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Functional and geographic components of risk for climate sensitive vertebrates in the Pacific Northwest, USA

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ABSTRACT

Rarity and life history traits inform multiple dimensions of intrinsic risk to climate and environmental change and can help systematically identify at-risk species. We quantified relative geographic rarity (area of occupancy), climate niche breadth, and life history traits for 114 freshwater fishes, amphibians, and reptiles in the U.S. Pacific Northwest. Our approach leveraged presence-only, publicly available data and traits-based inference to evaluate area of occupancy, climate sensitivity (i.e., climate niche breadth), and a Rarity and Climate Sensitivity (RCS) index of all species across multiple geographic extents, grain sizes, and data types. The RCS index was relatively stable across extents, grains, and data types, with climate sensitivity differentiating species with otherwise similar areas of occupancy. We also found that species with sensitivity-associated traits (e.g., long generation time, low fecundity) were not necessarily the same species identified as at-risk with geographical approaches (small range size, small climate niche breadth). Many multispecies assessments using coarse-scale data (e.g., entire range maps or convex-hull approaches) often focus on a single dimension of intrinsic risk; others rely on data-intensive models only applicable to a few well-studied species. What remains is a need for an approach that enables multispecies, multidimensional assessment efforts. This is particularly true at regional scales, where management needs require assessments that are intermediate to coarse- and fine-scale approaches. We demonstrate that by considering multiple dimensions of intrinsic risk to climate change (range size, climate sensitivity, and traits), site-specific locality data may offer a pathway for ensuring vulnerable, understudied species do not go overlooked in conservation.

1. Introduction

With climate change outpacing the rate at which climate vulnerability is studied and understood for many species, advances in multispecies assessments are critical to identify at-risk taxa (Williams et al., 2008) and to prioritize conservation efforts. Species vulnerability to climate change is a complex and multidimensional problem (Foden et al., 2013). Along two dimensions, vulnerability has been considered in terms of intrinsic sensitivity (capacity of a species to persist in its current range, inclusive of other intrinsic-biotic factors such as physiology, behavior, or phenotypic plasticity) and extrinsic exposure (external drivers of responses related to changes in climate) (Williams et al., 2008). Adaptive capacity, a third dimension, is the ability to cope with climate change through dispersal or evolutionary adaptation (Foden et al., 2013). Whereas these definitions of species vulnerability provide much conceptual clarity, operationalizing them in the form of multispecies risk assessments remains a major challenge.

Multispecies risk assessments have employed rarity- and traits-based classifications of species to inform sensitivity and adaptive capacity to climate change. Rare species are typically characterized by restricted range sizes, specific habitat requirements, and small populations (Rabinowitz, 1981) – factors that can increase sensitivity to environmental changes and reduce adaptive capacity (Harnik et al., 2012). Accordingly, rarity classifications have been used to systematically evaluate risk and vulnerability for a variety of taxa, including herpetofauna (Rey Benayas et al., 1999), plants (Murray et al., 2002), and freshwater fishes (Olden et al., 2008; Pritt and Frimpong, 2010; Giam and Olden, 2017). Species' sensitivity and adaptive capacity are also linked to other attributes such as life history, behavior, phenology, and genetic traits that modulate population size and dispersal capacity (Murray et al., 2002; Pacifici et al., 2015). Multispecies, traits-based assessments of species responses to climate change are growing in application (e.g., Rey Benayas et al., 1999; Harnik et al., 2012; Foden

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et al., 2013; Bland et al., 2014; Pacifici et al., 2017). Life history traits such as generation time, longevity, fecundity, and parental investment are particularly relevant for multispecies studies because they can be quantitatively assessed and efficiently compared among species (McGill et al., 2006). Moreover, traits-based analyses include aspects of both species' sensitivity and adaptive capacity – two dimensions of vulnerability (Pacifici et al., 2015). Thus, these approaches have high potential in assessing risk because together life history traits drive population vital rates and modulate the potential and timeframe for evolutionary response to environmental change (Williams et al., 2008), providing a proxy for adaptive capacity (Nicotra et al., 2015).

Inclusive multispecies comparisons of rarity and traits may help set regional priorities for future species management and conservation efforts, both in a general sense and relative to specific threats. To this end, approaches are needed that accommodate a mix of data types, a common challenge when multiple rare species are examined simultaneously. For example, records of species occupancy may range from highly detailed (e.g., systematic sampling throughout multiple years in many locations) to sparse (e.g., few records collected opportunistically), and may differ in spatial resolution (e.g., summary range maps versus point occurrence data) and level of verification. Such discrepancies complicate direct comparisons among species, and approaches are thus required to compare species for which different types of data are available.

A combination of both rarity- and traits-based approaches also provides promise for more meaningful multispecies assessments. Taken together, life history traits and spatial characteristics of species' ranges – such as those captured by rarity – may be the most important contributors to species' extinction risk due to climate change (Pearson et al., 2014). Moreover, life history traits and geographic rarity have strong interactions that drive species' sensitivity to climate change, indicating that these two factors together may provide a more comprehensive understanding of the multiple dimensions of intrinsic risk to climate change than if considered independently (Pearson et al., 2014; Pacifici et al., 2017). For example, multispecies comparisons can help identify previously overlooked or poorly understood species that may be vulnerable to climate change (Bland et al., 2014; Jetz and Freckleton, 2015), and such approaches also can help prioritize allocation of conservation resources (Gerber, 2016).

Multispecies assessments typically leverage existing data and information about species and their attributes to compare species to one another and to build predictive frameworks for assessing vulnerability (e.g., Rabinowitz, 1981; Harnik et al., 2012; Foden et al., 2013). Historically, multispecies assessments have used surrogate species (e.g., umbrella or flagship species), analyzed species assemblages or guilds, or focused on specific geographic areas (Caro, 2015). However, these approaches may overlook rare taxa (Stewart et al., 2017) and may introduce biases such that not all at-risk taxa benefit, particularly when congruence in taxonomic and biodiversity patterns is low across ecosystem types and regions (Darwall et al., 2011). Furthermore, evidence is mounting that intrinsic risk to climate change is multidimensional, with range size, climate niche breadth, species traits, and their interactions contributing in concert to species' sensitivity and adaptive capacity (Estrada et al., 2015; Saupe et al., 2015).

In this study, we developed a multidimensional, multispecies assessment approach to evaluate intrinsic risk to climate change as a function of geographic rarity, climate niche breadth (interpreted as a measure of climate sensitivity), and life history traits. We demonstrated our approach using publicly available occurrence data for 114 ectothermic vertebrates (freshwater fishes, amphibians, and reptiles) native to the U.S. Pacific Northwest, a large and climatically diverse region encompassing 656,000 km^2 (Dalton et al., 2013). The study area includes the intersection of multiple mountain ranges and a latitudinal gradient in climate resulting in several ecoregions characterized by forest, desert, montane, valley, and range ecosystems – hence, the study has potentially broad ecological application. Taxonomically, the area has numerous endemic species as well as species at the northward edge of their range – such that the study extent can yield results capable of distinguishing between different types of rarity: global versus local. Furthermore, ectothermic vertebrates are highly relevant for climate change assessments across this region because they rely upon external sources of heat for body temperature regulation and thus may be particularly sensitive to changes in environmental temperature across this vast area with its diverse physical habitat conditions. Also, aquatic forms are tied to water availability, another highly variable habitat attribute tied to physiographic and climatic factors.

Our goals were to: 1) develop a Rarity and Climate Sensitivity (RCS) index that jointly assessed area of occupancy and sensitivity to variation in climate metrics, and characterize life history traits for this regional species pool; 2) examine the effects of alternative geographic study extents (i.e., jurisdictional study boundaries versus ecological boundaries), data types, and grain sizes on RCS classifications to assess bias and robustness of values under different study designs; and 3) evaluate geographic rarity, climate sensitivity, and life history traits within taxonomic groups (fishes, amphibians, and reptiles) and for all species combined, to characterize multiple dimensions of intrinsic rarity and determine whether they are redundant at this scale. Additionally, we examined whether RCS values varied significantly according to species' primary habitat types (aquatic, semiaquatic, or terrestrial), their taxonomy (order), or their conservation status at the state and federal levels. Systematic, regional assessments such as this provide an important tool for prioritizing monitoring and management of resources among many species in the face of rapidly changing climates and biomes.

2. Methods

2.1. Species occurrence data

Baseline data for analyses described below were organized into different spatial extents and data types. First, to assess the effect of study area size on rarity classifications, we considered three geographical study extents in the U.S. Pacific Northwest. We focused on two jurisdictional delineations: Oregon state (255,000 km^2); and Oregon, Idaho, and Washington (656,000 km^2). To assess influence or bias of arbitrary jurisdictional delineations, we also examined an extent defined by ecological boundaries that included the full spatial extent of all Level III Ecoregions that overlapped with Oregon (571,000 km^2) and extended outside the Oregon state boundaries to include portions of California, Nevada, Washington, and Idaho (U.S. Environmental Protection Agency, 2005) (Fig. 1).

Species occurrence data were obtained from three sources. First, museum records for all freshwater fishes, amphibians, and reptiles collected from 1930 to 2002 within the study extent were compiled from 43 collections through the publicly available web-based tool VertNet (Constable et al., 2010; see Table A.1 for list of all collections and Supplementary Methods in Appendix for additional detail on VertNet record database assembly). All VertNet data used in this publication, including updates to taxonomy and filtering of records, are publicly available via U.S. Geological Survey (Mims and Hockman-Wert, 2018). Two additional data sources were used for reptile and fish occurrences. First, we used a comprehensive, multi-state (Oregon, Washington, and Idaho) reptile occurrence database assembled by the U.S. Forest Service and U.S. Geological Survey that included occurrence data from museum records, state databases, and federal databases (data sources: Table A.1). Second, we used native freshwater fish occurrence records within the state of Oregon assembled from the Oregon State University Fish Collection by the Oregon Department of Fish and Wildlife (ODFW). The ODFW fish database contained records with associated voucher specimens that were examined and identified by expert ichthyologists (Table A.1).

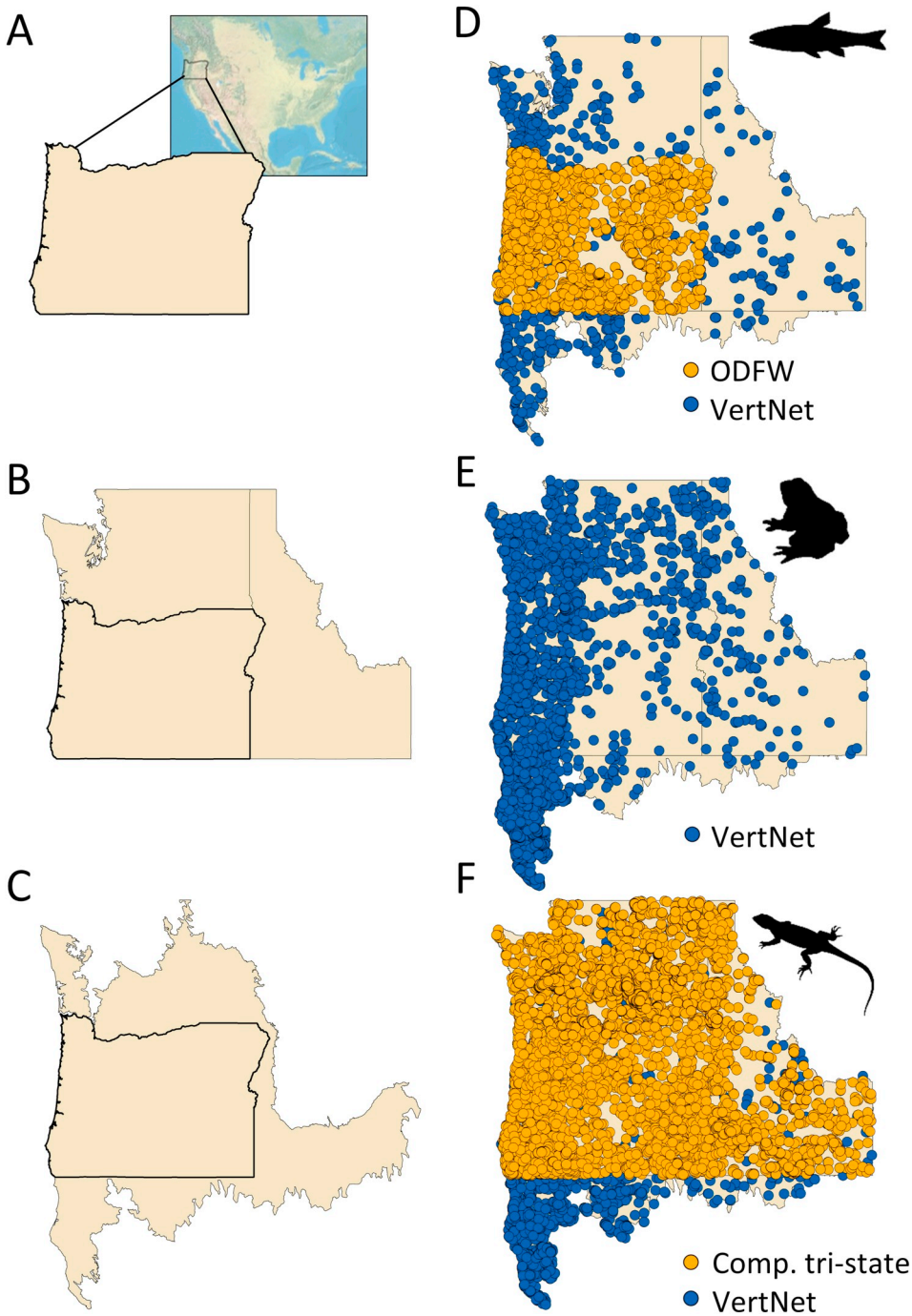

Fig. 1. Three geographic study extents analyzed for native fishes, amphibians, and reptiles of Oregon, USA, including: (A) the Oregon state boundary; (B) three-state extent (Oregon, Washington, Idaho); and (C) Ecoregional overlap with Oregon. Ectothermic vertebrate occurrence data for (D) freshwater fishes, (E) amphibians, and (F) reptiles native to Oregon, USA. VertNet data are shown in blue (D–F), Oregon Department of Fish and Wildlife fish dataset is shown in orange (D), and comprehensive tri-state reptile dataset is shown in orange (F). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Rarity and Climate Sensitivity index

Area of Occupancy (AOO) was calculated for each species having a minimum of 10 occurrence points and represents the total area (km^2) occupied by a species in a given study extent. We selected $N = 10$ as an arbitrary minimum number of occurrence points to include as many species as possible while retaining a reasonable representation of climate conditions across species' localities. AOO is typically calculated by tessellating a landscape with a uniform grid and summing the total area, or number of grid cells, occupied by a species. We used a modified grid-based approached in which we summed the area of buffered circles centered on each occurrence point. Grain size, or in this case buffer diameter, is known to influence rarity classifications (Hartley and Kunin, 2003), and the use of multiple grain sizes can help avoid bias from use of a single measurement. Buffers that overlapped for a given species were merged such that heavily sampled areas did not artificially inflate AOO measures. Additionally, smaller grain sizes offer higher precision, because AOO and climate-derived niche breadth are closely coupled with a specific point occurrence. However, smaller grain sizes more closely approximate the number of observations of a species, and this may introduce bias when comparing multiple species with potentially different sampling efforts. Therefore, a range of grain sizes can help account for sampling biases among species as well. We considered grain sizes of 1 km, 5 km, 10 km, and 20 km buffer diameters. Finally, the cumulative buffer area (km^2) for each species at each grain size was summed to produce an AOO measure.

Climate niche breadth, in addition to range size, has been linked to species' extinction risk over geological time scales (Saupe et al., 2015).

Climate niche breadth, described here as Climate Sensitivity (CS), was calculated for each species with a minimum of 10 occurrence points. In our analyses, CS was a derived metric describing the composite breadth of historical climate conditions associated with the range size (AOO) of each species. Historical climate data statistically downscaled to a 30-second grid of the northwest United States were available for a range of variables throughout our study extent (Shafer and Bartlein, 2015) (Table A.2). Variables were selected to capture the magnitude, predictability, and seasonality of dimensions of precipitation and temperature. We selected six climate variables for analysis, including total annual precipitation, total annual snowfall snow-water equivalent, number of frost-free days, mean annual temperature, mean temperature of the warmest month minus mean temperature of the coldest month (monthly temperature range), and total monthly precipitation of the wettest month minus total monthly precipitation of the driest month (monthly precipitation range) (Table A.2). These variables were intended to capture a range of climate conditions relevant to the species and the region we studied. The mean and standard deviation of each of variable were calculated across all years for which data were available (1901–2002). To retain as many species occurrence records as possible, we elected to retain all years of available climate data (1901–2002) to characterize contemporary climate conditions rather than subsetting climate data to a specific temporal window. This resulted in twelve climate descriptors. The breadth of historical climate conditions was assessed per species using the composite areas of their AOO buffers to extract the standard deviation of each climate descriptor. These were then relativized on a scale from 0 to 1, and finally subtracted from 1, such that 1 indicated the highest sensitivity (lowest standard deviation) for a given group of species and 0 indicated the lowest sensitivity (highest standard deviation). The mean relative climate breadth of all variables was then calculated to provide the Climate Sensitivity (CS) metric for each species at each study extent and grain size (see Appendix: Supplementary Methods for additional information on CS calculations). Time lags between earlier occurrence records (e.g., 1930s) and more recent climate conditions (e.g., late 20th century) could temporally decouple an observation with local climate conditions. This could be problematic for species distribution models or other approaches that evaluate species' exposure to a changing climate or environmental conditions. However, we did not use these occurrence data to evaluate range shifts, expansions, or contractions, but rather used them to estimate species' putative, contemporary ranges. Our aim was then to characterize overall climate niche breadth (using standard deviations of climate conditions) throughout that range. For that reason, we retained all years of climate data available for this study to estimate climate niche breadth (CS).

Finally, AOO and CS were combined to create a spatially derived rarity metric, the Rarity and Climate Sensitivity index (RCS). All AOO values were subtracted from 1 and then averaged with CS values, such that resultant RCS values near 1 indicated species with small AOO and a low range of climate variables found within their range (rare species); and values near 0 indicated species with large AOO and a large range of climate variables found within their range (common species). RCS values were produced for each species, study extent, data type, and grain size (N = 2360 values). The mean and standard deviation (SD) of species-specific RCS values, as well as AOO and CS independently, were then calculated to produce a species-composite RCS value (mean) and a metric of discordance and possible bias (SD). High SD can indicate discordance between rarity values due to sensitivity to grain size (e.g., geographic sampling bias within a species), study extent (e.g., different parts or proportions of a species' range), or data type (e.g., differential sampling efforts by data set). The RCS mean and SD were then compared among species within each major taxonomic group (fishes, amphibians, and reptiles). All spatial analyses were performed in ArcGIS Version 10.3.1.

2.3. Species life history traits

Life history traits were assembled from published databases where available (Mims et al., 2010; Myhrvold et al., 2015) and from trait values compiled from the literature (Mims and Hockman-Wert, 2018). Five primary life history traits were considered: body size measured as the natural log of maximum reported adult body length (mm) for fishes and amphibians and adult body mass (g) for reptiles; generation time (measured as age at maturity); longevity; fecundity; and parental investment (taxa-dependent combination of egg size, body size, and parental care behavior; defined in Appendix: Supplementary Methods). These traits were widely available and were selected because they characterize key energetic tradeoffs between longevity, generation time, and juvenile survivorship (Pianka, 1970; Stearns, 1976; Winemiller and Rose, 1992). See Appendix (Supplementary Methods and Table A.3) for additional details on life history traits.

Multivariate life history trait patterns among species were summarized and visualized for each of the three primary taxonomic groups using a principal coordinate analysis (PCoA). PCoA is a statistical methodology to explore and visualize similarities/dissimilarities in multivariate data by optimally representing the variability of a multidimensional data matrix in ordination space (distance) with reduced dimensionality (Legendre and Legendre, 2012). A species similarity matrix was constructed using the five continuous life history traits for species of each major taxonomic group. Four traits were log-transformed for all taxa (body size, fecundity, age at maturity, and generation time). Parental investment was scaled from 0 to 1 for species within our major groups (fishes, amphibians, and reptiles) and was log-transformed for fishes (log[parental investment] + 1). Trait similarity between species was calculated according to Gower's similarity coefficient (Gower, 1971). Statistical significance of the principal coordinates (eigenvalues) and trait contributions (eigenvectors) were assessed using Monte Carlo randomization (9999 permutations).

2.4. Evaluating relationships between RCS, traits, and conservation status

Vulnerability is widely acknowledged as multidimensional, and the intrinsic components of risk that contribute to vulnerability, including sensitivity and adaptive capacity (Foden et al., 2013), are likely to be multidimensional as well (Nicotra et al., 2015). Therefore, a single metric or approach (geographic vs. life history) may not capture all components of intrinsic risk for a given species. We conducted a series of analyses to evaluate relationships between species-composite mean Rarity and Climate Sensitivity index (RCS) values and a suite of species attributes, or traits, with theoretical and empirically-supported links to species' climate sensitivity and adaptive capacity. For these analyses, we calculated the RCS values across the Ecoregional study extent (all grain sizes for VertNet data) for all species. We then evaluated the relationships between RCS values (at the Ecoregional study extent) across all three taxonomic groups and species' life history traits using univariate Spearman rank correlation coefficients and visually using multivariate ordinations (PCoA) where we coded RCS values categorically (by symbol size) per species in the ordination graphics. In addition to life history traits, we also examined whether RCS values differed significantly according to primary habitat types (aquatic, semiaquatic, or terrestrial), taxonomy (order), or species conservation status at the state and federal levels. AOO and CS were also examined according to species conservation status to compare how these individual components differed from the combined RCS index. Comparisons of RCS values for species in different categories of each variable were performed using a Kruskal-Wallis test by ranks (Kruskal and Wallis, 1952), and a Dunn's test of multiple comparisons using rank sums (Dunn, 1964) was used for post-hoc evaluation of pairwise differences between categories where Kruskal-Wallis results were significant. Finally, regression tree and

random forest approaches were used to evaluate whether (and how strongly) species attributes predicted RCS values across all species (Breiman et al., 1984; Breiman, 2001). Body mass was calculated from body lengths of fishes using length-weight parameters published in FishBase (Froese and Pauly, 2016). For comparisons across all taxonomic groups (rather than within taxonomic groups), parental investment was not included due to the taxon-specific nature of the trait itself. Body size (log scaled), fecundity (log scaled), age at maturation, longevity, taxonomic order, and primary habitat types were evaluated as predictors of rarity using the R function "rpart" (method = "anova") (Therneau et al., 2015). All continuous variables were evaluated for correlations prior to inclusion in models. In random forest models, variables explaining the least amount of variation were removed in a stepwise fashion to identify a final model explaining the highest percentage variance. All analyses were performed in R (R Development Core Team, 2011) using the package "Hmisc" for correlations (Harrell, 2016), "dunn.test" for Kruskal-Wallis and Dunn's tests (Dinno, 2016), "rpart" for regression trees (Therneau et al., 2015), and "randomForest" for random forest analysis (Breiman et al., 2018).

3. Results

3.1. Rarity and Climate Sensitivity of ectothermic vertebrates in the Pacific Northwest, USA

Occurrence datasets across taxa (Fig. 1, Figs. A.1, and A.2; 42,052 total occurrence records analyzed) permitted calculation of Rarity and Climate Sensitivity (RCS) index values for 114 species of ectotherms native to Oregon. These included 73% of known freshwater fish species ($N = 54$), 100% of amphibian species ($N = 31$), and 97% of reptile species ($N = 29$) native to Oregon (Tables A.3, A.4; Figs. 2, 3). Correlations between RCS values across study extents, data types, and grain sizes were strong overall, and ranged from an average of 0.88 to 0.99 for fishes, 0.90 to 0.99 for amphibians, and 0.80 to > 0.99 for reptiles (Table 1). Study extent had the greatest effect on the RCS values of reptiles (lowest mean correlation across taxonomic groups, $r = 0.89$), followed by amphibians ($r = 0.91$) and then by fishes ($r = 0.93$). RCS values were highly correlated across grain sizes for all taxonomic groups, with the lowest mean correlation for fishes ($r = 0.96$) followed by reptiles ($r = 0.97$) and amphibians ($r = 0.99$). Rankings of RCS values within taxonomic groups were generally consistent across study extent, grain size, and data types (Figs. 2 and 3). Across taxonomic groups, the contributions of Area of Occupancy (AOO) and Climate Sensitivity (CS) to the RCS index of each species showed similar general patterns (Fig. 2), particularly for the rarest taxa (Figs. A.7–A.9). The standard deviations of both AOO and CS for each species across all study extents, data types, and grain size (e.g., buffer width) were generally small (Fig. 2). Among the more common taxa (low RCS rankings), fishes tended to be most congruent across RCS, AOO, and CS rankings. In contrast, AOO and CS values were more asynchronous for the most common amphibians and reptiles compared to the most common fishes. Distribution of RCS values as calculated within the three major taxonomic groups varied, with high (> 0.8) RCS values for 37% of fish species, 23% of amphibians, and 17% of reptiles (Fig. 3, Figs. A.7–A.9). RCS values were also calculated across all species combined for directly comparable values across all taxonomic groups (at the Ecoregional scale, $N = 111$ species with 48% fishes, 28% amphibians, and 24% reptiles). Across all taxa, the species with the highest (> 0.8) RCS values were primarily fishes (70%), followed by amphibians (19%) and reptiles (11%) (Combo_RCS, Table A.3.B).

3.2. Life history traits and variation

Principal coordinate analysis (PCoA, Fig. 4) revealed different tradeoffs between life history traits by taxa. Freshwater fishes had strong positive correlations between fecundity, longevity, age at maturity, and body size, and a negative relationship between parental investment and all other traits examined (Table 2). These same relationships for fishes were supported in multivariate space where a single primary axis (PC 1) explained over 87% of the variation (Fig. 4A) and distinguished the same correlations as revealed in univariate space. A second axis explaining < 5% of the variance (PC 2) distinguished body size from all other traits examined (Fig. 4A). Univariate and multivariate analyses supported a correlation between amphibian age at maturity and parental investment ($r = 0.62$) and indicated a tradeoff between those two traits and fecundity (age at maturity, $r = -0.45$; parental investment, $r = -0.55$) (Table 2). This tradeoff also was captured along the primary axis of the PCoA (PC 1), which explained over 63% of the variation observed across amphibian species (Fig. 4B). We also found support for relationships between body size and three life history traits: fecundity ($r = 0.52$), generation time ($r = -0.51$), and parental investment ($r = -0.64$) (Table 2, Fig. 4B). PCoA supported that strong three-way correlation as well as a tradeoff between fecundity and all other examined life history traits of reptiles (Fig. 4D, PC 2, 29.6% variation explained). However, univariate analyses suggested the tradeoff between fecundity and other life history traits was not significant (Table 2). Univariate and multivariate analyses supported strong correlations between longevity and body size ($r = 0.82$), longevity and generation time ($r = 0.55$), and body size and generation time ($r = 0.69$) for reptiles (Table 2).

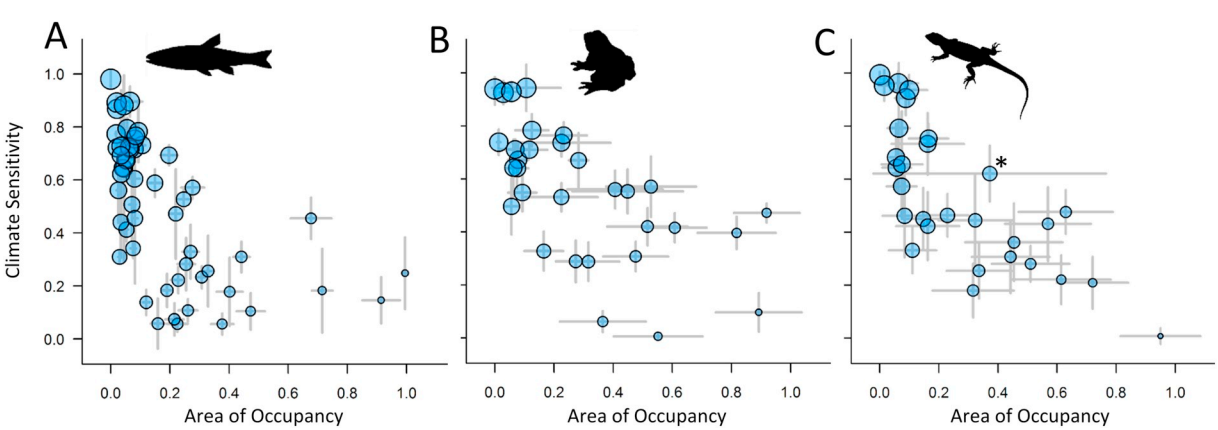

Fig. 2. Two components of the species-specific Rarity and Climate Sensitivity (RCS) index: Area of Occupancy (AOO, x-axis) and Climate Sensitivity (CS, y-axis) for (A) freshwater fishes, (B) amphibians, and (C) reptiles native to Oregon, USA. Symbol size scaled by RCS values, and the standard deviation of AOO and CS values across all grain sizes, data types, and study extents indicated by grey lines. Asterisk (*) identifies *Actinemys marmorata*, a pronounced example of the potential effect of data type on AOO.

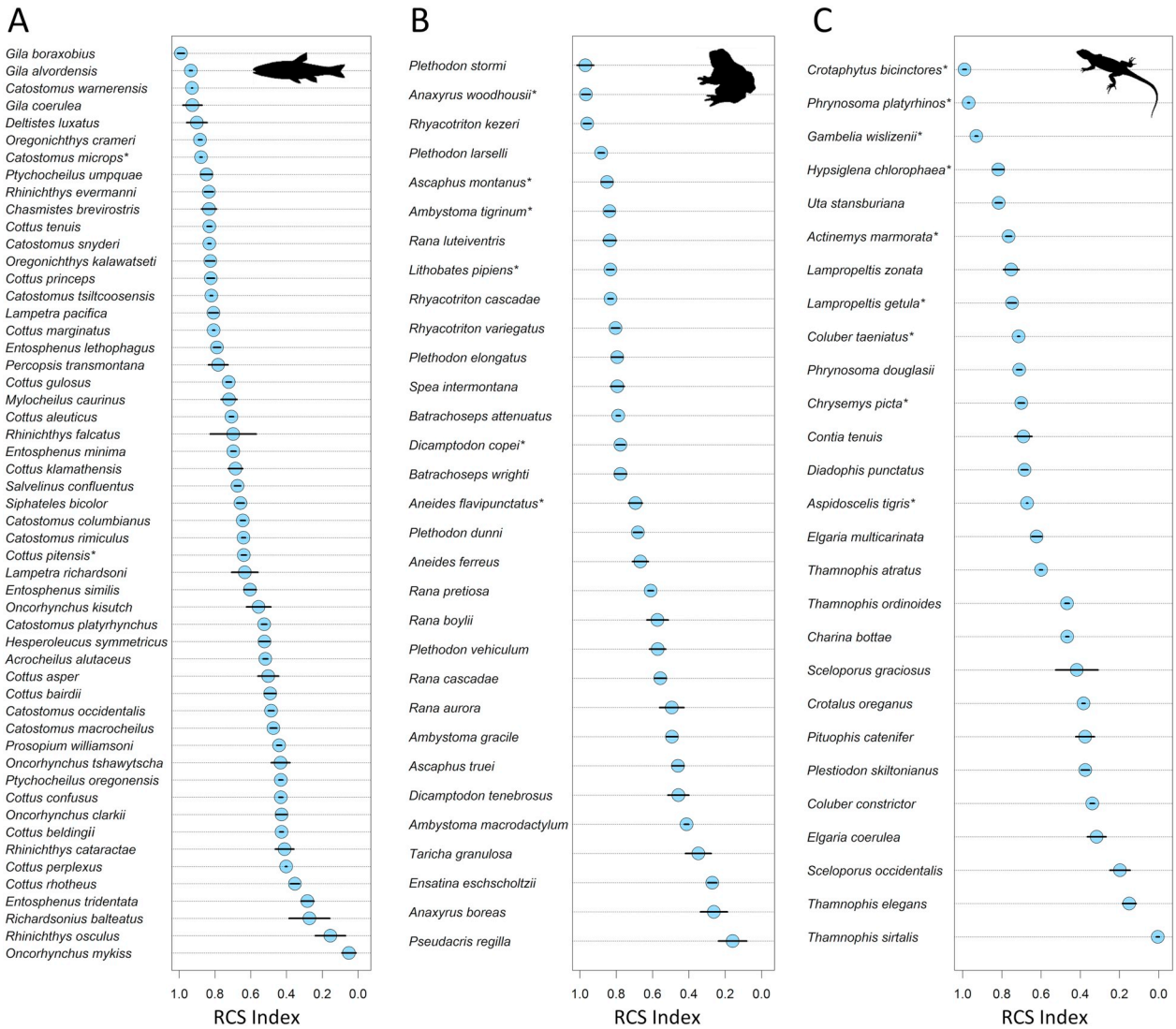

Fig. 3. Rarity and Climate Sensitivity (RCS) index values for all (A) freshwater fishes, (B) amphibians, and (C) reptiles native to Oregon, USA, with species ranked from most rare (top; left points) to most common (bottom; right points). Values averaged across grain sizes for the Ecoregional study extent (VertNet data only). Circle indicates mean RCS value, and standard deviation of RCS value indicated by black error bars. Species marked with an asterisk (*) were not assessed for at least one study extent due to data limitations (too few occurrence points).

Table 1
Spearman's rank correlation coefficients of Climate Sensitivity (Sensitivity), standardized Area of Occupancy (AOO), and Rarity and Climate Sensitivity (RCS) index values for each study design component of each taxonomic group.

Taxa	Study design	Sensitivity			AOO			RCS		
	Component	Average	Min	Max	Average	Min	Max	Average	Min	Max
Fishes	Extent	0.87	0.78	0.99	0.98	0.96	0.99	0.93	0.88	0.99
	Grain size	0.92	0.80	0.99	0.97	0.92	0.99	0.96	0.89	0.99
	Data type	0.98	0.95	0.99	0.99	0.99	0.99	0.98	0.97	0.99
Amphibians	Extent	0.93	0.86	0.99	0.86	0.80	0.90	0.91	0.90	0.93
	Grain size	0.96	0.87	> 0.99	0.98	0.92	0.99	0.99	0.97	> 0.99
	Data type	na	na	na	na	na	na	na	na	na
Reptiles	Extent	0.75	0.35	0.87	0.91	0.86	0.96	0.89	0.82	0.93
	Grain size	0.87	0.61	0.98	0.98	0.91	1.00	0.97	0.87	> 0.99
	Data type	0.79	0.48	0.82	0.87	0.75	0.93	0.87	0.79	0.93

Correlation coefficients were summarized (average, minimum (min), and maximum (max)) among studies for which only one component of study design (either extent, grain size, or data type) differed to assess the effect of that component on geographic rarity index values.

3.3. RCS and species attributes

A relationship between species' RCS values and life history traits at this regional scale was supported for only one trait for amphibian and reptiles. For amphibians, we found a positive relationship between age at maturity and RCS values ($r = 0.36$, $p = 0.05$, Table 2; Fig. 4B). For reptiles, this same RCS-maturity age relationship was inverse and a bit weaker ($r = 0.35$, $p = 0.07$, Table 2, Fig. 4C). There were no relationships between RCS values and the life history traits examined for fishes (Table 2).

Post-hoc exploratory analyses indicated that for species in this study, RCS values were generally higher among species of conservation concern at both the federal and state level, but these relationships were weakened if sub-species status was considered. When conservation status was considered at the species level only (e.g., protected or conservation status considered if applied to the entire species, not sub-species or other conservation units), RCS values differed among status categories at both the state and federal level (Fig. 5A and B, Table A.6). At the federal level, both Endangered species and Species of Concern had higher RCS values than species with no status ("None"); however, RCS values were not different between threatened species and those with no status (Fig. 5A, Table A.7). At the state level, both Critical and Vulnerable species had higher RCS values than species with no conservation status ("None", Fig. 5B, Table A.7). When sub-species status was considered, fewer differences in RCS values were observed between categories of protected status; only one was observed at the federal level (endangered species had higher RCS values than those with no protected status; Fig. 5C, Table A.7). No differences were present

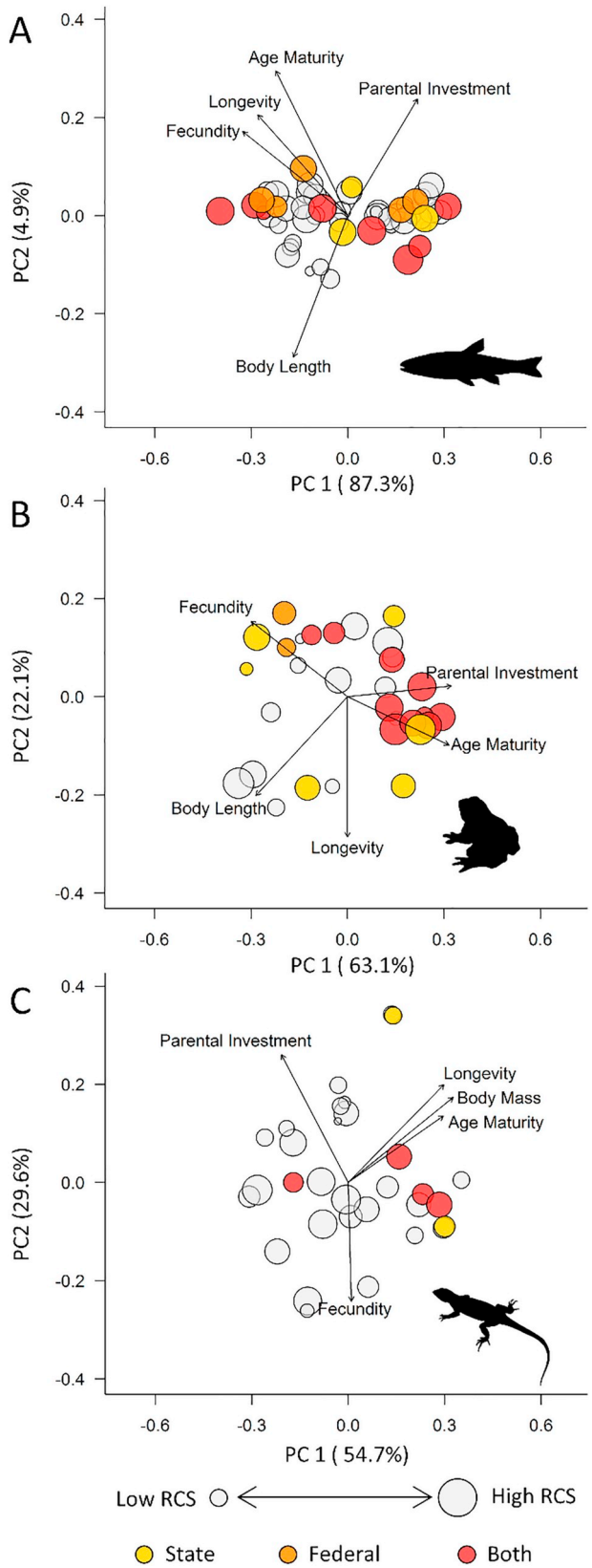

Fig. 4. Principal coordinate analysis of trait data for (A) freshwater fishes, (B) amphibians, and (C) reptiles native to Oregon, USA. Species are represented by circles, and the rarest species (high RCS values) are indicated by larger circles. Species protected status is indicated by color as federally threatened, endangered, or a species of concern (orange); a statewide sensitive or vulnerable species (yellow); or both (red). Species with no protected status or sub-species protected status are shown in grey. Trait vectors are indicated by black arrows and labeled by trait, and percent variation explained by principal components is shown on each axis. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Spearman rank correlation coefficients (top triangular matrix) and asymptotic *p*-values (bottom triangular matrix) between life history traits and the mean Rarity and Climate Sensitivity (RCS) index for each major taxonomic group.

	RCS	LogMass	Long	Mat	LogFec	ParInv
Fishes						
RCS		−0.19	−0.01	0.03	0.21	−0.07
LogBodySize	0.16		0.75	0.76	0.77	−0.72
Long	0.92	< 0.01		0.78	0.74	−0.68
Mat	0.81	< 0.01	< 0.01		0.82	−0.70
LogFec	0.13	< 0.01	< 0.01	< 0.01		−0.80
ParInv	0.64	< 0.01	< 0.01	< 0.01	< 0.01	
Amphibians						
RCS		−0.13	0.15	0.36	−0.28	0.21
LogBodySize	0.48		0.16	−0.51	0.52	−0.64
Long	0.43	0.38		0.25	−0.17	0.07
Mat	0.05	< 0.01	0.18		−0.45	0.62
LogFec	0.12	< 0.01	0.36	0.01		−0.55
ParInv	0.27	< 0.01	0.70	< 0.01	< 0.01	
Reptiles						
RCS		−0.20	−0.26	−0.35	−0.06	−0.21
LogBodySize	0.30		0.82	0.69	−0.08	−0.35
Long	0.17	< 0.01		0.55	−0.17	−0.24
Mat	0.07	< 0.01	< 0.01		0.09	−0.29
LogFec	0.76	0.68	0.38	0.63		−0.20
ParInv	0.27	0.06	0.22	0.12	0.29	

RCS Rarity and Climate Sensitivity index; LogBodySize, natural log of adult length (mm) for fishes and amphibians and mass (g) for reptiles; Long, longevity (in years); Mat, age at maturity (in years); LogFec, ln(fecundity); ParInv, parental investment (defined in Appendix: Supplementary Methods). See Supplementary Methods for additional details on life history traits.

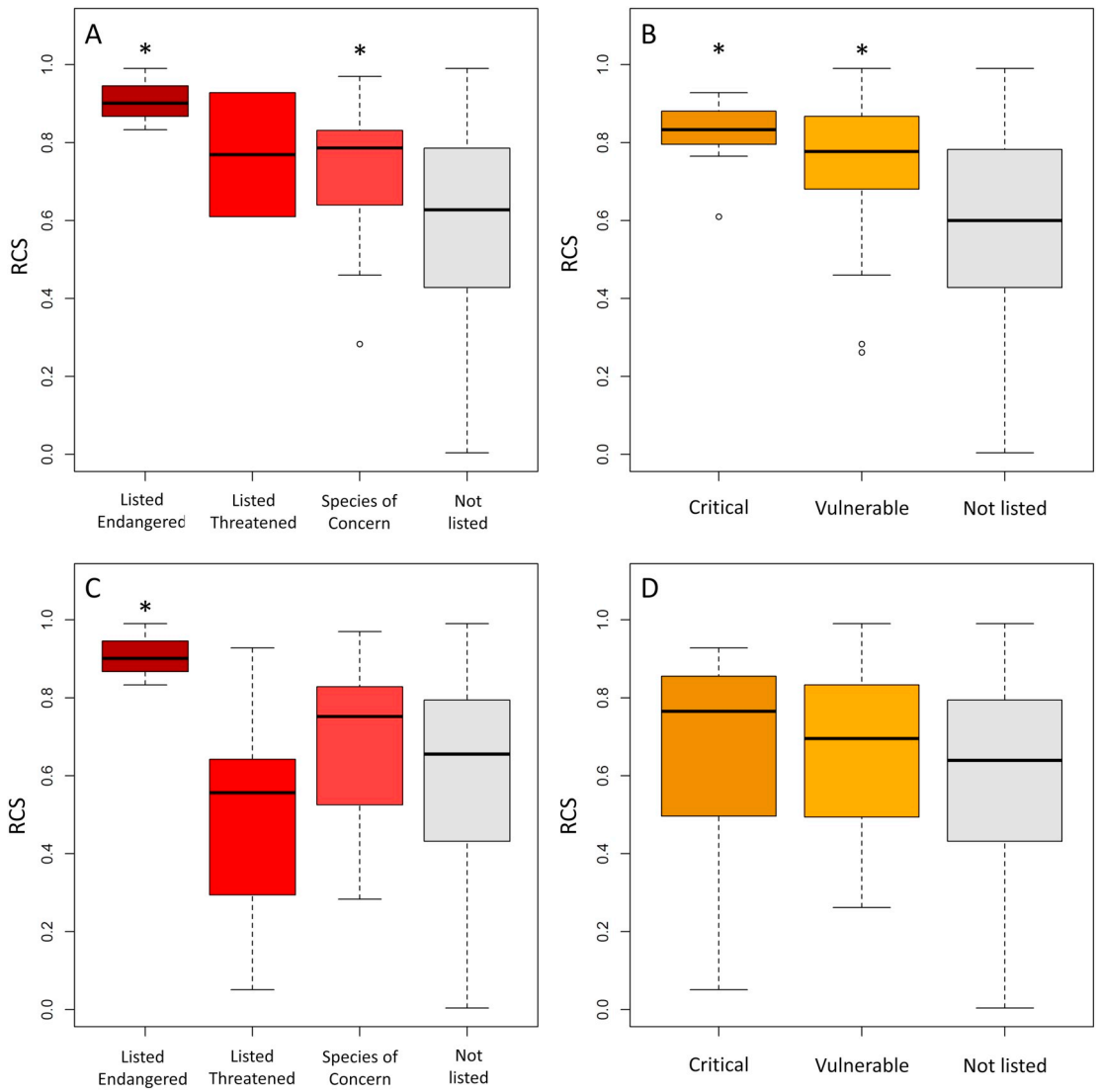

Fig. 5. Rarity and Climate Sensitivity (RCS) index values (y-axis) of native (Oregon, USA) ectothermic vertebrate species by species protected status at the federal (A, C) and state level (B, D); with status granted at the species level (A, B) or for any sub-species unit within a species (C, D). *Indicates groups significantly different from unlisted species. Each box delineates the upper and lower quartiles (75th and 25th percentile, respectively), and the line indicates the median (50th percentile). Whiskers indicate the range of values, and values outside a range of 1.5 times the interquartile range (e.g., 150% the length of the box) are shown as outliers (open circles).

between conservation status at the state level (Fig. 5D, Table A.6). Differences between AOO and CS for categories of protected status largely aligned with results from the RCS index comparisons (Figs. A.4 and A.5).

We found no differences in RCS values across species' primary habitat types or order (Fig. A.6, Table A.6). Correlations between continuous variables were not over the typical threshold of 0.7 (maximum Pearson's $r = 0.58$ between longevity and mass); thus, all predictor variables were retained. Regression tree analysis provided no support for traits, habitat, or taxonomy as predictors of rarity as measured by RCS values (cross-validated standard error increased with number of splits, for all combinations of predictors in regression tree analysis; Table A.5). Random forest also provided no support for species attributes as predictors of RCS values, with negative % variation explained for all models evaluated.

4. Discussion

4.1. Rarity and Climate Sensitivity index supports direct comparisons between climate-sensitive species

Multispecies assessments are urgently needed given the vast biodiversity at risk of decline or extinction due to environmental changes in an increasingly human-affected world. To project intrinsic risk of multiple species to climate change, we used an analytical approach combining geographic rarity attributes, climate niche breadth, and life history traits to provide a multidimensional assessment that allowed for regional cross-taxonomic comparisons. For most species, rarity and climate sensitivity (as measured by the Rarity and Climate Sensitivity index, RCS) were similar across three geographic study extents, four grain sizes, and two data types analyzed, supporting a simplification of

broad-based future analyses. We found that Climate Sensitivity (CS) was generally constrained by Area of Occupancy (AOO), but CS values varied substantially for species with smaller range sizes.

In terms of niche theory (Soberón and Nakamura, 2009) our treatment of CS was based on actual occupancy and thus most closely corresponded to a species' realized niche within the extent that we considered for species' ranges. Realized climate niche breadth has been identified as an important predictor of extinction risk in addition to geographic range of an organism (Saupe et al., 2015). Our findings indicate that inclusion of realized climate niche breadth (measured here as CS) may indeed offer additional insight into species' intrinsic risk to a changing climate over range size alone (Saupe et al., 2015). Among species included in this study, differences in CS between species with otherwise similar areas of occupancy could be related to a number of underlying factors. These include bona-fide differences in sensitivity to physical factors related to climate variability (e.g., the Grinnellian niche; Soberón and Nakamura, 2009), differences in species' capacities to behaviorally respond to climate (Beever et al., 2017), or results of our specific methodologies (e.g., scale or time-related biases). Regardless of the underlying cause, consideration of CS in addition to AOO can help to identify species that may merit additional investigation with respect to CS, adaptive capacity, or other factors potentially contributing to intrinsic risk.

The RCS index is valuable to consider for multi-species comparisons of climate vulnerability because it jointly weighs rarity (area of occupancy) and sensitivity to climate variation, allows a direct comparison among species, and highlights taxa predicted to be intrinsically vulnerable to climate change effects. The strength of the RCS is in the ability to identify taxa that may be at considerable risk due to combined, spatial intrinsic climate sensitivities (AOO + CS). Although RCS, AOO, and CS are largely concordant for the rarest taxa, the RCS can be broken down into its individual components to determine primary drivers of rarity should AOO and CS be discordant. Additionally, the RCS index provides a relative metric that allows for direct comparison of species within a region to one another. In our analyses, RCS values varied considerably among species, providing objective insights for those taxa with relatively little information regarding their intrinsic sensitivity and potential adaptive capacity, especially relative to species that may have protected status and be more heavily studied. For example, we found that a large proportion of fishes (37%) have high (> 0.8) RCS values, indicating that many freshwater fishes native to Oregon and the Pacific Northwest may have high intrinsic sensitivity. This is consistent with other regional assessments; for example, Moyle et al. (2013) found that 50% of California's native fishes have high intrinsic (or "baseline") vulnerability to extinction. We also found that freshwater fishes made up a higher proportion of taxa with high RCS values, in comparison to RCS values calculated across all taxa (fishes, amphibians, and reptiles). Although incomplete assessments and information can make cross-taxa comparisons difficult, other regional assessments also indicate disproportionately high intrinsic vulnerability of freshwater fishes compared to other fully, or partially, aquatic taxa (Howard et al., 2015). This is likely due to constrained freshwater habitats (i.e., stream networks at high risk of fragmentation) and limited dispersal ability of freshwater fishes compared to taxa with partial or full capacity to disperse across terrestrial habitats (e.g., frogs; Pilliod et al., 2015). Such conclusions can help provide context and guidance for regional monitoring and prioritization efforts.

We also found little to no support for correlations between RCS values and species' life history traits, indicating that geographic rarity and life histories may inform multiple dimensions of species sensitivity and adaptive capacity (i.e., intrinsic risk) to climate change (see also Pearson et al., 2014), particularly at the regional scale of this study. Assessing vulnerability is a multidimensional challenge, and our results support the use of a combination of rarity- and traits-based approaches to provide a relative assessment of potential risk of extinctions and declines due to climate change for multiple species at broad geographic extents.

The use of combined approaches provides multiple opportunities to identify species that may be intrinsically at-risk due to environmental change, but that may not be identified as such using a one-dimensional approach. Furthermore, the use of both AOO and CS provide a two-dimensional geographic rarity assessment that can be combined into the RCS used in this study or evaluated independently to identify individual, geographic components of risk. Thus, our results support deploying multiple approaches that incorporate both geographic and functional species attributes to help identify potentially at-risk species in a multispecies context.

Our approach has important methodological considerations. For example, we weighted AOO and CS equally in our RCS index; however, these two geographic components of intrinsic risk could be weighted differently should empirical or theoretical evidence suggest one is more important than the other for some taxa (e.g., Saupe et al., 2015). Additionally, we calculated CS over the entire temporal period for which we had climate data available to examine the breadth of climate conditions for a species' putative, contemporary range. Given the opportunistic nature of these data, we temporally aggregated all occurrence points. However, if species ranges have shifted or contracted during the time period represented by our study, the realized climate niche may be more restricted than the values presented here. CS values should be interpreted with this caveat in mind.

4.2. Considerations of grain size, data type, and study extent

Multispecies vulnerability assessments often must consider a trade-off between high-quality, systematically-collected data for well-studied species and limited, often opportunistically-collected data for poorly studied species. Consideration of as many species as possible, as was the aim of this study, often relies upon data collected in opportunistic or differing ways that may introduce biases within species or among species due to differential sampling efforts. Despite general congruence in RCS values within species, we found that some species' RCS values were affected by grain size, data type, or study extent. RCS values generally agreed between analyses derived from multiple datasets. However, some differences emerged (as highlighted by high standard deviation) and emphasize the importance of considering biases associated with differential sampling efforts, detectability, or sampling sizes when opportunistically compiling data for multispecies comparisons. For example, the western pond turtle, *Actinemys marmorata* (Fig. 2C*), had nearly two orders of magnitude more occurrence points ($N = 995$) in the comprehensive dataset than in the VertNet dataset ($N = 10$) at the three-state extent – a greater proportional difference between the two datasets than most other reptiles. Using multiple grain sizes provided a balance between precision and standardization (Hartley and Kunin, 2003) and helped assess whether sampling effort may affect RCS scores; additionally, variable RCS values across grain sizes for a species enabled identification of species with disproportionately high or low sampling effort, or detection relative to other species (e.g., Lost River Sucker, *Deltistes luxatus*; Fig. A.3). These potential effects of differential sampling efforts are not typically detectable with coarse-filter approaches that rely only on range maps or convex hull approaches (Peterson et al., 2017). Still, a relationship between sample size and RCS was detectable (Pearson's R ranged from −0.68 to −0.71 across grain sizes for VertNet Ecoregional data for all taxa). This relationship may be due to rarity of species (e.g., species that are rare are generally represented by fewer samples), or it could be associated with "true" sampling error (e.g., non-random collection of sampling) or observation error (e.g., detectability of species). Future empirical and simulation-based studies could help parse these processes to evaluate the sensitivity of RCS to sample size.

Our approach of buffered occurrence points at different grain sizes

also allowed for direct comparison of three distinct taxonomic groups: freshwater fishes, amphibians, and reptiles. For aquatic species such as lotic-affiliated freshwater fishes and amphibians, an alternative approach for sampling unit (or "grain") would be the use of watershed, catchments, or other stream network-based units – particularly for climate sensitivity metrics. Future research could expand the current study to compare modified grid-based based approaches to network-based approaches for aquatic organisms, where data allow. This comparison is likely an important step in setting regional priorities for monitoring or conservation efforts and exploring possible biases and limitations of the RCS approach – particularly if aquatic species are the primary focus.

We found a high congruence of RCS values across different spatial extents (Oregon only, three-state, and Ecoregional). However, study extents constrained by jurisdictional boundaries resulted in higher RCS values for some species with only a small extent of their total range within Oregon (e.g., California slender salamander [*Batrachoseps attenuatus*], Sacramento sucker [*Catostomus occidentalis*], and western whiptail [*Aspidoscelis tigris*]). For species at the periphery of their range, or if data availability is constrained within jurisdictional boundaries (e.g., within a state or province), rarity assessments should be tempered by species-specific geospatial and ecological contexts (i.e., accounting for edges of species' ranges or endemism within the region). Ecologically-defined study extents may provide a more reliable spatial framework for multiple species comparisons and may align with intraspecific differences in widely distributed species. Our focus on a regional extent and a particular state (Oregon) and its neighbors reflects jurisdictional boundaries at which species are managed. In our case, this regional focus allowed for the use of species occurrence data and climate data uniquely available within the spatial scope of our study. The alternative is to dispense with jurisdictional boundaries and consider an entire species' range, if data availability permits (Akçakaya et al., 2006). Both approaches provide useful insights.

Our results also highlight the utility of VertNet (Constable et al., 2010) as a tool for coarse yet systematic assessments of rarity across a wide range of species. VertNet records are verified by experts with confirmed species identifications, addressing the problem of misidentifications of cryptic species. This was of particular concern for the freshwater fishes in the study region, some of which are difficult to identify to species outside of a laboratory setting (P. Scheerer, Oregon Department of Fish and Wildlife, personal communication). However, some species had too few or no occurrence records in VertNet, and 27% of Oregon's native fishes were not assessed in this study due to too few occurrence points (Table A.4) (Markle, 2016). As analytical approaches for assessing species vulnerability to climate change continue to advance (Pacifici et al., 2015), the absence of many species in even the most basic framework highlights the importance of coupling analytical advances with empirical monitoring and assessment efforts. Ultimately, leveraging occurrence data collected opportunistically to inform sensitivity to climate change is most promising for datasets that have undergone expert evaluation or used highly-sensitive techniques (e.g., Biggs et al., 2015; Handley, 2015) to facilitate standardized comparisons between common, easily identified species and rare or cryptic species.

4.3. Geographic and traits-based approaches provide insight into multiple dimensions of intrinsic risk at a regional scale

Traits-based analyses revealed different suites of trade-offs between key life history traits among taxonomic groups. These results indicated that traits may inform an additional dimension of intrinsic risk when compared to geographic approaches. Additionally, the nature of trade-offs between life history traits and energetic investments differs among major taxonomic groups. In general, later-maturing species with lower fecundity (e.g., K-selected species; Pianka, 1970) are considered to be more at risk from a changing environment due to reduced evolutionary response capacity (Williams et al., 2008; Pearson et al., 2014). Relationships between life history traits for the region's freshwater fishes revealed a primary trade-off between longer-lived, later-maturing, highly fecund species and shorter-lived, early-maturing species with high parental investment per offspring. These trade-offs are characteristic of the larger suite of North American freshwater fishes (Mims et al., 2010). Generation time is one of the primary correlates of extinction risk (Pearson et al., 2014), and consequently fishes exhibiting a longer-lived, later-maturing life history may be expected to be more sensitive to climate change. Interestingly, we found no relationship between body size and RCS values for freshwater fishes in this region; this contrasts with evidence of positive correlations between range size and body size at the national scale (Giam and Olden, 2017). This finding may be due to restricted range sizes for many large-bodied native fishes in Oregon, such as native suckers (Catostomidae) including the Lost River sucker (RCS = 0.92), the shortnose sucker (*Chasmistes brevirostris*, RCS = 0.86), and the Klamath largescale sucker (*Catostomus snyderi*, RCS = 0.86). This finding underscores the need for regional studies to complement those at the scale of continents to inform management priorities that are often set by jurisdictional boundaries smaller than the entire extent of many species, particularly those with widespread distributions (Akçakaya et al., 2006). For the region's amphibians, life history traits distinguished later-maturing, longer-lived species with high parental investment from early-maturing, short-lived species with higher fecundity. In the only case of correlation between a life history trait and rarity and climate sensitivity, longer generation time was associated with higher geographic rarity for amphibians. As such, species with small range sizes and longer generation times, including Siskiyou Mountains salamander (*Plethodon stormi*), Larch Mountain salamander (*P. larselli*), and Columbia torrent salamander (*Rhyacotriton kezeri*), may have elevated risk due to multiple, potentially interacting, dimensions of intrinsic risk along axes of geography and life history. Reptiles also exhibited a tradeoff (albeit less pronounced) between later-maturing, longer-lived species and highly fecund species with shorter generation times. However, rarity and climate sensitivity were randomly distributed throughout the trait space of reptiles. Rare reptiles that exhibit K-selected life history attributes may be especially sensitive to climate change, and further investigation to characterize their vulnerability may be warranted.

Although life history traits offer a promising first step in addressing biological (or "functional") components of intrinsic risk, they are not a perfect predictor of adaptive capacity (Foden et al., 2013). Adaptive capacity was only partially addressed by the traits considered here. Behavior, movement ability, refuge use, ecophysiological factors – and the plasticity associated with these traits – are all critical in the ability of a species to respond to a changing climate (Nicotra et al., 2015; Beever et al., 2016). However, these traits can be difficult to quantify and are poorly characterized for many taxa. Life history traits, which tend to be more widely available, offer a surrogate or "proxy" for adaptive capacity in the absence of measures of behavior, refuge use, and the plasticity of these traits and others (Nicotra et al., 2015). The use of proxies for adaptive capacity must be considered in terms of the uncertainty they introduce when evaluating intrinsic risk. However, with the wide – and growing – availability of trait data, use of life history traits as proxies for these more mechanistic components of adaptive capacity offers a first step in assessing dimensions of intrinsic risk that are not captured by geographic methods alone. Efforts to synthesize evolutionary, genetic, and ecophysiological components of adaptive capacity should help improve the representation of adaptive capacity in vulnerability assessments in the future (Beever et al., 2016).

4.4. Placing species on the same scale: conclusions and future directions

Assessing vulnerability of species to a changing climate is a complex and multidimensional problem that includes the evaluation of both intrinsic and extrinsic components of risk. The multispecies approach

we developed shows promise as a useful primary filter for identifying species with intrinsic risk of extinction, but additional factors must be considered to fully describe species vulnerability to climate change (Williams et al., 2008; Foden et al., 2013). Understanding climate exposure or the velocity of climate change (Loarie et al., 2009; Burrows et al., 2014) within a species' range, as well as associated uncertainties (Wenger et al., 2013), is a key component of a more complete vulnerability assessment. For example, a rare species in a relatively stable environment may be less threatened than a common species occupying rapidly changing environments. Historical, trend-based analyses are known to perform better than strictly trait-based approaches in assessing risk of species to climate change (Wheatley et al., 2017).

Though multispecies assessments of intrinsic vulnerability and risk (i.e., with a focus on sensitivity and adaptive capacity) are subject to limitations, it is highly unlikely that timely and detailed ecological data will ever be available for most species of concern. Consequently, a means of screening or filtering regional species pools, such as the approach implemented here, is necessary to identify species most in need of additional information. Though the protected status of a species (or sub-species) typically accounts for many elements of exposure to environmental change or extrinsic threats, the range of rarity values within the "Not Listed" category – including some of the rarest species in this study – is notable. Species identified as rare, but unprotected, may warrant additional investigation, and this approach may provide an early warning for highly-sensitive species (Pritt and Frimpong, 2010; Stanton et al., 2015).

In summary, we found that the RCS index was relatively stable across extents, grains, and data types, with climate sensitivity differentiating species with otherwise similar areas of occupancy. We also found that species with traits associated with climate sensitivity and low adaptive capacity (e.g., long generation time, low fecundity) were not necessarily the same species identified as at-risk via the RCS index. This does not mean one approach is better than another, or that one is incorrect; rather, it highlights the utility of considering multiple dimensions of rarity to provide multiple opportunities for identifying species of potential conservation concern. This may prove to be critical for species with little information available, as they may not appear as intrinsically sensitive with only one means of exploration. Conversely, a single mode of analysis may artificially inflate sensitivity due to issues related to artificially low area of occupancy (e.g., undersampling or edge-of-range issues), and exploration along different dimensions could shed light on such scenarios. This approach equips managers with the option of exploring multiple metrics at once, including AOO, CS, the RCS index (a streamlined way to consider both AOO and CS), and traits. Regional approaches such as this would benefit significantly from future evaluations of the behavior within and among these dimensions of intrinsic sensitivity, including how they are affected by scale, data type, and sampling design (or, in the case of opportunistic data, distribution of locality information). Such approaches could be performed for species for which systematic surveys and opportunistic data are available, as well as in simulation studies.

Our approach enables multispecies, multidimensional efforts to quantify intrinsic sensitivity to climate change and provides a direct comparison between data-deficient and data-rich species. Furthermore, this approach is intermediate in scale, scope, and aim to very coarse-scale efforts (e.g., range-wide unidimensional multispecies approaches more appropriate for inference at continental or global scales), and those that involve data-hungry modeling techniques that may only be applicable to a few well-studied species. This is particularly important at regional scales in which managers operate at these intermediate scales and need tools that allow inclusion of the totality of a region's species pool – not simply those that are well-studied. We demonstrate that by considering multiple dimensions of intrinsic risk to climate change (range size, climate sensitivity, and traits), site-specific locality data may offer a pathway for ensuring vulnerable, understudied species do not go overlooked in conservation. By placing all species on the same scale, natural resource managers can reasonably evaluate a much broader complement of biological diversity than is typically true in practice. Such assessments can provide important guidance for investments to address species that require more information before decisions can be made, and identify species that may have been overlooked in current management and conservation plans.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.10.012.

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