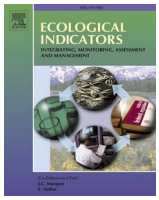
Ecological Indicators 174 (2025) 113488

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Amphibians reveal unexpectedly large differences in potential climate change responses among ecologically similar habitat specialists

Sky T. Button [a,*], Donald J. Brown [b], Jonah Piovia-Scott [a]

[a] School of Biological Sciences, Washington State University, 14204 NE Salmon Creek Ave, Vancouver, WA 98686, USA
[b] U.S. Forest Service, Pacific Northwest Research Station, 42218 NE Yale Bridge Road, Amboy, WA 98601, USA

ARTICLE INFO

Keywords:
Indicator species
Species distribution model
SDM
Niche model
ENM
Climate-smart management
Conservation

ABSTRACT

Climate change is substantially impacting earth's biodiversity, with a massive number of affected species that are difficult to study comprehensively. An "indicator species" approach that generalizes species-specific climate change impacts to broader groups (e.g., ecological groups) could theoretically help overcome this challenge and streamline climate-smart conservation planning. We assessed this approach's viability using four specialist amphibians (*Ascaphus montanus*, *Dicamptodon copei, Plethodon idahoensis*, and *Plethodon vandykei*), for which we expected convergent forecasted trajectories under climate change given that all four species belong to the same group of narrowly groundwater-dependent amphibians in the Pacific Northwest, USA. Using boosted regression trees, we constructed species distribution models (SDMs) for each species and (if applicable) major intraspecific lineage, then forecasted species' trajectories under two climate change scenarios (SSP370 and SSP585) and timeframes (mid-century and late-century). Contrary to our expectation, potential trajectories varied widely among species; most notably, a late-century three-fold potential gain in highly-suitable areas for *P. idahoensis* was contrasted with a potential three-fold loss for the sister species *P. vandykei*. Further, lineage-specific SDMs for *P. vandykei* suggested negligible climate change vulnerability for coastal populations but major vulnerability for Cascades populations. Thus, divergent climate change projections persisted even at an intraspecific scale. Based on our findings, the use of climate change "indicator species" to represent broader groups can be misleading, even within narrowly-defined groups wherein organisms have considerable genetic and ecological overlaps. Lastly, species-tailored variables (e.g., stream or cliff-face seep refugial properties) had consistently high explanatory power, yet many lacked the necessary data to forecast future species' trajectories, highlighting an important future research need.

1. Introduction

Climate change is increasingly jeopardizing biodiversity (Bellard et al. 2012, Kattel 2022, Lindner et al. 2010, Luedtke et al. 2023, Urban 2015), making "climate-smart" conservation approaches increasingly critical (Stein et al. 2014). However, knowledge that can guide these conservation efforts (e.g., regarding species' niches in relation to climate change) remains scarce or unavailable for many species (Howard and Bickford 2014, Pureswaran et al. 2018). A key challenge in obtaining this knowledge is that conservation funding levels are currently dwarfed by the immense magnitude of earth's climate-sensitive biodiversity, meaning that not all climate-sensitive species can be studied (Shortridge et al. 2017). Thus, approaches that can accurately streamline knowledge of species' climate change vulnerabilities hold significant conservation value given current research constraints.

The use of climate change "indicator species" as surrogates for broader climate-sensitive groups has gained traction as a means to facilitate efficient climate-smart management without needing to study every species (Leasi et al. 2021, Pearman et al. 2011, Siddig et al. 2016, Zhang et al. 2020). However, identifying "indicator species" requires demonstrating that these species co-vary in some manner (e.g., in population trends or occupancy) with the broader ecological groups they correspond to (Caro 2010, Lindenmayer and Likens 2011). While many studies have utilized the concept of climate change indicator species (Cruz et al. 2013, de Groot et al. 1995, Leasi et al. 2021, Osipova and Sangermano 2016, Yousefi et al. 2020), the applicability of this label has rarely been critically examined. Nevertheless, viable climate change indicator species have demonstrated utility in at least some limited

* Corresponding author at: 147 Pleasant St., Windsor, CT 06095, USA.
E-mail address: sky.tc.button@gmail.com (S.T. Button).

https://doi.org/10.1016/j.ecolind.2025.113488
Received 27 November 2024; Received in revised form 11 April 2025; Accepted 14 April 2025
Available online 18 April 2025

cases, such as when assessing changes in certain bird communities (Butler et al. 2012), flowering plant phenology (Hufft et al. 2018), and edible Nearctic plant occurrence patterns (Higa et al. 2013). Yet, other empirical studies have found evidence of divergent species-specific climate change impacts (e.g., among forest insects) that render climate change "indicator species" invalid (Pureswaran et al. 2018). In other cases, climate change "indicator species" may appear initially viable but then vanish over time or within certain land use contexts (Clavero et al. 2011, Mair et al. 2018, Zettler et al. 2013). Given these complexities, climate change "indicator species" may streamline ecological research and conservation in certain cases but are also questionable until tested in others, highlighting a crucial need to better evaluate this concept across study groups.

Habitat specialists are one key group for which the viability of climate change "indicator species" is understudied. Notably, specialist ecological groups span a narrower range of environmental conditions than more generalist groups that lack climate change "indicator species" (Pureswaran et al. 2018)—this presumably minimizes within-group niche differences and may therefore allow members of specialist ecological groups to serve as more interchangeable indicators of each other. If feasible to infer group-level climate change impacts, the use of indicator species may reduce the need to collect more exhaustive data on understudied (yet equivalent under climate change) habitat specialists, freeing up resources to conduct more sophisticated research on key indicator species. If viable, this option would hold considerable conservation value for habitat specialists, of which many are disproportionately vulnerable to environmental change (Biesmeijer et al. 2006, Fourcade et al. 2021, Mendoza-Fernández et al. 2022).

Groundwater-dependent amphibians in the Pacific Northwest (PNW), USA represent an excellent candidate ecological group to assess the viability of climate change "indicator species" among different habitat specialists. This group, like many other specialist ecological groups, tolerates a narrow range of environmental conditions, with constituent species using largely overlapping but non-identical microhabitats (Stebbins and McGinnis 2018). In addition, groundwater-specific variables have recently been estimated for the PNW (Button et al., in prep; output metrics available online at doi.org/10.5066/P1989RPN), improving opportunities to study potential climate change trajectories in this group using modern tools such as species distribution models (SDMs; Santini et al. 2021). Further, watercourses used by this group are projected to be highly impacted by changing precipitation and snowmelt patterns under climate change (Melillo et al. 2014, Olson and Burton 2019), making its members potentially important targets for future climate-smart management.

We constructed SDMs for four groundwater-associated specialist amphibians to assess whether potential climate change impacts on individual species would be generalizable across this group. Our study species included the Rocky Mountain tailed frog (*Ascaphus montanus*), Cope's giant salamander (*Dicamptodon copei*), Coeur d'Alene salamander (*Plethodon idahoensis*), and Van Dyke's salamander (*Plethodon vandykei*). We selected these four species based on sufficient range-wide occurrence records to construct informative SDMs. We predicted that all four species would have broadly similar potential climate change trajectories (e.g., shrinking suitability in warm regions), consistent with a tension between climate warming and their shared affinity for cool habitats (Thurman et al. 2022). Our study improves knowledge about whether individual habitat specialists can represent group-wide potential climate change impacts, while also enabling better climate-smart management for study species. Notably, all four of these species are listed as Species of Greatest Conservation Need (SGCN) in at least one state where they occur (USGS 2015) and use habitats likely to be heavily impacted by climate change (Melillo et al. 2014, Olson and Burton 2019).

2. Methods

2.1. Study species

Despite using broadly overlapping habitats, our study species varied in important life history characteristics and genetic structures, thus representing a wide breadth of specialist niches and evolutionary histories for amphibian species in PNW groundwater-based habitats. For example, *A. montanus* and *D. copei* are most closely associated with headwater streams, while *P. idahoensis* and many *P. vandykei* populations depend more heavily on cliff-face seeps (Stebbins and McGinnis 2018). In addition, *D. copei* is usually fully aquatic (Foster et al. 2014), while *A. montanus* has a biphasic life cycle (Olson 2011) and *Plethodon* spp. are non-aquatic direct-developers (Stebbins and McGinnis 2018). Rocky Mountain species (*A. montanus* and *P. idahoensis*) have distinct northern and southern genetic clusters (Carstens et al. 2004, Metzger et al. 2015), while *D. copei* exhibits a more continuous isolation-by-distance pattern (Steele et al. 2009) and *P. vandykei* occurs in three disjunct range segments. Range segments for *P. vandykei* include the Cascades, Olympic Peninsula, and Willapa Hills; the latter two of which may be more isolated from Cascades populations than from each other (Howard et al. 1993). Due to genetic and evolutionary differences among lineages for three of our four study species, these lineages may also have different distributional constraints, making this an important consideration to construct meaningful SDMs (Goudarzi et al. 2021, Hu et al. 2021, Peñalver-Alcázar et al. 2021, Schwalm et al. 2016). For example, coastal (Olympic Peninsula and Willapa Hills) and Cascades *P. vandykei* populations may have different habitat preferences, as the former lineage is often associated with coarse downed wood along headwater stream corridors, while the latter is more strongly associated with cliff-face seeps (McIntyre 2003, Olson and Crisafulli 2014).

2.2. Occurrence points and study regions

We obtained occurrence points for each species from a combination of wildlife agency databases (Washington Department of Fish and Wildlife, U.S. Forest Service, Idaho Department of Fish and Game, and the British Columbia Ministry of Water, Land and Resource Stewardship), online resources (GBIF, VertNet, BISON, and iNaturalist), and new observations from field-based surveys (Button et al., in prep). We discarded records older than 30 years for each species, roughly matching timeframes captured by most historical climate datasets in our analyses. To acknowledge that our study species may have declined to some extent over the past 30 years, we refer to SDMs constructed from the above occurrence points and past climate data as "recent historical" (i.e., reflecting relatively recent conditions) rather than "current".

We removed occurrence records with imprecise coordinates (i.e., those with $>$ 100 m locational uncertainty) and minimized impacts of sampling bias by thinning the remaining occurrence points with the "spThin" package in R for each species (Aiello-Lammens et al. 2015). We used a 1 km distance threshold while thinning, representing a balance between addressing spatial autocorrelation while maintaining a sufficient sample size to construct accurate SDMs (Santini et al. 2021). We defined $>$ 50 valid occurrence points as sufficient for SDMs based on a recent review of the topic (Moudrý et al. 2024), but we acknowledge that models with $>$ 50 yet less than a few hundred occurrence records can still face some limitations (Liu et al. 2019). Finally, we manually delineated species-specific study regions based on a combination of accurate occurrence records and qualitative expert knowledge about where each species may presently occur or be able to disperse to (Fig. 1; P. Ohanjanian, D. Olson, A. McIntyre, and R. Ojala-Barbour pers. comm.).

2.3. Pseudoabsence point selection

Geographic sampling biases often impact occurrence data and can

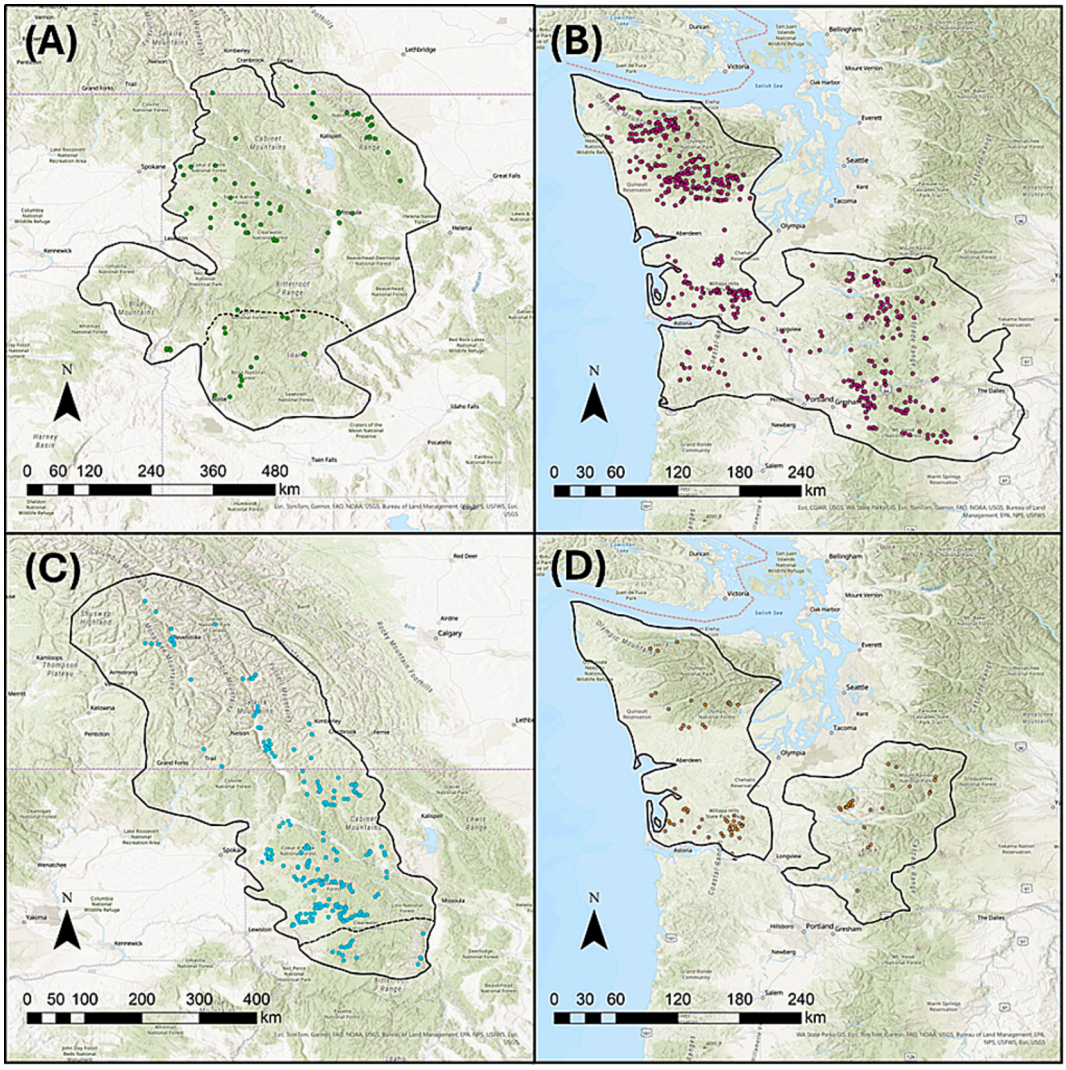


Fig. 1. Species occurrence records retained after thinning and removing non-recent and imprecise records, as well as SDM study areas delineated for (A) *A. montanus* (Rocky Mountain tailed frog), (B) *D. copei* (Cope's giant salamander), (C) *P. idahoensis* (Coeur d'Alene salamander), and (D) *P. vandykei* (Van Dyke's salamander).

cause SDMs to incorrectly conflate undersampled and unsuitable areas, unless pseudoabsence points are designed to account for such biases (Phillips et al. 2009). Therefore, we further minimized bias in SDM outputs by restricting pseudoabsence points to areas where amphibians (including non-target species) had been documented, as well as in areas that we knew in advance were unsuitable for our study species. First, we downloaded recent (1989–2024) records for all PNW amphibian species (including non-target species) using GBIF, VertNet, BISON, and iNaturalist. We removed all records with imprecise coordinates, then buffered the remaining occurrence points by 1 km using ArcGIS Pro (Esri Inc., Redlands USA). We used these polygons to approximate regions that had been sampled for amphibians in general. Next, we created as many pseudoabsence points as possible within these well-sampled regions while constraining points to be $>$ 2 km apart from each other to minimize spatial autocorrelation (Guélat and Kéry 2018), and $>$ 1 km away from the nearest target species record to avoid predicting suitable areas as unsuitable. Using the same distance criteria, we also augmented our pseudoabsence points for each species by selecting additional random points from manually defined areas that fell within the geographic range of each species but were unambiguously unsuitable based on the species' biology (e.g., glaciers, dry grasslands, and large lentic waterbodies). We combined the two sources of pseudoabsence points for each study species, then merged them with each species' occurrence records. The number of resulting pseudoabsence points was 1,615 for *A. montanus*, 3,265 for *D. copei*, 1,777 for *P. idahoensis*, and 1,851 for *P. vandykei*.

2.4. Predictor variables

Based on a shared relationship between our study species and high-gradient lotic habitats, we downloaded 64 initial SDM predictor variables reflecting a large set of plausible distribution-limiting factors related to topography, vegetation/cover, climate, groundwater, and geology (Table S1) under recent historical conditions (Brun et al. 2022, Chen et al. 2022, Isaak et al. 2017, Jaeger et al. 2019, Krosby et al. 2018, Welty and Jeffries 2020, Wenger et al. 2010, Wolock 2003). We included topographic, vegetative/cover-related, and geologic variables given their combined influence on fine-scale microclimate conditions pertinent to non-vagile species (De Frenne et al. 2021, Stoutjesdijk and Barkman 2015, Zellweger et al. 2019). Predictors related to groundwater (e.g., likelihood of seep occurrence) similarly warranted inclusion, based on the groundwater-dependent biology of our study species (Stebbins and McGinnis 2018). Moreover, we considered geology (e.g., dominant rock type) a potentially distribution-limiting for our study species, as it can impact not only the distribution of their key habitats (e.g., cliff-face seeps; Button et al. in prep), but also understudied groundwater dynamics manifesting within those habitats (Briggs et al. 2018, Jefferson et al. 2007). We prioritized using CHELSA-BIOCLIM +

climate data (Brun et al. 2022) over analogous climate datasets, due to a combination of this dataset's fine spatial resolution (~1km), global coverage, and greater accuracy at representing PNW precipitation patterns than other datasets (e.g., WorldClim; Fick and Hijmans 2017).

Predictor variables spanned resolutions of 30 m to ~ 1 km, with the finest resolution approximating plausible home ranges of our study species and the coarsest determined by resolution-based limits of available climate data (Brun et al. 2022). To enable fine-scale predictions consistent with the non-vagility of our study species, all variables with a coarser resolution than 30 m were resampled to 30 m using bilinear interpolation; this enabled the creation of predictor variable raster stacks, which were needed to generate SDM output maps. However, we acknowledge that resampling coarse (e.g., 1 km) variables to finer (e.g., 30 m) spatial scales does not improve their true precision. We also included five seep-related predictor variables generated in a previous study (Button et al., in prep), which were designed to specifically predict habitat characteristics associated with seep-dependent species like *P. idahoensis* and *P. vandykei*. In addition, we included the presence or absence of fire within 40 years as a predictor variable for Rocky Mountain species (*A. montanus* and *P. idahoensis*), as broad-scale and high-intensity fires are becoming more frequent in this region (Riley and Loehman 2016). Lastly, we included sympatry or allopatry with *D. tenebrosus* (based on current range boundaries) as a binary predictor variable for *D. copei*, as co-occurrence between these two species has been linked to lower densities of *D. copei* than elsewhere (Lannoo 2005), potentially due to competition.

To account for species-specific differences in ecological traits, we used a biologically tailored approach to construct SDMs for each species (Irving et al. 2020). First, we constructed a matrix of pairwise correlations for the potential predictor variables, then assigned each variable a subjective 1–5 score based on its hypothesized biological importance for the study species, given personal observations and previous studies (Table S1). For example, 30 m-scale seep-related variables received the highest scores for seep-dependent species (*P. idahoensis* and *P. vandykei*), while stream-related variables received higher scores for the remaining species (*A. montanus* and *D. copei*) based on their primarily stream-based habitat use. If two variables were highly correlated (i.e., Pearson's $R^2 > 0.8$, after standardizing all quantitative variables such that mean = 0 and standard deviation = 1), we retained the one with higher expected species-specific biological relevance and discarded the other, avoiding potentially misleading SDM predictions (Santini et al. 2021). Variables lacking any high pairwise correlations were included in our initial SDMs regardless of their exact subjective score, as overlapping habitats used by our study species meant that each variable was at least moderately plausible as a potential distribution-limiting factor for each species. We accounted for spatial autocorrelation related to these predictor variables by using Moran's eigenvector map (MEM) components as additional predictor variables in our SDMs (Borcard and Legendre 2002, de Mendoza et al. 2018, Dray et al. 2006), using the "PCNM" package in R (Legendre et al. 2012).

2.5. Modeling approaches

We constructed SDMs using two separate modeling approaches, which had separate, complementary purposes. First, we constructed SDMs for contemporary conditions with model predictor variables selected amongst all those that had historical data available (Table S1). The purpose of these models—referred to as "holistic SDMs" hereafter—was to predict contemporary species distributions as accurately as possible to improve immediate research and monitoring capabilities (e.g., prospects to detect new populations and range extensions). In addition, we constructed a second set of SDMs that included only predictor variables with future projections under climate change. The purpose of these models—referred to as "climate projection-constrained (CPC) SDMs" hereafter—was to determine the most likely long-term trajectories of each species under climate change. For this approach, we generated contemporary model predictions to serve as a comparable baseline, then compared these to future projections under climate change (described below) to evaluate potential shifts in suitability over time. We used contemporary estimates from CPC SDMs (and not holistic SDMs) as the sole reference when comparing to future CPC model-based projections, ensuring that these comparisons were grounded in equivalent and thus directly comparable metrics across time.

As a lack of future projections available for many biologically-relevant variables constrained us to using less comprehensive sets of topography-related and CHELSA-BIOCLIM + predictor variables (Brun et al. 2022) for CPC SDMs, during model construction we sought to improve the biological relevance of CPC SDMs by maximizing proxy-based relationships to holistic model variables. To maximize concordance between holistic and CPC SDMs when determining which predictor variable to retain in cases of pairwise redundancy for the latter, we prioritized whichever variable had the higher contemporary correlations with variables that were influential in holistic SDMs yet could not be directly included in CPC SDMs (i.e., due to a lack of future data). This procedure allowed influential, biologically-tailored variables from our holistic SDMs to shape CPC SDMs even when they could not be included in those models directly. However, we acknowledge that the utility of this approach may become more limited over time, if contemporarily associated variables become decoupled under future climate change.

Using each of the two approaches above (holistic and CPC), we constructed species-level SDMs for all study species, as well as lineage-specific SDMs for species with distinct genetic clusters—*A. montanus*, *P. idahoensis*, and *P. vandykei* (Carstens et al. 2004, Howard et al. 1993, Metzger et al. 2015). We apportioned species-level study area boundaries into lineage-specific boundaries based on the spatial extent of each major genetic cluster for each relevant species, then overlaid lineage-specific output maps with each other, to generate range-wide maps for each lineage-split species.

2.6. Model fitting algorithm

We used boosted regression trees (BRTs) and the "dismo" package in R to construct SDMs for each study species (Hijmans et al. 2017), for both of the two modeling approaches above. As BRTs rely on iterative decision trees (each improving on the previous one) instead of curve-fitting algorithms (Elith et al. 2008), they are optimal for accommodating threshold-based relationships (e.g., species-habitat relationships) that can impact habitat specialists, both contemporarily and under climate change (Yu et al. 2020). We maximized the repeatability of BRTs by using the lowest learning rate feasible given tradeoffs with model runtime ($lr = 0.0005$), then further optimized model performance by repeatedly manipulating the tree complexity and bag fraction settings and choosing the combination that yielded the highest cross-validated (CV) AUC score (Greenwell et al. 2019). Cross-validation was carried out using 10 randomly-generated folds, each using 50–75 % of the data for model training (see bag fraction [*bf*] details below). This randomized cross-validation approach can sometimes underestimate prediction error (Roberts et al. 2016), but we deemed this drawback acceptable given that (1) we had previously thinned occurrence records to limit adverse effects of spatial autocorrelation (see above), and (2) alternative approaches to cross-validation (e.g., spatial filtering to select training data) often require large reductions in the training data sample size (Veloz 2009), potentially leading to worse SDM performance overall for species that have modest occurrence datasets to begin with (Liu et al. 2019). We used $tc = 5$ and $bf = 0.5$ for most models, but we occasionally adjusted down to tc = 2–3 and up to bf = 0.65–0.75 to accommodate more modest (e.g., lineage-specific) datasets. In addition to BRTs, we also considered MaxEnt models as a potential alternative for *A. montanus* given the small sample size ($n = 77$) for this species (Wisz et al. 2008), but this option was ultimately abandoned due to consistently poorer model performance metrics (e.g., CV AUC).

After constructing initial SDMs for each species, we repeatedly

refined these models by iteratively removing the least influential variable until all variables had a ≥ 5 % relative influence on the revised model. This "recursive feature elimination" can improve out-of-sample prediction accuracy for BRTs with modest sample sizes (Elith et al. 2008), whereas overly complex tree-based models can lead to poorer model transferability (Wenger and Olden 2012). We finalized each of our revised SDMs after visually inspecting the resulting output maps to ensure that predictions appeared biologically plausible within each species' pre-defined study area (e.g., no "high suitability" predictions within areas known in advance to be unsuitable).

2.7. Generating future projections and comparing SDM outputs

We projected potential shifts in environmental suitability for each species within CPC SDMs based on mid-century (2041–2070) and late-century (2071–2100) climate projections under "SSP370" and "SSP585" socio-economic pathways (Riahi et al. 2017), loosely corresponding to moderate-to-high and severe climate change, respectively. We refer to the former of these two scenarios as "moderate" in the relative sense hereafter. We did not consider more optimistic climate change scenarios, as we aimed to provide wildlife managers with a precautionary framework for conserving our study species (Kriebel et al. 2001), given that these managers have little individual ability to impact overall global carbon emissions. We used the GFDL-ESM4 Earth System Model to forecast future climate data, given its emphasis on ecological processes (Dunne et al. 2020), and because its agreement with other global climate models (GCMs) was qualitatively high within our study region, making it unnecessary to consider multiple GCM forecasts. This decision also improved simplicity when interpreting certain results (e.g., projected changes in suitability over time) that can become more uncertain when using multiple GCMs (Thuiller et al. 2019).

We compared SDM outputs using multiple approaches. For each climate change scenario and timeframe, we visualized projected suitability by color-coding map pixels based on their number of standard deviations above or below the species-specific (or lineage-specific) mean recent historical suitability value in our CPC SDMs, enabling more direct visual comparisons among maps for different species. To determine how well CPC SDMs replicated holistic SDMs under recent historical conditions, we computed the average difference in pixel values between holistic and CPC SDMs, after z-score standardizing both variables to place

Table 1
Cross-validated (CV) AUC scores of holistic SDMs and relative influences of final variables used to construct them for each species and/or lineage. Aug Flow = average discharge for streams within 300 m; Aug STemp = average August water temperature for streams within 300 m; BFI = base flow index; Bio1 = annual mean temperature; Bio2 = mean diurnal range; Bio3 = isothermality; Bio4 = temperature seasonality; Bio15 = precipitation seasonality; Bio17 = precipitation of the driest quarter; Can Cov = percentage canopy cover; CMI = climate moisture index; Curvature = topographic curvature; Dist NHD = distance to nearest NHD flowline; GSP = growing season precipitation; GST = growing season temperature; Max Flow Acc = maximum flow accumulation within 30 m; Max RCCI = maximum riparian climate-corridor index within 90 m; MEM1 = Moran's eigenvector component 1; MEM2 = Moran's eigenvector component 2; NSRH = near-surface relative humidity; PROSPERm = mean 12-year probability of streamflow permanence within 300 m; PROSPERsd = standard deviation of 12-year PROSPER prediction within 300 m; Rock Type = dominant bedrock type; Seep Perm Pred = predicted probability of seep permanence; Seep WTemp Var = predicted relative variation in seep water temperature; Slope = topographic slope; Stand Hgt = stand height; SWE = snow water equivalent; Tot SRef Pred = total abiotic seep refugial potential; Vol Tree = volume of live trees. ASMO = *A. montanus* (Rocky Mountain tailed frog), DICO = *D. copei* (Cope's giant salamander), PLID = *P. idahoensis* (Coeur d'Alene salamander), and PLVA = *P. vandykei* (Van Dyke's salamander). Several other variables were tested in initial models (Table S1) but discarded in all cases due to minimal influence on models and/or inferior species-specific relevancy compared to a highly correlated variable. Results are not shown for southern lineages of *A. montanus* and *P. idahoensis*, due to a lack of model convergence.

	ASMO range-wide holistic	ASMO north holistic	DICO range-wide holistic	PLID range-wide holistic	PLID north holistic	PLVA range-wide holistic	PLVA east holistic	PLVA west holistic
CV AUC	0.935	0.925	0.840	0.925	0.912	0.819	0.840	0.870
Aug Flow	5.3	—	—	—	20.6	—	—	—
Aug STemp	8.6	11.6	16.6	—	—	8.1	—	7.0
BFI	—	—	—	—	—	—	—	—
Bio1	—	—	—	—	—	—	—	—
Bio2	—	—	—	—	—	—	—	—
Bio3	—	—	—	—	—	—	—	—
Bio4	5.2	—	—	—	—	—	8.2	—
Bio15	—	—	—	10.0	—	—	7.5	—
Bio17	—	—	—	—	—	—	—	—
Can Cov	—	—	—	—	—	—	—	—
CMI	7.8	—	17.3	—	—	—	—	—
Curvature	—	—	—	—	—	—	7.0	—
Dist NHD	30.2	26.1	—	7.9	8.9	9.8	5.2	9.6
GSP	—	—	—	—	—	—	—	9.7
GST	—	—	7.2	—	—	—	—	—
Max Flow Acc	14.3	26.0	11.5	5.3	6.4	11.3	7.4	12.6
Max RCCI	10.0	15.6	11.8	11.4	—	—	—	—
MEM1	—	—	7.9	—	—	—	—	—
MEM2	—	—	9.2	—	—	12.6	16.1	8.7
NSRH	10.2	—	—	7.3	—	—	10.5	—
PROSPER Mean	—	—	—	—	—	7.5	6.7	6.1
PROSPER SD	—	—	—	7.9	9.5	6.5	5.9	6.6
Rock Type	8.3	12.1	9.3	9.0	15.0	11.4	—	8.5
Seep Perm Pred	—	—	—	—	—	—	—	8.5
Seep WTemp Var	—	—	9.3	7.5	7.5	13.4	6.1	13.5
Slope	—	—	—	6.2	7.9	—	—	—
Stand Hgt	—	—	—	—	—	5.9	9.8	9.1
SWE	—	8.5	—	20.8	17.5	—	—	—
Tot. SRef Pred	—	—	—	6.7	6.6	7.1	9.6	—
Vol Tree	—	—	—	—	—	6.4	—	—

them on the same scale. We also estimated relative uncertainty in our predictions for each SDM based on CV AUC scores (Greenwell et al. 2019). We used the same general cutoffs as Araújo et al. (2005) to infer qualitative predictive accuracy from AUC (e.g., AUC > 0.9 reflecting excellent fit, AUC < 0.7 reflecting poor fit, etc.). Lastly, we computed relative changes in suitability by subtracting predicted recent historical suitability (specifically for CPC SDMs) from projections under future climate scenarios and timelines, then dividing by the standard deviation of recent historical suitability (Oliver et al. 2012).

3. Results

3.1. Occurrence points and model performance

After discarding unusable occurrence data (i.e., points with imprecise coordinates or that were > 30 years old) and thinning points, there were 77 valid remaining occurrence points for *A. montanus*, 451 for *D. copei*, 235 for *P. idahoensis*, and 202 for *P. vandykei* (Fig. 1). These sample sizes yielded relatively well-performing holistic SDMs, with CV AUC scores of 0.935, 0.840, 0.925, and 0.819, respectively, consistent with low-to-moderate model uncertainty (Table 1). In general, CPC SDMs performed similarly or slightly worse than holistic SDMs, yielding CV AUC scores of 0.914, 0.828, 0.917, and 0.849 for the above species, respectively. Predicted recent historical suitable areas appeared more fragmented and granular within holistic SDMs than CPC SDMs based on visual inspection (Figs. 2-7).

Compared to the range-wide holistic model for *P. vandykei* (CV AUC = 0.819), lineage-specific models yielded a moderately higher model performance for this species' eastern lineage (CV AUC = 0.840), and notably higher model performance for the western lineage (CV AUC = 0.870). For CPC SDMs, all three models for *P. vandykei* were within 0.04 AUC units of each other (range = 0.845–0.849). In contrast, splitting *A. montanus* and *P. idahoensis* into distinct lineages had negative consequences on SDM performance; southern-lineage models failed to converge for *A. montanus* and *P. idahoensis*. Modeled suitability estimates in Canada were sometimes impacted by a lack of data for certain predictor variables within the country, representing a practical modeling limitation for *A. montanus* and *P. idahoensis*.

Comparing model types and geographic trends.

Holistic and CPC SDMs yielded similar predictions overall for our study species (Figs. S1-S4), which—after z-scoring both outputs—were on average, 0.14, 0.42, 0.27, 0.45, 0.48, and 0.29 standard deviations apart from each other for *A. montanus*, *D. copei*, *P. idahoensis*, and *P. vandykei* (species-wide, Cascades, and coastal models), respectively. In general, areas predicted as most suitable under recent historical conditions for *A. montanus* consisted of small riparian pockets scattered across the species' range (Fig. 2), although this result should be interpreted cautiously due to our small sample size of valid occurrence points for this species (n = 77). Relative suitability was highest overall in portions of the Olympic Peninsula for *D. copei*, with more limited and geographically isolated suitability predicted in the Cascades. For *P. idahoensis*, predicted recent historical suitable areas were aligned with steep-sided canyons such as the North Fork Clearwater, Selway, Lochsa, and other climatically similar drainages in the Northern Rockies, with overall more localized suitability in Canada. Lastly, the Cascades and Willapa Hills were predicted as most suitable for *P. vandykei* within both species-level and lineage-specific SDMs, with additional localized suitable pockets in the Olympic Peninsula.

3.2. Important predictor variables

Primary rock type, distance to National Hydrography Dataset (NHD) flowline, and maximum flow accumulation within 30 m were consistently influential for predicting our study species' distributions overall,

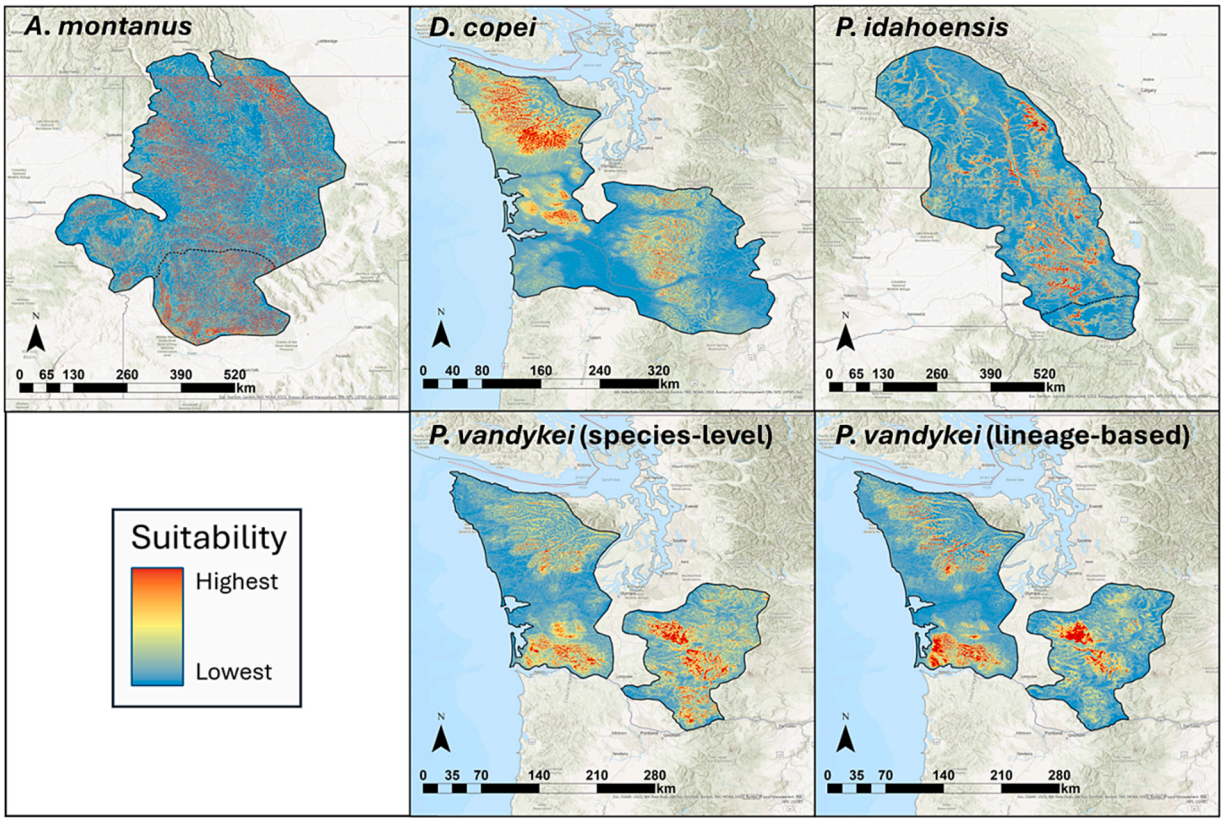


Fig. 2. Recent historical suitability, based on standard deviations above or below the overall mean for species-level models of *A. montanus* (Rocky Mountain tailed frog), *D. copei* (Cope's giant salamander), *P. idahoensis* (Coeur d'Alene salamander), and species-level or lineage-specific models *P. vandykei* (Van Dyke's salamander), based on holistic SDMs (Table S1). Dashed lines within SDM regions divide major genetic lineages for each applicable species.

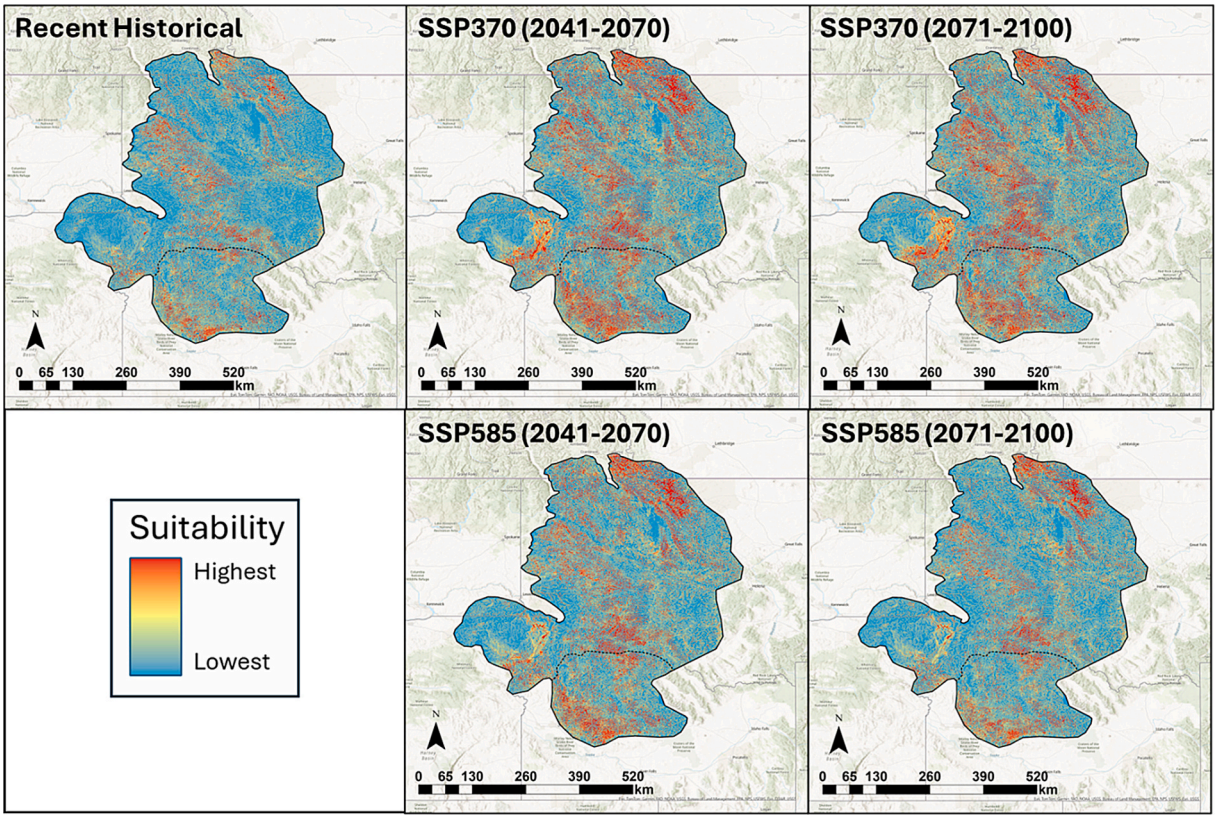


Fig. 3. Current and projected future suitability for *A. montanus* (Rocky Mountain tailed frog) under different climate change scenarios and timelines, based on a range-wide, species-level SDM, with predictor variables limited to those with climate change projections. Dashed line within SDM region divides major genetic lineages.

and these were retained in at least one model for each species (Tables 1-2). In both holistic and CPC SDMs, favorable rock types showed species-specific rather than group-wide patterns, with high predicted suitability most closely linked to *meta*-argillite and andesite for *A. montanus*, tholeiite for *D. copei*, siltstone for *P. idahoensis*, and a wider variety of rock types for *P. vandykei*. However, consistent with biological overlaps among species, predicted habitat suitability was highest for all four species and both SDM types when pixels were located immediately adjacent to watercourses and had at least marginal flow accumulation (i.e., a non-zero total upslope area draining into the pixel), with clear thresholds (i.e., steep changes in predicted suitability above or below a certain value of the predictor variable) related to both of these variables for all species (Figs. S5-S20). In addition, *P. idahoensis* and *P. vandykei*—the two most seep-dependent species—were each associated with at least two variables developed specifically to represent their preferred cliff-face seep habitats within holistic SDMs. High predicted suitability was associated with low seep water temperature variation and high overall predicted seep refugial capacity (which combines the likelihood of seep occurrence with expected thermal and hydrologic stability) for both species, as well as a high predicted probability of seep permanence for the western clade of *P. vandykei*. These two species were also associated with steep slopes in most models. In comparison, *A. montanus* and *D. copei* were more closely associated with relatively cool August stream temperatures (Table 1). All four study species were positively linked to cool and/or moist climates via at least one predictor variable, in both holistic and CPC SDMs (Figs. S5-S20). Relative to the other species, *P. idahoensis* was instead associated with relatively warm climates with long growing seasons—except for in dry climates wherein aridity (based on the Miami Model for calculating net primary productivity [NPP], which was an influential predictor variable) became limiting regardless of warmth (Fig. S10).

3.3. Projected climate change responses

Projected changes in pixel suitability under different climate change scenarios and timeframes differed widely among species (Tables 3-5; Figs. 3-8 and S21). A moderate increase in average suitability (35–42 %) was projected for *A. montanus* during both mid-century (2041–2070) and late-century (2071–2100) timeframes under the moderate climate change scenario (SSP370), although this increase was more modest under a more severe (SSP585) climate change scenario (15–27 %). Average range-wide suitability decreased under all climate change scenarios for *P. vandykei* using a species-level modeling approach, including by 25 % and 40 %, respectively, for mid-century and late-century outputs under a moderate (SSP370) climate change scenario, and by 32 % and 37 % for these same timeframes under a more severe (SSP585) scenario. Modeling *P. vandykei* as two separate lineages, in contrast, resulted in negligibly positive changes in projected suitability for the western (coastal) lineage under climate change (increasing 0–6 %), but similarly negative changes in projected suitability as in the species-level model for the eastern (Cascades) lineage (decreasing 25–44 %; Table 3). In stark contrast, environmental suitability for *P. idahoensis* was projected to increase 68 % by 2041–2070 and 132 % by 2071–2100 under moderate (SSP370) climate change. This trend was even more pronounced under severe (SSP585) climate change, wherein average suitability for *P. idahoensis* was projected to increase 93 % by 2041–2070 and 213 % by 2071–2100. Lastly, for *D. copei*, average suitability was projected to negligibly decrease 1 % by 2041–2070 and negligibly increase by 4 % by 2071–2100 under moderate (SSP370) climate change. The more severe scenario (SSP585) yielded modest gains in average suitability for this species: 5 % by 2041–2070, and 17 % by 2071–2100. Changes in highly suitable habitat (defined as the pixels scoring above the 90th percentile value within recent historical maps) for each species (or lineage) followed overall similar patterns relative to

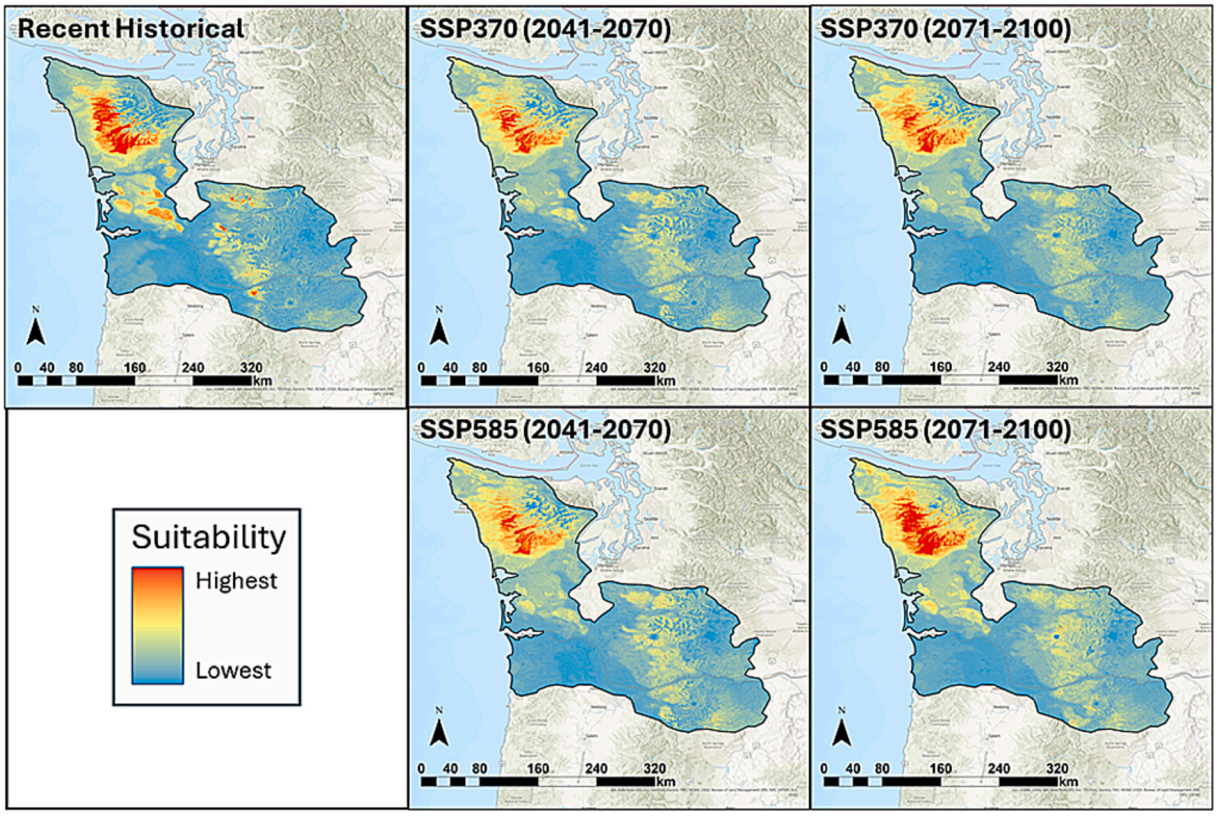


Fig. 4. Current and projected future suitability for *D. copei* (Cope's giant salamander) under different climate change scenarios and timelines, based on a range-wide, species-level SDM, with predictor variables limited to those with climate change projections.

changes in projected average suitability, albeit with wider variation (Tables 3-5). By exception, suitability in these pixels decreased by 4–19 % for *D. copei*, contrasting with modest gains in overall pixel suitability described above.

Geographic shifts in environmental suitability scores were also highly variable among our study species (Fig. 8). Suitability for *A. montanus* was expected to increase in several different portions of its range—modestly in most cases. In addition, *P. idahoensis* gained additional projected suitability—much more notably than *A. montanus*—within its pre-existing most favorable regions, as well as in a large area around (but especially north of) these regions. This geographic trend for *P. idahoensis* intensified with both time and climate change intensity (Figs. 5 and 8). Conversely, environmental suitability for *P. vandykei* was projected to decrease sharply overall within contemporarily suitable areas. This was not accompanied by any notable increases in suitability elsewhere for the eastern lineage, other than in highly localized pockets; the western lineage had more variable results depending on whether species-level or lineage-specific models were used (Figs. 6-8). Similarly, the highest suitability areas for *D. copei* did not exhibit long-distance geographic shifts overall (except for reduced suitability in throughout most of Willapa Hills region), although short-distance shifts were more common (e.g., from east to west within the Cascades and Olympic Peninsula) and the spatial extent of these areas was projected to either shrink or grew, depending on the climate change scenario and timeframe (Figs. 5 and 8). When modeling *P. vandykei* as two separate lineages, the western (Olympic/Willapa Hills) lineage exhibited virtually no projected geographic shifts under future climate change, whereas the eastern (Cascades) lineage lost considerable projected suitability in foothill regions and retained or gained suitability within only a few small patches surrounding taller and more glaciated peaks (Figs. 7-8).

4. Discussion

Our study assessed whether four Pacific Northwest (PNW) endemic and groundwater-dependent amphibians would have similar potential climate change trajectories, consistent with the concept of specialist climate change indicator species. However, our results did not support the use of indicator species—potential climate change trajectories diverged considerably among study species, spanning a wide range between sharply declining and sharply increasing suitability. Notably, none of our study species were projected to experience generalized poleward shifts in suitable areas under climate change as hypothesized, and the magnitude of geographic shifts in suitability varied widely among species. These divergent results occurred despite shared traits among all species (e.g., narrow, overlapping niches, sufficient occurrence and climate data for high-quality SDMs, and a shared influence of biologically relevant factors like watercourse proximity), which appeared anecdotally favorable for convergent climate change trajectories among study species. Given our overall findings, the use of specialist climate change "indicator species" would be misleading in our study system and may have a negative net impact on the conservation of specialist ecological groups. However, a lack of projected data under future climate change limited the usability of many species-tailored variables for projecting potential future climate change impacts. This also made it infeasible to compare projected future suitability to holistic estimates of contemporary suitability (i.e., due to statistical non-equivalence of the two models) and represents a notable (but not unique) constraint of our study.

The most notable interspecific disparity in our results was, surprisingly, between two sister species: *P. idahoensis* and *P. vandykei*. Despite a close evolutionary relationship, our SDMs projected a three-fold increase in highly suitable areas by 2071–2100 under a severe climate change scenario (SSP585) for *P. idahoensis*, but a three-fold loss for *P. vandykei* (Figs. 5-6). Variables contributing to these divergent results

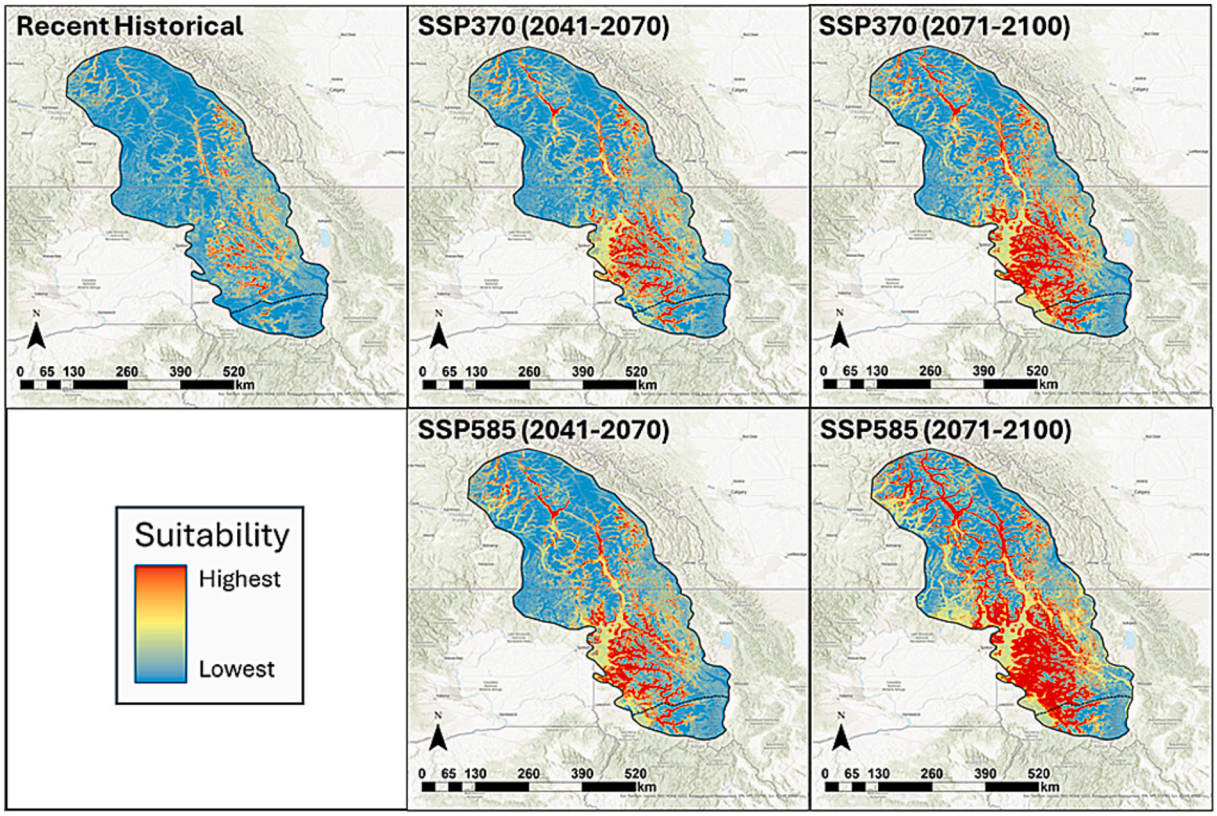


Fig. 5. Current and projected future suitability for *P. idahoensis* (Coeur d'Alene salamander) under different climate change scenarios and timelines, based on a range-wide, species-level SDM, with predictor variables limited to those with climate change projections. Dashed line within SDM region divides major genetic lineages.

were associated with subtle but unique ecological traits for each study species. For example, geographic trends in suitability projections for *P. idahoensis* matched this species' avoidance of chronically frigid or arid climates (including in areas with seeps; SB unpubl. data), which were accounted for simultaneously by the most influential predictor variable in the CPC SDM for this species (NPP; Table 2). Further, while this species tends to be most active during mild spring and fall conditions (Lynch 1984), it also appears capable of surface activity during unseasonably warm winter days (pers. obs.), which, along with thermally stable seeps, may limit foraging constraints imposed by a seasonal expansion of mid-year heat under climate change. In contrast, this adaptive behavior has not been documented for *P. vandykei*, and numerous cold, snowmelt-driven seeps once occupied by this species in the Cascades appear to have vanished under recent historical climate change (Button et al., in review). Moreover, regional variation in land use impacts has not been documented for *P. idahoensis*, whereas *P. vandykei* may be less ecologically sensitive to logging in the Olympic Peninsula than Willapa Hills (Olson and Crisafulli 2014, Raphael et al. 2002). This region-dependent sensitivity for *P. vandykei* may be partly explained by predictions of much higher environmental suitability in the Willapa Hills than Olympic Peninsula, which could theoretically improve fitness and thus better insulate Willapa Hills populations from land use change.

Large projected expansions in suitable areas for *P. idahoensis* under climate change were also analogous to its > 50 m/yr straight-line rate of northward range expansion following the retreat of the Cordilleran Ice Sheet (CIS) under historical climate warming (Carstens et al. 2004). In contrast, *P. vandykei* did not achieve comparable northerly range expansion during this period and appears to be highly non-vagile (McIntyre 2003). However, despite its presumably superior range expansion capabilities to *P. vandykei*, many areas projected to become suitable for *P. idahoensis* are nonetheless unlikely to be colonized within the timeframe of this study. Based on a range expansion rate of ~ 50–200 m/yr (the upper estimate assumes that range expansion capabilities are equal to the approximate historical maximum rate of CIS retreat; Reyes et al. 2024), only ~ 4–16 km of range expansion is expected by 2100 for *P. idahoensis*.

Our finding of highly divergent potential climate change impacts among species was similarly tied to biology of *A. montanus* and *D. copei*. For example, *A. montanus* occurs in areas with relatively high temperature variation due to its overall more southerly distribution than other endemic Rocky Mountain species in the Pacific Northwest (e.g., *Dicamptodon aterrimus* and *P. idahoensis*; Stebbins and McGinnis 2018), consistent with a positive association with temperature seasonality in our CPC SDM for this species, and potentially conferring benefits under climate change (Fig. S6). However, this result should be treated with caution considering the low final sample size of valid occurrence points for *A. montanus* ($n = 77$). Counterintuitively, the moderate (SSP370) climate change scenario resulted in a greater increase in projected suitability for *A. montanus* than the more severe (SSP585) scenario (Table 3). This pattern appears best explained by temperature seasonality, which—driven by a combination of cold winters and hot summers—was highest under the moderate climate change scenario, lower under the severe scenario, and lowest under contemporary conditions. This non-monotonic relationship arose because summer temperatures were projected to increase faster than winter temperatures in both scenarios, but the severe scenario had more evenly distributed warming across seasons, reducing overall temperature seasonality compared to the moderate scenario. In contrast to the moderate positive impacts of climate change projected for *A. montanus*, *D. copei* was projected to be the least impacted by climate change among our study species, which may reflect its more fully-aquatic life history than our other three study species (Foster et al. 2014), given that aquatic habitats are more thermally buffered than terrestrial ones.

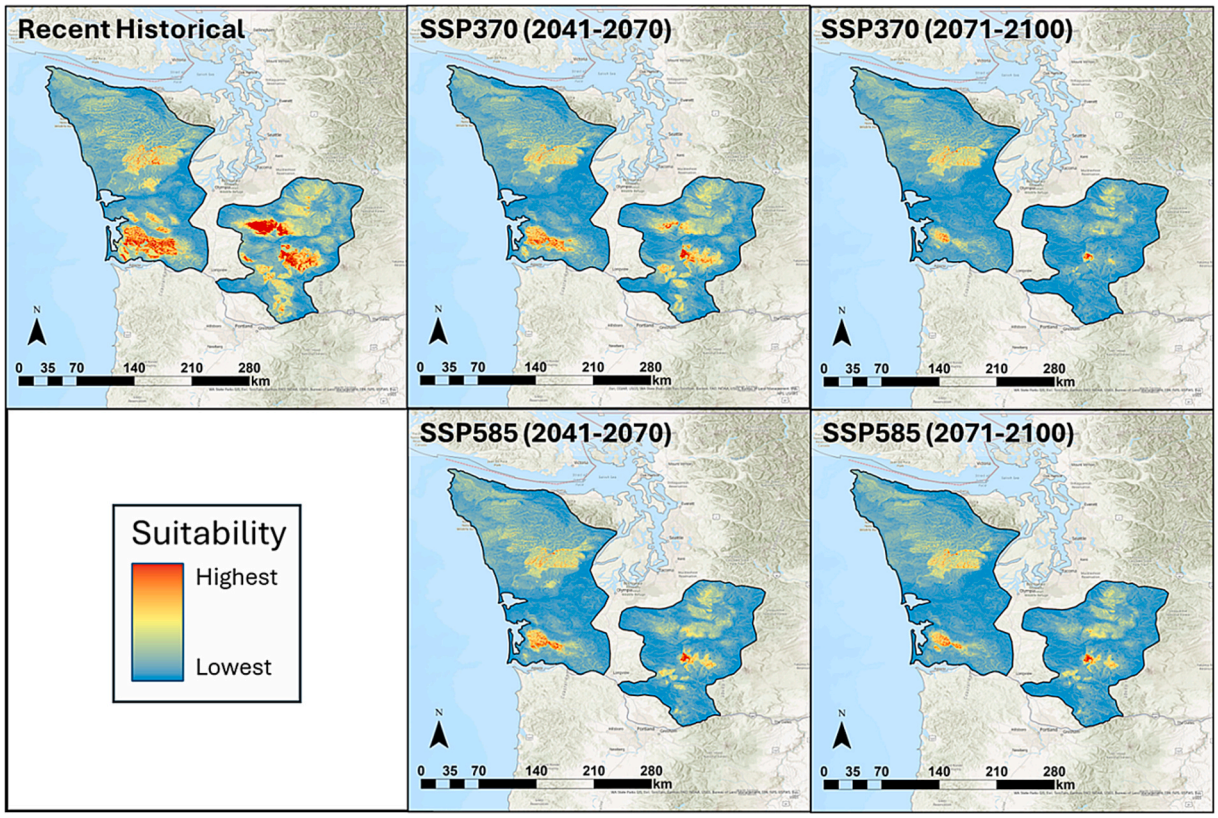


Fig. 6. Current and projected future suitability for *P. vandykei* (Van Dyke's salamander) under different climate change scenarios and timelines, based on a range-wide, species-level SDM, with predictor variables limited to those with climate change projections.

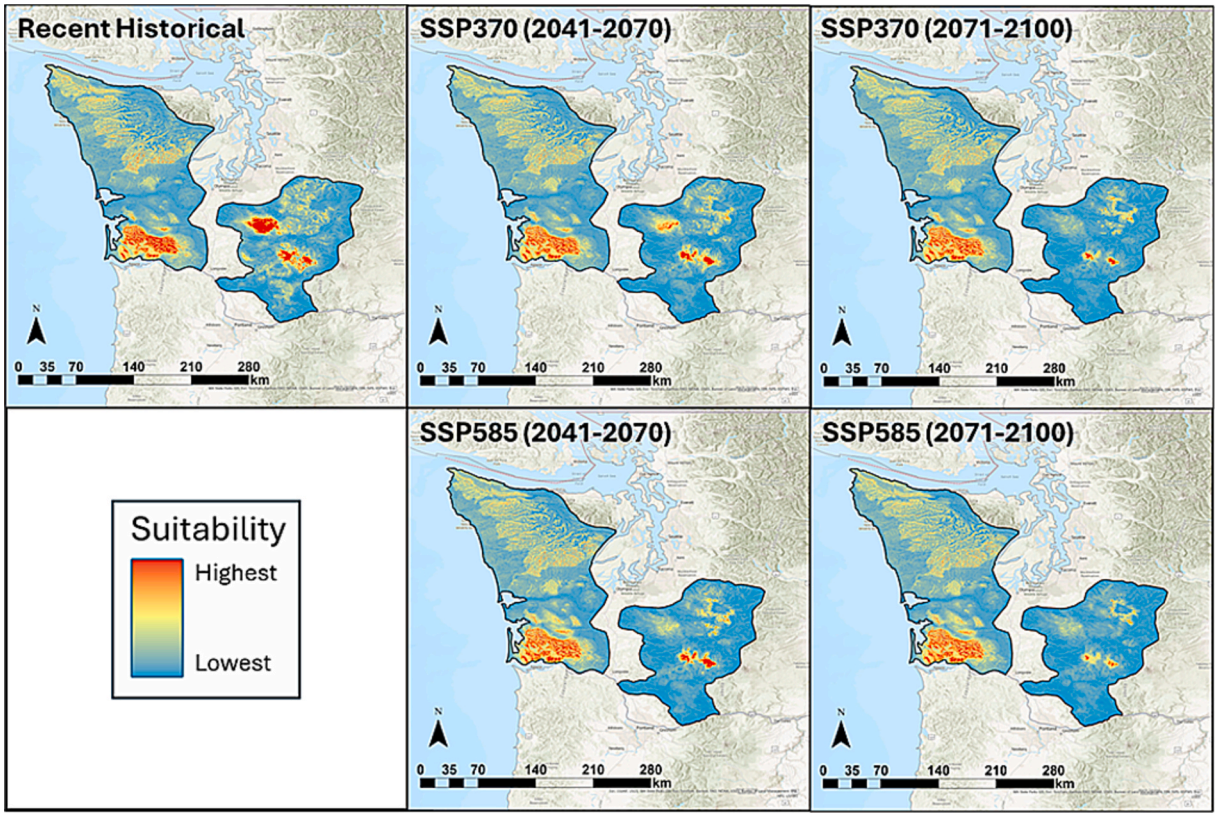


Fig. 7. Current and projected future suitability for *P. vandykei* (Van Dyke's salamander) under different climate change scenarios and timelines for two overlaid lineage-based SDMs (eastern and western lineages), built using predictor variables limited to those with climate change projections.

Table 2
Cross-validated (CV) AUC scores for SDMs constrained to predictor variables projectable under climate change, as well as relative influences of final predictor variables for each species and/or lineage. Bio1 = annual mean temperature; Bio2 = mean diurnal range; Bio3 = isothermality; Bio4 = temperature seasonality; Bio12 = annual precipitation; Bio15 = precipitation seasonality; Bio17 = precipitation of the driest quarter; Curvature = topographic curvature; Diff North = angular difference (in degrees) between pixel aspect and northerly aspect; Dist NHD = distance to nearest NHD flowline; FCF = frost change frequency; GDD = annual growing degree days; GSL = growing season length; GSP = growing season precipitation; GST = growing season temperature; Max Flow Acc = maximum flow accumulation within 30 m; Max TWI = maximum topographic wetness index within 30 m; MEM1 = Moran's eigenvector component 1; MEM2 = Moran's eigenvector component 2; NPP = net primary productivity; Rock Type = dominant bedrock type; Slope = topographic slope; SWE = snow water equivalent. ASMO = *A. montanus* (Rocky Mountain tailed frog), DICO = *D. copei* (Cope's giant salamander), PLID = *P. idahoensis* (Coeur d'Alene salamander), and PLVA = *P. vandykei* (Van Dyke's salamander). Several other variables were tested in initial models (Table S1) but discarded in all cases due to minimal influence on models and/or inferior species-specific relevancy compared to a highly correlated variable. Results are not shown for southern lineages of *A. montanus* and *P. idahoensis*, due to a lack of model convergence.

	ASMO range-wide	ASMO north	DICO range-wide	PLID range-wide	PLID north	PLVA range-wide	PLVA east	PLVA west
CV AUC	0.914	0.898	0.828	0.917	0.914	0.849	0.845	0.849
Bio1	—	—	—	—	—	—	—	5.7
Bio2	—	—	—	—	—	—	—	—
Bio3	—	—	7.8	—	—	—	—	—
Bio4	10.5	7.6	—	—	—	—	—	—
Bio12	6.9	—	—	—	—	—	8.0	—
Bio15	—	—	5.1	8.8	7.8	7.6	7.2	—
Bio17	—	6.6	—	—	—	14.0	9.2	—
Curvature	—	—	—	—	—	7.1	—	7.5
Diff North	—	—	—	—	—	—	—	12.8
Dist NHD	36.7	28.3	7.3	13.9	15.1	11.2	8.8	12.2
FCF	—	—	—	—	—	—	—	—
GDD	—	—	7.0	—	—	—	—	—
GSL	—	—	—	—	6.0	—	—	—
GSP	—	—	13.6	—	—	—	8.1	15.1
GST	—	—	11.1	—	—	—	—	—
Max Flow Acc	25.0	34.8	11.2	8.7	8.5	15.9	11.0	17.3
Max TWI	—	—	5.6	—	—	5.9	—	6.3
MEM1	—	—	9.9	8.6	—	—	8.7	—
MEM2	—	—	11.1	8.3	9.2	16.1	19.1	11.1
NPP	—	—	—	11.5	10.8	—	—	—
Rock Type	13.8	12.2	13.5	10.0	11.5	17.0	5.0	12.0
Slope	—	—	—	12.0	14.3	5.2	7.2	—
SWE	7.0	10.4	—	18.3	16.9	—	7.8	—

Table 3
Projected proportional changes in overall average pixel suitability for each species, under each climate change scenario and timeframe. Comparisons are relative to outputs of recent historical SDMs generated with climate projection-limited sets of predictor variables. In addition, lineage-specific outputs are shown for P. vandykei, as both CPC lineage-based models for this species resulted in improved model performance (based on cross-validated AUC score) compared to a range-wide model (Table 2). ASMO = *A. montanus* (Rocky Mountain tailed frog), DICO = *D. copei* (Cope's giant salamander), PLID = *P. idahoensis* (Coeur d'Alene salamander), and PLVA = *P. vandykei* (Van Dyke's salamander).

		Moderate climate change (SSP370)		Severe climate change (SSP585)	
Taxon	Average Raw Pixel Score	Mid-century (2041–2070)	Late Century (2071–2100)	Mid-century (2041–2070)	Late Century (2071–2100)
ASMO	0.026	0.035 (+35 %)	0.037 (+42 %)	0.033 (+27 %)	0.030 (+15 %)
DICO	0.100	0.099 (−1%)	0.104 (+4%)	0.105 (+5%)	0.117 (+17 %)
PLID	0.060	0.101 (+68 %)	0.139 (+132 %)	0.116 (+93 %)	0.188 (+213 %)
PLVA species-level	0.075	0.056 (−25 %)	0.045 (−40 %)	0.051 (–32 %)	0.047 (−37 %)
P. vandykei eastern lineage	0.081	0.061 (−25 %)	0.046 (−43 %)	0.054 (–33 %)	0.045 (−44 %)
P. vandykei western lineage	0.067	0.067 (±0%)	0.068 (+1%)	0.071 (+6%)	0.071 (+6%)

Table 4
Projected proportional changes in average suitability under each climate change scenario and timeframe, strictly among historically highly-suitable pixels for each species. Pixels were defined arbitrarily as "historically highly-suitable" if their scores ranked among the top 10 % among all pixels within the modeling area for their respective species, based on outputs from recent historical SDMs generated with climate projection-limited sets of predictor variables. In addition, lineage-specific outputs are shown for P. vandykei, as both lineage-based models for this species resulted in improved performance (based on cross-validated AUC score) compared to a range-wide model (Table 2). ASMO = *A. montanus* (Rocky Mountain tailed frog), DICO = *D. copei* (Cope's giant salamander), PLID = *P. idahoensis* (Coeur d'Alene salamander), and PLVA = *P. vandykei* (Van Dyke's salamander).

		Moderate climate change (SSP370)		Severe climate change (SSP585)	
Taxon	Average Raw Score in Top 10 % Pixels	Mid-century (2041–2070)	Late Century (2071–2100)	Mid-century (2041–2070)	Late Century (2071–2100)
ASMO	0.162	0.245 (+51 %)	0.258 (+59 %)	0.228 (+41 %)	0.197 (+22 %)
DICO	0.343	0.277 (−19 %)	0.278 (−19 %)	0.281 (−18 %)	0.328 (−4%)
PLID	0.314	0.456 (+45 %)	0.530 (+69 %)	0.484 (+54 %)	0.570 (+82 %)
PLVA species-level	0.297	0.192 (−35 %)	0.132 (−56 %)	0.164 (−45 %)	0.146 (−51 %)
P. vandykei eastern lineage	0.330	0.206 (−38 %)	0.127 (−62 %)	0.162 (−51 %)	0.096 (−71 %)
P. vandykei western lineage	0.273	0.260 (−5%)	0.260 (−5%)	0.271 (−1%)	0.268 (−2%)

Table 5
Change in the total proportion of pixels surpassing a historical "high suitability" threshold for each species by 2071–2100 compared to recent historical suitability, under a moderate (SSP370) climate change scenario. Pixels were arbitrarily defined as "high suitability" if their score would have ranked among the top 10 % of all pixels within the recent historical SDM generated using climate projection-limited sets of predictor variables for each species. In addition, lineage-specific outputs are shown for P. vandykei, as both lineage-based models for this species resulted in improved model performance (based on cross-validated AUC score) compared to a range-wide model (Table 2). ASMO = *A. montanus* (Rocky Mountain tailed frog), DICO = *D. copei* (Cope's giant salamander), PLID = *P. idahoensis* (Coeur d'Alene salamander), and PLVA = *P. vandykei* (Van Dyke's salamander).

Taxon	Historical Top 10 % Scoring Threshold	Historical Proportion Above Threshold	Late Century (2071–2100) Proportion Above Threshold Under SSP370 Scenario
ASMO	0.037	0.100	0.122 (+22 %)
DICO	0.212	0.100	0.098 (−2%)
PLID	0.130	0.100	0.296 (+196 %)
PLVA species-level	0.153	0.100	0.031 (−69 %)
P. vandykei eastern lineage	0.178	0.100	0.033 (−67 %)
P. vandykei western lineage	0.122	0.100	0.103 (+3%)

Despite highly divergent potential climate change trajectories among our study species, all four were linked to the presence of non-zero flow accumulation and nearby watercourses, suggesting that traits present across the ecological group were successfully captured in our SDMs. In addition, geology has played an important role beyond climate in modifying habitat suitability for these species (e.g., through the creation of large, thermally stable basaltic aquifers in the Cascades following past volcanic eruptions; Jefferson et al. 2006), and dominant bedrock type was a top-ranking variable for all four species (Tables 1-2). This finding was particularly consistent with field observations for *P. idahoensis* and *P. vandykei*, which often depend heavily on impermeable, fracture-prone rock types that force groundwater to the surface at preferred cliff-face seeps (Briggs et al. 2018, McIntyre et al. 2006, Wilson et al. 1997). These shared findings among our study species suggest that their divergent projected climate change trajectories were not due merely to inadequate variables to capture ecological commonalities in our SDMs.

Notably, estimated changes in overall suitability may have been misleadingly optimistic for some study species. For example, although overall suitability scores increased slightly for *D. copei* over time under all climate change scenarios evaluated, this could be overshadowed by a modest net decrease in initially highly suitable areas (Tables 3-5), considering the species' narrow ecological preferences (Foster et al. 2014). Similarly, while overall average pixel suitability was projected to decline by 43 % for the eastern (Cascades) lineage of *P. vandykei* by 2071–2100 under a realistic SSP370 climate change scenario, this projected decline increased to 62 % among historically highly suitable pixels, accompanied by a 67 % projected decrease in the proportion of pixels that fell above our "highly suitable" threshold (Tables 3-5).

The design of our SDMs had both strengths and limitations. For instance, newly-created metrics for cliff-face seeps (SB unpubl. data) helped ensure that SDMs for *P. idahoensis* and *P. vandykei* were (appropriately) highly biologically relevant. Although diminutive in size, these specialized habitats are critical for both species (McIntyre et al. 2006, Wilson et al. 1997), making seep-related GIS layers a key prerequisite to construct biologically relevant SDMs for these species. Notably, our SDM

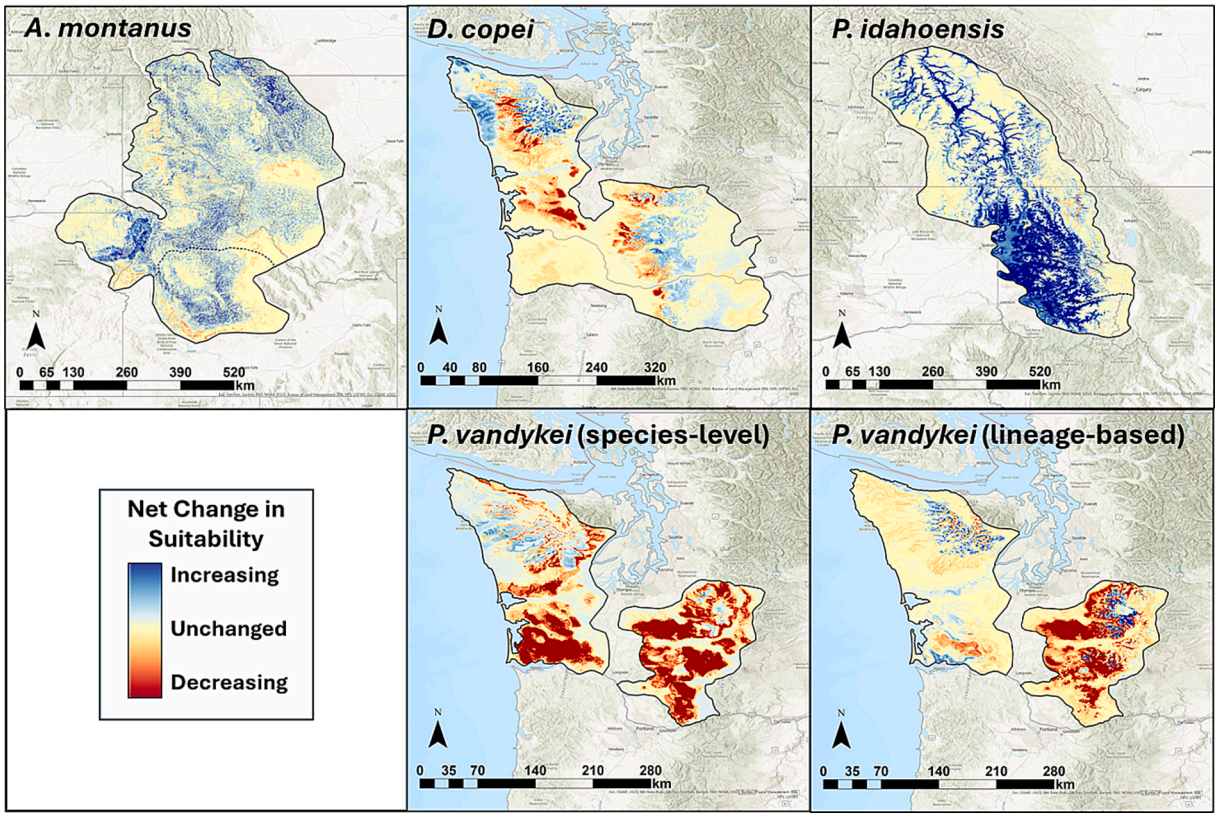


Fig. 8. Geographic variation in projected changes in suitability over time for (A) *A. montanus* (Rocky Mountain tailed frog), (B) *D. copei* (Cope's giant salamander), (C) *P. idahoensis* (Coeur d'Alene salamander), and *P. vandykei* (Van Dyke's salamander) based on either a range-wide model (D) or lineage-specific model (E). Outputs were calculated by subtracting recent historical suitability from late-century (2071–2100) projected suitability under a moderate climate change scenario (SSP370). Colors are centered on zero, with standard deviations matching those of maps from recent historical SDMs constructed from CPC predictor variables for each species.

projections for *P. idahoensis* and *P. vandykei* differed considerably from those of an earlier study that used a more generic set of predictor variables (Nottingham and Pelletier 2021), highlighting the importance of biologically tailored SDM inputs (Santini et al. 2021, Sofaer et al. 2019, Zangiabadi et al. 2021). Projected data under climate change have become increasingly available for biologically tailored variables in recent years (Brun et al. 2022) but remain non-existent for many metrics. For example, seep-related metrics, August stream temperature, and streamflow metrics were all key predictors of at least one study species within our holistic SDMs (Table 1), yet these were unusable to infer potential climate change impacts on our study species due to a lack of future projections. This made our CPC SDM approach necessary yet also reflective of a key limitation of this study. However, as holistic SDMs and CPC SDMs tended to have similar numbers of final predictor variables (Tables 1-2), the two approaches were likely to have similarly avoided overfitting.

In addition, while we were able to recreate general spatial patterns predicted by holistic SDMs using CPC SDMs, this ability was impacted by spatial scale, as CPC SDM-based suitability estimates were often relatively coarse across space (Figs. 3-7) despite the de facto patchy distributions of our study species (Stebbins and McGinnis 2018). Moreover, future decoupling between biologically-tailored holistic (e.g., groundwater-specific) and CPC SDM variables could—if it occurs—potentially limit the accuracy of future CPC SDM projections, further highlighting the need for future climate change projections for more biologically-relevant variables (e.g., seep-related variables; Stark and Fridley 2022, Zangiabadi et al. 2021). The small number of species in our study ($n = 4$) also reflects a potential limit on its overall generalizability. We ultimately selected only these four amphibian species—among dozens co-occurring in the same habitats and region—because they were among the only species that met simultaneous criteria of (1) having sufficient occurrence records to build reasonable SDMs, (2) occurring in habitats with existing data (e.g., raster layers) for biologically-tailored predictor variables, (3) not having already been modeled with SDMs using a highly species-tailored approach, and (4) being of potential conservation concern in at least one state or province where they occur. Thus, our findings require validation across other ecological groups; this will be infeasible in many cases until addition data (e.g., additional occurrence records for poorly-studied species) have been collected to enable more robust SDMs. Lastly, as MEM components were poorly correlated with all other predictor variables yet modestly influential in most SDMs, our predictor variables likely failed to capture all drivers of our study species' distributions (Borcard and Legendre 2002, Dray et al. 2006), potentially causing small-to-moderate biases in our projections under future climate change.

Our finding of reduced environmental suitability for *P. vandykei* under climate change depended on the taxonomic level (i.e., species-level or intraspecific lineage-level) used to construct SDMs (Figs. 6-8), adding to existing evidence for a need to consider potential intraspecific niche variation when studying potential climate change impacts (Schwalm et al. 2016, Smith et al. 2019). Given our results, is plausible that eastern (Cascades) and western (coastal) lineages differ considerably in climate vulnerability, as lineage-specific SDMs for *P. vandykei* performed universally better (based on CV AUC) than a species-level model within our holistic (and thus most realistic) SDMs, despite smaller sample sizes for the former (Tables 1-2). While SDMs consistently projected high vulnerability to climate change for Cascades *P. vandykei* populations, the projected vulnerability of coastal populations was high within the species-level SDM but negligible in a lineage-specific SDM (Tables 3–5; Figs. 3–8). Therefore, the presence or absence of intraspecific niche variation within *P. vandykei* is likely to have major impacts on its conservation status in coastal regions. Our findings do not confirm intraspecific niche differences (i.e., it is possible that differential coastal and Cascades SDM results were statistical artefacts arising from imperfect predictor variables) but suggest it as a reasonable possibility. Therefore, our finding of differential SDM results for different *P. vandykei* lineages is consistent with previous evidence that species-level or taxonomically coarser SDMs can be insufficient in some contexts for capturing pertinent niche variation (Schwalm et al. 2016). Thus, additional field surveys and genetic analyses are necessary to confirm whether coastal and Cascades *P. vandykei* lineages differ in their potential responses to climate change.

Regardless of ambiguous results for coastal *P. vandykei* populations, Cascades populations were projected to be severely impacted by climate change regardless of the SDM approach used (Figs. 6–8), potentially reflecting the instability of montane perched aquifers (e.g., those that feed most headwall seeps) under rapidly changing precipitation regimes (Allocca et al. 2015, Melillo et al. 2014). Unfortunately, multiple former seeps once occupied by this species near Mount Saint Helens appear to have vanished under recent historical climate change (pers. obs.), and three surveys of a nearby stream that harbored an exceptional population ~ 20 years ago (McIntyre 2003) yielded no *P. vandykei* observations during 2021 (Button et al., in review). In addition, while McIntyre (2003) observed *P. vandykei* at ~ 38 % of seeps in the vicinities of Mount Saint Helens and Mount Rainier in 2002, multiple surveys ($n = 2$–5) of similar seep habitats in these areas detected *P. vandykei* at only ~ 10 % of seeps in 2021–2022 (pers. obs.). Further, Button et al. (in review) found clear evidence of *P. vandykei* declines at historically occupied localities, including protected areas in the Cascades. Taken together, the collective evidence therefore suggests that Cascades *P. vandykei* populations have a potentially dire need for climate-smart management actions, such as identifying, maintaining, protecting, and potentially augmenting climatic refugia (Cartwright et al. 2020, Cartwright and Johnson 2018, Kurylyk et al. 2015). Based on our projections, climatic refugia for *P. vandykei* in the Cascades may eventually become more restricted to headwaters of glacially-fed watersheds (e.g., surrounding Mount Rainier); these were among the only areas in the region where suitability was projected to increase over time (Fig. 8).

4.1. Conclusion

Given highly variable potential climate trajectories among our study species, we caution against using a limited number of well-studied specialists (which are often taxonomically biased towards birds, mammals, and game fishes, yet can underrepresent vulnerable groups like amphibians; Clark and May 2002) to represent lesser-studied species within the same ecological group under climate change. Despite lacking empirical support in most contexts, this approach is relatively common under present-day habitat management schemes (Lindenmayer and Likens 2011), which may jeopardize a potentially large, understudied proportion of species that have divergent conservation needs from purported "indicator species" under climate change. The precise conservation needs of these overlooked species are, moreover, difficult to infer without more resources allocated to understanding their ecology and distributions (Gratwicke et al. 2012, Howell and Rodger 2018). Thus, species-specific approaches—rather than group-wide "indicator species"—are likely critical to understand potential climate change impacts on many specialists. By extension, caution may be warranted when interpreting previous SDM approaches that treat closely related yet ecologically varying species (e.g., *P. vandykei* and *P. larselli*) as equivalent despite clear interspecific niche differences (Nottingham and Pelletier 2021). Moreover, efforts to map additional species-tailored predictor variables—including under future climate change—are a critical future research need. Our findings also affirm that even species-level SDMs can be insufficient to infer potential climate change impacts on some organisms, underscoring major potential consequences of intraspecific niche variation among allopatric lineages when assessing vulnerability to climate change (Schwalm et al. 2016).

In the absence of viable "indicator species", better ecological data are a key species-specific prerequisite to understand and plan for potential climate change impacts on understudied habitat specialists. These

species are simultaneously massive in number (Bland et al. 2017), disproportionally less targeted than other vertebrates for research and management (Clark and May 2002, Gratwicke et al. 2012), and disproportionately impacted by human stressors (McKinney 1999). Given the combined magnitude of these factors, substantial additional research effort may be required to limit "silent extinctions" among understudied specialists. Pending additional research on other specialist groups, individual species appear unsupported as surrogates for the diverse conservation needs of habitat specialists under climate change. Similarly, our study also highlights the importance of species-specific SDM methods when modeling these organisms, such as by using species-specific predictor variables and visually inspecting output maps to ensure consistency with pre-existing knowledge. However, this approach becomes less logistically feasible when several species must be modeled simultaneously, unless resources like funding, labor, and time are also scaled upwards to maintain a similar level of effort per species (Shortridge et al. 2017). As this dilemma spans both social and ecological dimensions, future studies may benefit from applying an interdisciplinary framework to identify optimal pathways for resolution.

CRediT authorship contribution statement

Sky T. Button: Writing – original draft, Writing – review & editing, Methodology, Conceptualization, Investigation, Validation, Formal analysis, Data Curation, Visualization. **Donald J. Brown:** Writing – review & editing, Methodology, Conceptualization. **Jonah Piovia-Scott:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank several interns and volunteers who assisted with fieldwork as part of this study, including Lara Tice-York, Pazao Lee, Kalie Morgan, Austin Robinson, and Leonard Swatosh. In addition, committee members Jesse Brunner and Caren Goldberg provided invaluable feedback on the manuscript prior to submission. This research was funded by the Northwest Climate Adaptation Science Center (NW CASC; Grant ID G22AC00411). Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this report are those of the authors and should not be construed to represent any official USDA or U. S. Government determination or policy.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113488.

Data availability

Data are available online at the following URL: https://doi.org/10.5066/P148UUAU

References

Allocca, V., De Vita, P., Manna, F., Nimmo, J.R., 2015. Groundwater recharge assessment at local and episodic scale in a soil mantled perched karst aquifer in southern Italy. J. Hydrol. 529, 843–853.
Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species-climate impact models under climate change. Glob. Chang. Biol. 11, 1504–1513.
Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15, 365–377.
Biesmeijer, J.C., Roberts, S.P., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A., Potts, S.G., Kleukers, R., Thomas, C., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313, 351–354.
Bland, L.M., Bielby, J., Kearney, S., Orme, C.D.L., Watson, J.E., Collen, B., 2017. Toward reassessing data-deficient species. Conserv. Biol. 31, 531–539.
Borcard, D., Legendre, P., 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecol. Model. 153, 51–68.
Briggs, M.A., Lane, J.W., Snyder, C.D., White, E.A., Johnson, Z.C., Nelms, D.L., Hitt, N.P., 2018. Shallow bedrock limits groundwater seepage-based headwater climate refugia. Limnologica 68, 142–156.
Brun, P., Zimmermann, N.E., Hari, C., Pellissier, L., Karger, D.N., 2022. Global climate-related predictors at kilometer resolution for the past and future. Earth Syst. Sci. Data 14, 5573–5603.
Butler, S.J., Freckleton, R.P., Renwick, A.R., Norris, K., 2012. An objective, niche-based approach to indicator species selection. Methods Ecol. Evol. 3, 317–326.
Caro, T., 2010. Conservation by Proxy: Indicator, Umbrella, Keystone, Flagship, and Other Surrogate Species. Island Press.
Carstens, B.C., Stevenson, A.L., Degenhardt, J.D., Sullivan, J., 2004. Testing nested phylogenetic and phylogeographic hypotheses in the Plethodon vandykei species group. Syst. Biol. 53, 781–792.
Cartwright, J.M., Freed, Z., Hammer, S.J., McLaughlin, B., Misztal, L.W., Schenk, E.R., Spence, J.R., Springer, A.E., Stevens, L.E., 2020. Oases of the future? Springs as potential hydrologic refugia in drying climates. Front. Ecol. Environ. 18, 245–253.
Cartwright, J.M., Johnson, H.M., 2018. Springs as hydrologic refugia in a changing climate? A Remote-sensing Approach. Ecosphere 9, e02155.
Chen, G., Li, X., Liu, X., 2022. Global land projection based on plant functional types with a 1-km resolution under socio-climatic scenarios. Sci. Data 9, 125.
Clark, J.A., May, R.M., 2002. Taxonomic bias in conservation research. Science 297, 191–192.
Clavero, M., Villero, D., Brotons, L., 2011. Climate change or land use dynamics: do we know what climate change indicators indicate? PLoS One 6, e18581.
Cruz, J., Garrido, S., Pimentel, M.S., Rosa, R., Santos, A.M.P., Re, P., 2013. Reproduction and respiration of a climate change indicator species: effect of temperature and variable food in the copepod *Centropages chierchiae*. J. Plankton Res. 35, 1046–1058.
De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D.M., Decocq, G., De Pauw, K., 2021. Forest microclimates and climate change: Importance, drivers and future research agenda. Glob. Chang. Biol. 27, 2279–2297.
de Groot, R.S., Ketner, P., Ovaa, A.H., 1995. Selection and use of bio-indicators to assess the possible effects of climate change in Europe. J. Biogeogr. 22, 935–943.
de Mendoza, G., Kaivosoja, R., Grönroos, M., Hjort, J., Ilmonen, J., Kärnä, O.M., Paasivirta, L., Tokola, L., Heino, J., 2018. Highly variable species distribution models in a subarctic stream metacommunity: Patterns, mechanisms and implications. Freshw. Biol. 63, 33–47.
Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol. Model. 196, 483–493.
Dunne, J.P., Horowitz, L., Adcroft, A., Ginoux, P., Held, I., John, J., Krasting, J.P., Malyshev, S., Naik, V., Paulot, F., 2020. The GFDL Earth System Model version 4.1 (GFDL-ESM 4.1): Overall coupled model description and simulation characteristics. J. Adv. Model. Earth Syst. 12, e2019MS002015.
Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77, 802–813.
Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315.
Foster AD, Olson DH, and Jones LL. 2014. A review of the biology and conservation of the Cope's Giant Salamander, *Dicamptodon copei* Nussbaum, 1970 (Amphibia: Caudata: Dicamptodontidae) in the Pacific Northwestern Region of the USA. Life: The Excitement of Biology 2:210.
Fourcade, Y., Åström, S., Öckinger, E., 2021. Decline of parasitic and habitat-specialist species drives taxonomic, phylogenetic and functional homogenization of sub-alpine bumblebee communities. Oecologia 196, 905–917.
Goudarzi, F., Hemami, M.-R., Malekian, M., Fakheran, S., Martínez-Freiría, F., 2021. Species versus within-species niches: a multi-modelling approach to assess range size of a spring-dwelling amphibian. Sci. Rep. 11, 597.
Gratwicke, B., Lovejoy, T.E., Wildt, D.E., 2012. Will amphibians croak under the endangered species act? Bioscience 62, 197–202.
Greenwell B, Boehmke B, Cunningham J, and Greenwell MB. 2019. Package 'gbm'. R package version 2.
Guélat, J., Kéry, M., 2018. Effects of spatial autocorrelation and imperfect detection on species distribution models. Methods Ecol. Evol. 9, 1614–1625.
Higa, M., Nakao, K., Tsuyama, I., Nakazono, E., Yasuda, M., Matsui, T., Tanaka, N., 2013. Indicator plant species selection for monitoring the impact of climate change based on prediction uncertainty. Ecol. Ind. 29, 307–315.
Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., Hijmans, M.R.J., 2017. Package 'dismo'. Circles 9, 1–68.
Howard, S.D., Bickford, D.P., 2014. Amphibians over the edge: silent extinction risk of Data Deficient species. Divers. Distrib. 20, 837–846.
Howard, S.D., Seeb, L.W., Wallace, R., 1993. Genetic variation and population divergence in the *Plethodon vandykei* species group (Caudata: Plethodontidae). Herpetologica:238-247.

Howell, L.G., Rodger, J.C., 2018. An examination of funding for terrestrial vertebrate fauna research from Australian federal government sources. Pac. Conserv. Biol. 24, 142–147.
Hu, Z.M., Zhang, Q.S., Zhang, J., Kass, J.M., Mammola, S., Fresia, P., Draisma, S.G., Assis, J., Jueterbock, A., Yokota, M., 2021. Intraspecific genetic variation matters when predicting seagrass distribution under climate change. Mol. Ecol. 30, 3840–3855.
Hufft, R.A., DePrenger-Levin, M.E., Levy, R.A., Islam, M.B., 2018. Using herbarium specimens to select indicator species for climate change monitoring. Biodivers. Conserv. 27, 1487–1501.
Irving, K., Jähnig, S.C., Kuemmerlen, M., 2020. Identifying and applying an optimum set of environmental variables in species distribution models. Inland Waters 10, 11–28.
Isaak, D.J., Wenger, S.J., Peterson, E.E., Ver Hoef, J.M., Nagel, D.E., Luce, C.H., Hostetler, S.W., Dunham, J.B., Roper, B.B., Wollrab, S.P., 2017. The NorWeST summer stream temperature model and scenarios for the western US: A crowd-sourced database and new geospatial tools foster a user community and predict broad climate warming of rivers and streams. Water Resour. Res. 53, 9181–9205.
Jaeger, K., Sando, R., McShane, R.R., Dunham, J.B., Hockman-Wert, D., Kaiser, K.E., Hafen, K., Risley, J., Blasch, K.W., 2019. Probability of Streamflow Permanence Model (PROSPER): A spatially continuous model of annual streamflow permanence throughout the Pacific Northwest. J. Hydrol. 2, 100005.
Jefferson, A., Grant, G., Rose, T., 2006. Influence of volcanic history on groundwater patterns on the west slope of the Oregon High Cascades. Water Resour. Res. 42, W12411.
Jefferson A, Grant GE, and Lewis SL. 2007. A river runs underneath it: geological control of spring and channel systems and management implications, Cascade Range, Oregon. US Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR (689, Part 2):391-400.
Kattel, G.R., 2022. Climate warming in the Himalayas threatens biodiversity, ecosystem functioning and ecosystem services in the 21st century: is there a better solution? Biodivers. Conserv. 31, 2017–2044.
Kriebel, D., Tickner, J., Epstein, P., Lemons, J., Levins, R., Loechler, E.L., Quinn, M., Rudel, R., Schettler, T., Stoto, M., 2001. The precautionary principle in environmental science. Environ. Health Perspect. 109, 871–876.
Krosby, M., Theobald, D.M., Norheim, R., McRae, B.H., 2018. Identifying riparian climate corridors to inform climate adaptation planning. PLoS One 13, e0205156.
Kurylyk, B.L., MacQuarrie, K.T., Linnansaari, T., Cunjak, R.A., Curry, R.A., 2015. Preserving, augmenting, and creating cold-water thermal refugia in rivers: Concepts derived from research on the Miramichi River, New Brunswick (Canada). Ecohydrology 8, 1095–1108.
Lannoo, M.J., 2005. Amphibian Declines: The Conservation Status of United States Species. University of California Press.
Leasi, F., Sevigny, J.L., Hassett, B.T., 2021. Meiofauna as a valuable bioindicator of climate change in the polar regions. Ecol. Ind. 121, 107133.
Legendre, P., Borcard, D., Blanchet, G., Dray, S., 2012. MEM spatial eigenfunction and principal coordinate analyses. R Package PCNM, Version 2, 2.
Lindenmayer, D.B., Likens, G.E., 2011. Direct measurement versus surrogate indicator species for evaluating environmental change and biodiversity loss. Ecosystems 14, 47–59.
Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 259, 698–709.
Liu, C., Newell, G., White, M., 2019. The effect of sample size on the accuracy of species distribution models: considering both presences and pseudo-absences or background sites. Ecography 42, 535–548.
Luedtke, J.A., Chanson, J., Neam, K., Hobin, L., Maciel, A.O., Catenazzi, A., Borzée, A., Hamidy, A., Aowphol, A., Jean, A., 2023. Ongoing declines for the world's amphibians in the face of emerging threats. Nature 622, 308–314.
Lynch, J.E., 1984. Reproductive ecology of *Plethodon idahoensis*. University of Idaho. Unpublished Master's thesis.
Mair, L., Jönsson, M., Räty, M., Bärring, L., Strandberg, G., Lämås, T., Snäll, T., 2018. Land use changes could modify future negative effects of climate change on old-growth forest indicator species. Divers. Distrib. 24, 1416–1425.
McIntyre, A.P., 2003. Ecology of Populations of Van Dyke's Salamanders in the Cascade Range of Washington State. Oregon State University. Unpublished Master's thesis.
McIntyre, A.P., Schmitz, R.A., Crisafulli, C.M., 2006. Associations of the Van Dyke's Salamander (*Plethodon vandykei*) with geomorphic conditions in headwall seeps of the Cascade Range, Washington State. J. Herpetol. 40, 309–322.
McKinney, M.L., 1999. High rates of extinction and threat in poorly studied taxa. Conserv. Biol. 13, 1273–1281.
Melillo, J.M., Richmond, T., Yohe, G., 2014. Climate change impacts in the United States. U.S. Global Change Research Program Technical Report, Third National Climate Assessment.
Mendoza-Fernández, A.J., Fernández-Ceular, Á., Alcaraz-Segura, D., Ballesteros, M., Peñas, J., 2022. The fate of endemic species specialized in island habitat under climate change in a mediterranean high mountain. Plants 11, 3193.
Metzger, G., Espindola, A., Waits, L.P., Sullivan, J., 2015. Genetic structure across broad spatial and temporal scales: Rocky Mountain tailed frogs (*Ascaphus montanus*; Anura: Ascaphidae) in the inland temperate rainforest. J. Hered. 106, 700–710.
Moudrý, V., Bazzichetto, M., Remelgado, R., Devillers, R., Lenoir, J., Mateo, R.G., Lembrechts, J.J., Sillero, N., Lecours, V., Cord, A.F., 2024. Optimising occurrence data in species distribution models: sample size, positional uncertainty, and sampling bias matter. Ecography:e07294.
Nottingham, S., Pelletier, T.A., 2021. The impact of climate change on western *Plethodon* salamanders' distribution. Ecol. Evol. 11, 9370–9384.
Oliver, T.H., Gillings, S., Girardello, M., Rapacciuolo, G., Brereton, T.M., Siriwardena, G. M., Roy, D.B., Pywell, R., Fuller, R.J., 2012. Population density but not stability can be predicted from species distribution models. J. Appl. Ecol. 49, 581–590.
Olson DH. 2011. Conservation Assessment for the Rocky Mountain Tailed Frog in Oregon and Washington (*Ascaphus montanus*). USDA Forest Service Region 6 and USDI Bureau of Land Management Interagency Task Force.
Olson, D.H., Burton, J.I., 2019. Climate associations with headwater streamflow in managed forests over 16 years and projections of future dry headwater stream channels. Forests 10, 968.
Olson DH and Crisafulli CM. 2014. Conservation Assessment for the Van Dyke's Salamander (*Plethodon vandykei*).
Osipova, L., Sangermano, F., 2016. Surrogate species protection in Bolivia under climate and land cover change scenarios. J. Nat. Conserv. 34, 107–117.
Pearman, P.B., Guisan, A., Zimmermann, N.E., 2011. Impacts of climate change on Swiss biodiversity: an indicator taxa approach. Biol. Conserv. 144, 866–875.
Peñalver-Alcázar, M., Jiménez-Valverde, A., Aragón, P., 2021. Niche differentiation between deeply divergent phylogenetic lineages of an endemic newt: implications for species distribution models. Zoology 144, 125852.
Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol. Appl. 19, 181–197.
Pureswaran, D.S., Roques, A., Battisti, A., 2018. Forest insects and climate change. Curr. For. Rep. 4, 35–50.
Raphael MG, Bisson PA, Jones LL, and Foster AD. 2002. Effects of streamside forest management on the composition and abundance of stream and riparian fauna of the Olympic Peninsula. United States Department of Agriculture Forest Service General Technical Report.
Reyes, A.V., Carlson, A.E., Clark, J., Guillaume, L., Milne, G.A., Tarasov, L., Carlson, E.C., He, F., Caffee, M.W., Wilcken, K.M., 2024. Timing of Cordilleran-Laurentide ice-sheet separation: Implications for sea-level rise. Quat. Sci. Rev. 328, 108554.
Riahi K, Van Vuuren DP, Kriegler E, Edmonds J, O'neill BC, Fujimori S, Bauer N, Calvin K, Dellink R, and Fricko O. 2017. The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. Global Environmental Change 42:153-168.
Riley, K.L., Loehman, R.A., 2016. Mid-21st-century climate changes increase predicted fire occurrence and fire season length, Northern Rocky Mountains. United States. Ecosphere 7, e01543.
Santini, L., Benítez-López, A., Maiorano, L., Čengić, M., Huijbregts, M.A., 2021. Assessing the reliability of species distribution projections in climate change research. Divers. Distrib. 27, 1035–1050.
Schwalm, D., Epps, C.W., Rodhouse, T.J., Monahan, W.B., Castillo, J.A., Ray, C., Jeffress, M.R., 2016. Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. Glob. Chang. Biol. 22, 1572–1584.
Shortridge, J., Guikema, S., Zaitchik, B., 2017. Robust decision making in data scarce contexts: addressing data and model limitations for infrastructure planning under transient climate change. Clim. Change 140, 323–337.
Siddig, A.A., Ellison, A.M., Ochs, A., Villar-Leeman, C., Lau, M.K., 2016. How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in Ecological Indicators. Ecol. Ind. 60, 223–230.
Smith, A.B., Godsoe, W., Rodríguez-Sánchez, F., Wang, H.-H., Warren, D., 2019. Niche estimation above and below the species level. Trends Ecol. Evol. 34, 260–273.
Sofaer, H.R., Jarnevich, C.S., Pearse, I.S., Smyth, R.L., Auer, S., Cook, G.L., Edwards Jr, T. C., Guala, G.F., Howard, T.G., Morisette, J.T., 2019. Development and delivery of species distribution models to inform decision-making. Bioscience 69, 544–557.
Stebbins, R.C., McGinnis, S.M., 2018. Peterson Field Guide to Western Reptiles & Amphibians of Western North America. Houghton Mifflin.
Steele, C., Baumsteiger, J., Storfer, A., 2009. Influence of life-history variation on the genetic structure of two sympatric salamander taxa. Mol. Ecol. 18, 1629–1639.
Stein, B.A., Glick, P., Edelson, N., Staudt, A., 2014. Climate-smart conservation: putting adaption principles into practice. National Wildlife Federation, Report Number.
Thuiller, W., Guéguen, M., Renaud, J., Karger, D.N., Zimmermann, N.E., 2019. Uncertainty in ensembles of global biodiversity scenarios. Nat. Commun. 10, 1446.
Thurman, L.L., Cousins, C.D., Button, S.T., Garcia, T.S., Henderson, A.L., Olson, D.H., Piovia-Scott, J., 2022. Treading water: Conservation of headwater-stream associated amphibians in northwestern North America. The Encyclopedia of Conservation (Elsevier Inc.), Imperiled.
Urban, M.C., 2015. Accelerating extinction risk from climate change. Science 348, 571–573.
USGS. 2015. Compiled National List of Species of Greatest Conservation Need: U.S. Geological Survey data release.
Veloz, S.D., 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. J. Biogeogr. 36, 2290–2299.
Welty, J.L., Jeffries, M.I., 2020. Combined wildfire datasets for the United States and certain territories. U.S. Geological Survey data release, 1878–2019.
Wenger, S.J., Luce, C.H., Hamlet, A.F., Isaak, D.J., Neville, H.M., 2010. Macroscale hydrologic modeling of ecologically relevant flow metrics. Water Resour. Res. 46, W09513.
Wenger, S.J., Olden, J.D., 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation: Model transferability. Methods Ecol. Evol. 3, 260–267.
Wilson, A.G., Wilson, E.M., Groves, C.R., Wallace, R.L., 1997. US Distribution of the Coeur d'Alene salamander (*Plethodon idahoensis* Slater and Slipp). The Great Basin Naturalist 57, 359–362.
Wolock DM. 2003. Base-flow index grid for the conterminous United States: Geological Survey data release.

Yousefi, M., Jouladeh-Roudbar, A., Kafash, A., 2020. Using endemic freshwater fishes as proxies of their ecosystems to identify high priority rivers for conservation under climate change. Ecol. Ind. 112, 106137.
Yu, H., Cooper, A.R., Infante, D.M., 2020. Improving species distribution model predictive accuracy using species abundance: Application with boosted regression trees. Ecol. Model. 432, 109202.
Zangiabadi, S., Zaremaivan, H., Brotons, L., Mostafavi, H., Ranjbar, H., 2021. Using climatic variables alone overestimate climate change impacts on predicting distribution of an endemic species. PLoS One 16, e0256918.
Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D., Coomes, D., 2019. Advances in microclimate ecology arising from remote sensing. Trends Ecol. Evol. 34, 327–341.
Zettler, M.L., Proffitt, C.E., Darr, A., Degraer, S., Devriese, L., Greathead, C., Kotta, J., Magni, P., Martin, G., Reiss, H., 2013. On the myths of indicator species: issues and further consideration in the use of static concepts for ecological applications. PLoS One 8, e78219.
Zhang, C., Zhu, R., Sui, X., Chen, K., Li, B., Chen, Y., 2020. Ecological use of vertebrate surrogate species in ecosystem conservation. Global Ecol. Conserv. 24, e01344.