESUs, but their exact consequences for geographic variation in the species' environmental niche are still unclear.	new SDMs for this species is largely limited by the fact that this is already a
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Oregon slender salamander (Batrachoseps wrighti)	50-100m grid cells; this species is expected to select habitat at fine spatial scales but uses slightly less localized microhabitats (e.g., coarse woody debris) than certain other philopatric species.	Microclimate variables (mean and variation of soil and air temperature, soil moisture, humidity, and precipitation), forest stand class, fire history, topographical variables (elevation, slope, aspect, and exposure), and availability of coarse woody debris	Medium	High	Medium	Medium	Medium	A reasonably high number of contemporary records exist for this species, but records are largely lacking from some wilderness areas that represent a moderate proportion of this species' range and may possess somewhat unique climate features. In addition, records for this species are relatively localized within parts of its range (e.g., the eastern side of the Cascades), but it is unclear whether this represents habitat specificity and rarity or is merely an artifact of low detection probability. This species is largely dependent on coarse woody debris, which is likely difficult to represent directly using GIS data, although forest stand class may serve as a viable proxy. Niche differences may exist between populations located on the western and eastern slopes of the Cascades.	(1) The spatial distribution of coarse woody debris should be modeled across this species' range, as these microhabitats are important for the species' persistence. (2) Lab-based studies should assess whether populations on the western and eastern slopes of the Cascades are physiologically different and should be modeled separately.
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Idaho giant salamander (Dicamptodon aterrimus)	30m grid cells overlapping watercourses; the core habitat of this species (headwater streams with pools) occurs at relatively fine spatial scales and the species is generally restricted to aquatic/riparian habitats and immediately adjacent areas based on current knowledge. A closely related species (D. tenebrosus) was never observed moving more than 15m at a time and had an estimated home range size of only 935m².	Microclimate variables (mean and variation of water temperature, air temperature, stream discharge, humidity, and precipitation), forest stand class, fire history, Strahler stream order, streamflow permanence, topographical variables (elevation, slope, aspect, and exposure), and geology	Medium	Medium	Low	High	Low	Large portions of this species' range are underrepresented by occurrence points due to their location in the middle of large swaths of wilderness, and there are a relatively modest number of contemporary occurrence records in general. Terrestrial adults are not necessarily expected to play an insignificant role in populations, but there are few records of terrestrial adults and little existing knowledge of their habitat requirements due to their extremely secretive nature.	appropriate SDM scale, studies should
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Cope's giant salamander (Dicamptodon copei)	30m grid cells overlapping watercourses; the core habitat of this species (headwater streams with pools) occurs at relatively fine spatial scales and the species is generally restricted to aquatic habitats, with very few known examples of terrestrial adults. A closely related species (<i>D. tenebrosus</i>) was never observed moving more than 15m at a time and had an estimated home range size of only 935m².	variation of water temperature and stream discharge), forest stand class, fire history, Strahler stream order, streamflow	Low	High	Medium	High	High	There are a reasonably high number of contemporary occurrence points for this species, but within the Olympic Peninsula, these points are highly biased towards lowlands. Occurrence points are sparse for moderate and high elevations in the Olympic Mountains, which likely represent a moderate (but unknown) proportion of this species' area of occurrence. In addition, this large, underrepresented wilderness area contains climatic conditions generally not found within more heavily sampled places within this species' range.	(1) Additional sampling effort is needed for wilderness areas within the Olympic Peninsula, which likely represent a moderate, undersampled portion of this species' range.
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Cascade torrent salamander (Rhyacotriton cascadae)	30m grid cells overlapping watercourses; this species is suspected to be highly philopatric and uses very specific, localized microhabitats (e.g., seeps).	fire history, Strahler stream order, streamflow permanence,	Medium	High	High	High	High (√)	Lots of contemporary occurrence points exist for this species, and ongoing studies should soon reveal the distribution of important microhabitat features (e.g., seeps) that are relatively important for the species. Habitat preferences appear to be broadly consistent across the species' range, although minor niche differences between populations north and south of the Columbia River may exist. Models for this species are already in development by Thurman et al. (in review).	coverage across this species' range will make it easier to infer forest stand class (based on vegetation height) for certain areas. (2) Lab-based studies should assess whether populations north and south of the Columbia River are physiologically different and should he modeled
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torrent salamander	30m grid cells overlapping watercourses; this species is suspected to be highly philopatric and uses very specific, localized microhabitats (e.g., seeps).	Microclimate variables (mean and variation of water temperature, air temperature, humidity, and precipitation), forest stand class, fire history, Strahler stream order, streamflow permanence, topographical variables (elevation, slope, aspect, and exposure), geology, and availability of seeps	Low	High	High	Medium	High (✔)	Lots of contemporary occurrence points exist for this species, and ongoing studies should soon reveal the distribution of important microhabitat features (e.g., seeps) that are relatively important for related species, but these analyses are geared towards areas other than the range of this species (although with moderate geographic proximity), thus they may have limited applicability for Columbia torrent salamanders, which may in turn limit possibilities for constructing accurate SDMs. Habitat preferences appear to be broadly consistent across the species' range, although minor niche differences between populations north and south of the Columbia River may exist. Models for this species are already in development by Thurman et al. (in review).	(1) The spatial distribution of groundwater-dependent ecosystems (e.g., seeps) should be modeled across this species' range, as these ecosystems are likely to be important for the species' persistence. (2) Lab-based studies should assess whether populations north and south of the Columbia River are physiologically different and should be modeled separately.
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Olympic torrent salamander (Rhyacotriton olympicus)	30m grid cells overlapping watercourses; this species is suspected to be highly philopatric and uses very specific, localized microhabitats (e.g., seeps).	Microclimate variables (mean and variation of water temperature, air temperature, humidity, and precipitation), forest stand class, fire history, Strahler stream order, streamflow permanence, topographical variables (elevation, slope, aspect, and exposure), geology, and availability of seeps	Low	High	Low	High	Medium	There are a reasonably high number of contemporary occurrence points for this species, but they are highly biased towards lowlands. Occurrence points are sparse for moderate and high elevations in the Olympic Mountains, which likely represent a moderate-to-high (but unknown) proportion of this species' area of occurrence. However, torrent salamanders often become scarce at slightly lower elevations than other lotic/riparian species, which may partially ameliorate the above problem. Regardless, the large, underrepresented wilderness area in the center of the Olympic Peninsula contains climatic conditions that are not found within more heavily sampled lowlands within this species' range. Ongoing studies should soon reveal the distribution of important microhabitat features (e.g., seeps) that are relatively important for the species, including in the Olympics.	(1) Substantial additional sampling effort is needed for wilderness areas within the Olympic Peninsula, which likely represent a large, undersampled portion of this species' range.
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Southern torrent salamander (Rhyacotriton variegatus)	30m grid cells overlapping watercourses; this species is suspected to be highly philopatric and uses very specific, localized microhabitats (e.g., seeps).	fire history, Strahler	Medium	High	High	Low	Medium	Lots of contemporary occurrence points exist for this species. Ongoing studies should soon reveal the distribution of important microhabitat features (e.g., seeps) that are relatively important for related species, but these analyses are taking place far away from the range of southern torrent salamanders and thus likely have limited transferability, making SDMs for this species more difficult. Multiple ESUs linked to niche differences are expected for this species, but the boundaries of these niche differences have not been fully resolved.	groundwater-
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Larch Mountain salamander (Plethodon larselli)	30m grid cells; this species is suspected to be highly philopatric and uses very specific, localized microhabitats (e.g., moist talus).	Microclimate variables (mean and variation of soil and air temperature, soil moisture, humidity, and precipitation), topographical variables (elevation, slope, aspect, and exposure), and talus availability	Medium	High	Medium	Low	Low	This species exclusively lives in talus, but there are currently no GIS resources for inferring the distribution of this habitat type, and it is notoriously difficult to model.	(1) GIS products that accurately portray the spatial distribution of talus on the landscape are critical for making it possible to construct accurate SDMs for this species. (2) Lab-based studies should clarify whether known ESUs for this species confer localized differences in physiology, which would necessitate the separate treatment of different ESUs in SDMs.
Siskiyou Mountains salamander (Plethodon stormi)	30m grid cells; this species is suspected to be highly philopatric and uses very specific, localized microhabitats (e.g., moist talus).	soil moisture,	Medium	High	High	Low	Low	This species exclusively lives in talus, but there are currently no GIS resources for inferring the distribution of this habitat type, and it is notoriously difficult to model.	(1) GIS products that accurately portray the spatial distribution of talus on the landscape are critical for making it possible to construct accurate SDMs for this species. (2) Lab-based studies should clarify whether known ESUs for this species confer localized differences in physiology, which would necessitate the separate treatment of different ESUs in SDMs.

Van Dyke's salamander (Plethodon vandykei)	30m grid cells overlapping watercourses; this species is suspected to be highly philopatric and uses very specific, localized microhabitats (e.g., seeps).	variation in	High	High	Medium	High	High	Lots of contemporary occurrence points exist for this species, including a moderately high number contemporary occurrence points due to recent survey efforts. In addition, ongoing studies should soon reveal the distribution of important microhabitat features (e.g., seeps) that are relatively important for the species. However, there are relatively few records from high elevations in the Olympic Peninsula due to this area being mostly inaccessible wilderness. Two major clades with corresponding niches are suspected, but the boundaries of these two clades is likely easy to delineate (Olympics/Willapa Hills versus Cascades) due to the disjunct nature of this species' range. Ongoing research suggests that this species is declining even in regions with seemingly intact habitat, which could indicate a link to climate change and makes this an especially compelling species to model using SDMs.	(1) More sampling effort is needed for wilderness areas within the Olympic Peninsula. (2) Lab-based physiology and phylogenetic research is needed to determine whether the two major clades of Van Dyke's salamander (Willapa Hills/Olympics and Cascades) are sufficiently different to warrant separate modeling exercises, and to assess whether this group represents one or two species.
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¹Likelihood of multiple, ecologically different ESUs inferred from past/ongoing studies on each species and its qualitative variety of occupied habitats relative to suspected dispersal/connectivity.

²Locality data were considered "high-quality" if locational accuracy was high relative to the spatial scale of an optimal SDM and if the data were qualitatively recent enough to reflect contemporary occupancy patterns.

³Environmental data were considered unbiased at occurrence points if high-quality occurrence points captured the, in general, full diversity of major climates/regions occupied by the species.

⁴Overall feasibility of SDMs was estimated based on a combination of the four preceding columns, as well as the redundancy or novelty of constructing new SDMs for each species. Check marks represent species that are already being modeled by others.

Species distribution modeling literature review for targeted Pacific Northwest amphibians

Rocky Mountain tailed frog (Ascaphus montanus)

This species occurs primarily in rocky, fast-flowing headwater streams (Nielson et al. 2001) and is possibly sensitive to warming temperatures and altered precipitation patterns (Metzger et al. 2015). Therefore, important SDM predictor variables include both physical properties of streams (e.g., Strahler stream order and slope) and fine-scale climate variables (e.g., air and stream temperatures). Wildfires can result in short-term declines for this species, but near-complete recovery to pre-fire population levels has been observed after approximately one decade (Hossack and Honeycutt 2017). Thus, wildfires are unlikely to play a major role in shaping the distribution of A. montanus. Annual migrations along stream corridors have been observed for this species (Adams and Frissell 2001), and individuals might move up to several hundred meters per year based on observations from closely related A. truei (Hayes et al. 2006). In general, this species is expected to move upstream (e.g., into 1st and/or 2nd order streams) during the non-breeding season each summer and move back downstream each fall to breed, and seasonal movements appear to be relatively restricted to riparian corridors than for A. truei (Olson 2011). Therefore, a 100-200m pixel resolution is likely sufficient to represent this species' core habitat using SDMs, but pixels should be clipped to stream segments. There are two clearly defined major clades of A. montanus, with a deep divergence pattern (~1.2 million years ago [MYA]) indicating a northsouth split in central Idaho (Metzger et al. 2015). The two clades occur in areas with different climatic conditions and may possibly possess different ecological niches, making it potentially useful to construct separate SDMs for each clade.

To our knowledge, three attempts have been made to construct SDMs for A. montanus; all with clear limitations. First, Carstens and Richards (2007) used Maxent models (Phillips et al. 2006) and WorldClim variables (Hijmans et al. 2005) at a resolution of 10 arc-minutes to assess current and historical (21,000 years before present [YBP]) climatic suitability for this species. Metzger et al. (2015) used a similar approach but with smaller (1km²) grid cells, an additional predictor variable (land cover), and added projections for 2070 climate suitability based on a worst-case (RCP 8.5) emissions scenario. The latter authors suggest a severe reduction in future habitat by 2070 under their worst-case emissions scenario. However, problems with SDMs in both papers include overly coarse grid sizes relative to the scale of habitat use, a lack of spatial bias correction techniques (e.g., point-thinning), probable overfitting due to the large number of predictor variables used (n = 19-20), a failure to consider the possibility of two clades with different niches and thus modeling needs, and the omission of biologically relevant predictor variables (e.g., slope and Strahler stream order). In addition, a third SDM publication (Elliott et al. 2022) used a subset of WorldClim variables and water temperature variables and general boosting/random forest models to predict current and future distributions of Ascaphus and several other aquatic species within Washington. While this paper more carefully selected predictor variables for their collective (but not individual) study species, all modeling pitfalls listed for the previous two approaches besides potential overfitting also apply to this publication, and the spatial scale used (15.7km², based on a 5km radius around each occurrence point) far exceeds areas used to select habitat by A. montanus. In addition, the authors treated Ascaphus as a single group, although this genus

contains two species that likely have separate niches, and the authors' training area (the state of Washington) did not conform to the boundaries of available habitats for either species. Similar to Metzger et al. (2015), the above authors also predicted future declines in *Ascaphus* habitat under climate change. However, all three SDM publications above should be treated with extreme caution due to their clear modeling pitfalls.

Cope's giant salamander (Dicamptodon copei)

This species is usually fully aquatic and prefers pool microhabitats within fast-flowing streams (Petranka 1998). It occurs only in humid portions of western Washington and a small portion of Oregon (Foster et al. 2014), is potentially impacted by logging and habitat fragmentation (Petranka 1998), and has a patchy distribution, particularly where sympatric with D. tenebrosus (Lannoo 2005). Therefore, important SDM predictor variables for D. copei likely include stream characteristics (e.g., slope and Strahler stream order), fine-scale climate characteristics (e.g., water temperature), land use characteristics (e.g., logging intensity and upstream road crossings), and biotic factors (e.g., the distribution of D. tenebrosus). Movements and home range sizes are unknown for this species, but closely related D. tenebrosus was observed moving a maximum of 15m at a time and had an estimated home range size of only 935m² (Johnston and Frid 2002). Notably, D. copei may be even less vagile than D. tenebrosus due to being fully aquatic with rare exceptions (Loafman and Jones 1996) and thus being generally unable to disperse over land or bypass features like large waterfalls. Therefore, a fine-scale pixel resolution (e.g., 30m) is likely needed to adequately model the distribution of D. copei. As the phylogenetics of this species suggest isolation by distance as the prevailing determinant of its population structure (Steele et al. 2009), there is no evidence for ecologically distinct clades within this species with separate modeling needs.

To our knowledge, no SDMs have not been published for *D. copei* specifically. However, Elliott et al. (2022) modeled the current and future distributions of Washington *Dicamptodon* (*D. copei* + *D. tenebrosus*) collectively and predicted an overall increase in climate suitability for the genus under climate change, contrary to earlier, qualitative predictions that future habitat for *D. copei* may decrease with future reductions in summer streamflow (Trumbo et al. 2013). Unfortunately, the above SDMs are probably uninformative for *D. copei* specifically, in part due to differing life histories between *D. copei* and *D. tenebrosus*. In addition, the above SDM approach suffered from multiple other pitfalls limiting its usability for *D. copei*, including overly coarse grid sizes relative to the scale of habitat use, a lack of spatial bias correction techniques (e.g., point-thinning), model training areas misaligned with areas accessible to the study species, and the omission of biologically relevant predictor variables (e.g., slope and Strahler stream order). Lastly, although predating the widespread use of SDMs, Adams and Bury (2002) did not detect *D. copei* in the relatively dry, northeastern rain shadow of Olympic National Park, providing evidence that this species is likely sensitive to precipitation.

Coeur d'Alene salamander (Plethodon idahoensis) and Van Dyke's salamander (Plethodon vandykei)

These two sister species are both habitat specialists, restricted to margins of seeps, waterfall splash zones, high-gradient headwater streams, and occasionally moist talus and cave entrances

(Petranka 1998, Wilson Jr and Ohanjanian 2002). Among these habitats, P. idahoensis appears to be most closely tied to seeps (pers. obs.), whereas P. vandykei habitat preferences may vary between regions (Olson and Crisafulli 2014). Both species possess narrow climatic niches and have likely shifted their distributions in response to past climatic changes (Carstens and Richards 2007, Pelletier et al. 2015). Therefore, important SDM predictor variables for these species include the spatial distribution of seeps (corresponding models are currently in development), other physical habitat characteristics (e.g., slope and bedrock geology), and fine-scale climatic variables (e.g., soil temperature). The preferred habitats of these species (e.g., seeps) are often small, discreet, and extremely geographically restricted in nature, and both species are expected to be philopatric based on their patchy distributions and the low movement rates observed in closely related species (Ovaska 1988). Thus, fine-scale pixels (e.g., 30m resolution) are likely needed to accurately model the distribution of each species. In addition, each species features multiple genetic clusters (Carstens et al. 2004). As these different clusters occur in regions with somewhat different climates for both species, they may possess different environmental niches, and thus the distribution of each major clade should potentially be modeled separately. For P. idahoensis, a major genetic divide exists between Selway/Lochsa Drainage populations and all populations farther north. For P. vandykei, a major genetic divide exists between coastal (Willapa Hills/Olympic Peninsula) and Cascades populations, with these two clades often using different microhabitats (Olson and Crisafulli 2014) and potentially representing separate species (Aimee McIntyre, pers. comm.).

Existing SDMs for P. idahoensis and P. vandykei have largely been constructed to help test hypotheses about paleoclimatic refugia. For example, Carstens and Richards (2007) and Pelletier et al. (2015) both used Maxent-based SDMs (Phillips et al. 2006) to predict climatically suitable regions for P. idahoensis and P. vandykei during a previous glacial maximum (21,000 YBP), although the latter paper did so using climate variables at a finer resolution (1km²). Coupled with clear genetic evidence, these models provide evidence that P. idahoensis likely has expanded its range considerably in the past 21,000 years, although patterns were less clear for P. vandykei. In addition, Maxent-based models developed by Nottingham and Pelletier (2021) predicted a geographic shift (but not reduction) in climatically suitable habitat for P. idahoensis by 2050-2070, and an increase in suitable habitat for P. vandykei/P. larselli (modeled together). Unfortunately, the above SDMs all suffer from common pitfalls, including overly coarse grid sizes relative to the scale of habitat use, a lack of spatial bias correction techniques (e.g., point-thinning), probable overfitting due to a large number of predictor variables used, a failure to consider the possibility multiple P. idahoensis and P. vandykei clades with different niches and thus different modeling needs, and the omission of biologically relevant predictor variables (e.g., slope, geology, and the spatial distribution of seeps). Further, P. idahoensis and P. vandykei are both highly dependent on factors other than macroclimate (e.g., seeps), compounding the severity of the above modelling pitfalls. Thus, while genetic data provide compelling evidence for range expansion by P. idahoensis since the last glacial maximum (Carstens and Richards 2007), we recommend against using the above publications to infer potential future climate change impacts on distributions of P. idahoensis and P. vandykei.

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