Modeling Climate Change Sensitivity of Californian Ephemeropteran Assemblages

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ABSTRACT

Mayflies (*Ephemeroptera*) are crucial taxa in freshwater ecosystems and are known for their high sensitivity to environmental disturbance. How these organisms will respond to climate change has been a topic of concern for researchers interested in the future health and resilience of streams, especially in highly variable Mediterranean climate regions (MCRs). Though temporal trends in community composition and size have been examined, a large-scale spatial model of Californian mayflies' response to climate change was previously nonexistent. The aim of this study was to identify and model sensitivities and projected changes in the current distribution of selected families within Ephemeroptera, a climate-sensitive taxa in the state of California, from 1980 to 2050. Projections indicate universal range contractions for all species studied, contracting in the direction of higher elevations and northern latitudes. Those most threatened, as demonstrated by greatest range contractions, are coastal species unable to disperse through inland regions. For example, species in the family Ameletidae exhibited a 73.2% range contraction, with a distinct clustering towards the coast and foothills of the Sierra Nevadas. Species distributions within Ephemerellidae contracted only 21.4%, yet underwent significant fragmentation and a complete excursion from the central valley. In contrast, the family Baetidae is projected to persist in inland regions, which may be due to its decreased dependency on temperature as a model driver. The data presented has implications for improving biomonitoring efforts, and directs future efforts towards generating more detailed collection records in Mediterranean regions.

KEYWORDS

species distribution modeling, climate change, Maxent, Mediterranean climate, benthic macroinvertebrates

INTRODUCTION

Mediterranean-climate regions (MCRs), unlike temperate regions, are characteristically variable, with stream flow and temperatures varying substantially across seasons (Ball et al 2013). In California specifically, high levels of biodiversity and the nation's second-largest number of streams and rivers are juxtaposed with intensive land-use change and the continuous threat of drought (Moyle 1995). Stream-dwelling species are especially threatened by climate change, as their dispersal capacity is inherently limited (Reiss et al. 2011). Under conditions of prolonged climate disturbance, freshwater taxa often exhibit extinction rates at or greater than those of terrestrial organisms (Heino et al. 2009). In MCRs the effects of climate change are projected to alter community structure, composition, and population size in benthic aquatic taxa, changes which may lead to consequences for overall stream health and resilience (Lawrence et al 2010). As a result, the resilience of aquatic taxa is especially precarious in the context of prolonged climate change, even though MCRs are adapted to annually variable climate regimes. Growing concern for the fate of stream biodiversity has brought benthic macroinvertebrates to the fore of freshwater conservation research. In view of the threats of climate change, and California's unique status as an MCR home to massive, diverse aquatic systems, it is imperative to investigate how environmental changes will influence freshwater taxa.

As concern has increased over the effects of climate change on freshwater streams, recent studies have tried to discern how taxa crucial for evaluating stream health will respond to prolonged environmental disturbance. Climate change is predicted to impact MCRs with regional variation in coastal, inland, and highland systems (Prat et al. 1999). Similarly, the responses of sensitive aquatic taxa are predicted to vary along species preferences. Bonada et al. (2006c) predicted that most occurring benthic species in northern Europe will survive climate change effects, indicating a disappearance of many mayfly genera to be replaced by more resilient taxa from the south (Bonada et al. 2006c). Bonada projected a disappearance in Ephemeroptera, Plecoptera, and Trichoptera (EPT) orders, especially those with low dispersal capacity (such as those living in springs), corresponding to a northward expansion of Mediterranean taxa. Hering et al. (2009) characterized 29 taxa-specific parameters to describe how species-selective sensitivities can modulate climate change response, including physiology, emergence period, and stream order preferences. Although quantifying the temporal and taxonomic component, these

studies did not consider EPT response across a large spatial scale. Currently, no such spatial model exists that describes predicted response of sensitive taxa in California's MCR. Considering the non-uniform nature of climate change's effects, merging environmental changes with EPT distributions in a spatial context could reveal how studied climactic variables will impact populations across space and time.

The selection of appropriate climactic variables for species distribution modeling of aquatic taxa requires an understanding of the habitats in which they reside, in addition to life-history strategies that render them sensitive to certain parameters. Precipitation and temperature are key variables identified in prior climate change studies as to predict population survivorship and distribution. Even in annually variable Mediterranean climates, the importance of precipitation and temperature to EPT population resilience, community composition, and range is retained (Heino et al. 2009, Lee et al. 2008). These two variables have been consistently cited as central to EPT survivorship, while being the most readily affected by climate change (Prat et al. 1999, Heino et al. 2009, Hering et al. 2009). Temperature is expected to increase while rainfall will decrease (Lawrence et al. 2010). As a corollary, annual snowmelt and runoff from seasonal snowpack are expected to decrease and become less consistent, respectively (Bonada et al. 2006a). These variables are especially important to California's water supply, and changes in the degree of water availability will effect human and aquatic populations alike. All four of these important parameters exhibit quantifiable changes across the next five decades, as modeled by the CalAdapt climate dataset (UC Berkeley, California Energy Commission 2014), which presents an opportunity to assess EPT distributions with variables crucial to their survival.

Ephemeropteran species are central to California's freshwater ecosystems and exhibit exquisite environmental sensitivity. Though these taxa have been used in bioassesment studies for decades, the literature lacks a large-scale spatial model incorporating both species distributions and projected climate changes across the region. The outcome would be a more coherent picture of how these indicative benthic taxa may adapt, migrate, or dissipate in response to these shifts.

In this study, I identify and model sensitivities and projected changes in the current distribution of selected families within *Ephemeroptera*. The result is a series of maps integrating current and potential climate and geographic data to model how populations may migrate, adapt or dissipate in future scenarios. Using Maxent (Phillips et al. 2006), I establish their realized niche while identifying the most significant environmental variables such as precipitation, temperature

and annual runoff beginning in 1980 and projected through 2050.

METHODS

Study system and subjects

This study examined populations and climate trends in freshwater streams west of the Sierra Nevada mountain range in California, from the San Francisco Bay Area north to the Klamath River. Collections were made from streams of different sizes with a variety of methods over a period of 60 years. In all cases, field researchers were not sampling for one taxon exclusively. In this study, I examined distribution records of three families within the order Ephemeroptera: Baetidae, Ameletidae, and Ephemerellidae. Within each family I sampled 1 to 4 species, which were chosen by their abundance within the collection record.

Data collection

To assemble collection records, I used geo-referenced collection event datapoints sourced from the Essig Museum's database and unpublished collection data (Patrick O'Grady, UC Berkeley, unpublished data). Each collection record has five corresponding categorical values: collector, verbal description of the locale, method of collection (e.g. flipping rocks, net swinging), identifier, and the count of total number of individuals in the sample from which it came. These collection attributes are in addition to the taxonomic classification (Order, Family, Genus, Species) and location coordinates in decimal degrees, provided by the data sources. Many of the collection identifications, (primarily O'Grady collections), are confirmed by genetic barcode. I imported these values via Excel into ArcMap's ArcGIS® 10.2.1 (ESRI 2012) as comma separated (delimited) file.

To assemble climatic variables, I resourced historic climate data from the CalAdapt (UC Berkeley, California Energy Commission 2014) platform. These climate datasets were generated using physiographic interpolation methods to generate continuous spatial data integrating climate observations over the last 60 years. I chose precipitation, maximum temperature, mean temperature, annual snowmelt and seasonal runoff (Anderson 2006). Using each website's query interface, I downloaded each variable as ASCII historical-mean rasters binned into 30-year

averages. The resolution of CalAdapt rasters is 1km²;

To assemble additional features for visualization, such as hydrography, elevation and state plane basemaps, I used the USGS Topographic Map Viewer (USGS 2013). I did not use the numerical values of the elevation data in my analysis, as these are closely correlated with temperature as elevation is used in interpolation in the climate datasets. Hydrographic shapefiles are in vector form and have no inherent traits, but were used as visual references.

Present-climate distribution model

To quantify the correlation between climactic variables underlying each collection point, I ensured that the comma separated values file included a single column each for species, longitude and latitude in decimal degrees. Using Maxent (Phillips et al 2010), I input this file and two 30-year PRISM normal means for data from 1981-2010. These were for precipitation and mean temperature (Bonada et al. 2006). The run was conducted using "Auto Features", with a logistic output in .asc format. The output consisted of maps (.png images) and graphical representations of the model's robustness. I then imported the resulting map files into ArcGIS to visualize the results. I reported these in both tabular and visual form, comparing the Maxent-modeled distribution against observed record distribution, under current conditions.

Projected distribution model under 2-degree Temperature Increase

To project future (25 and 40-year) distributions, I input the .csv file into the Maxent model under the same parameters, using climate data from the CalAdapt projections which includes an approximate. I continued in an iterative fashion, adjusting the parameters according to the outputs from the Maxent model. I imported each result into ArcGIS. The hydrography and state plane maps were layered into the map to better communicate the spatial aspects of projected distributions.

Percent Habitat Change

To quantify the percent contraction of habitat under present scenarios, I aggregated observation

events constraining for individuals within a 200km radius in both the current and projected scenarios in ArcMap 10.1.2 (Taft et al. 2008). I exported each polygon and performed a percentarea change function to quantify how the habitat had changed, by spatial extent. Then I performed a Map Algebra subtraction from the projected and present model, across all layers.

RESULTS

Present-climate distribution model

The current distribution of the family Baetidae, based on four examined California species, occupied a range of 4470km², extending through the Central Valley into the foothills of the Sierra Nevadas, with a separate population on the south-central coast. Their regions were characterized by a high snowmelt and annual precipitation (Figure 1a).

This distribution contrasts, albeit mildly, with the current distribution of selected species within Ephemerellidae, which preferred both the highest snowmelt and lowest minimum temperatures of all taxa studied, while occupying a smaller range of 1170km² that clustered near either the Sierra Nevadas or on the northern coasts, avoiding the warmer central regions entirely (Figure 1b). It is important to note that while Ephemerellidae's overall range is smaller than that of Baetidae, there was a greater density of multiple species in a given range.

Ameletidae were generally less abundant and much more constrained to a range of only 890km², in the northern latitudes, typically within 50km of the coast, characterized by low mean temperatures (Figure 1c). Table 1 provides the environmental parameters of each studied species' established niche.



Figures 1a, 1b, 1c. GIS visualization of current (a)Baetidae, (b)Ephemerellidae, and (c)Ameletidae distributions. Maxent outputs for each species under present and future conditions in Appendix A.

				cm/yr*	°C*	°C*	**	**
Family	genus	species	observations	precip	t_min	t_max	snowmelt	runoff
Baetidae	Baetis	tricaudatus	43	72.33	4.47	19.51	16.58	12.62
	Callibaetis	californicus	7	93.64	19.41	3.89	27.29	9.77
		ferrugineus	32	63.21	5.34	19.94	13.29	9.86
		pictus	49	61.09	7.39	20.83	4.92	11.30
Ameletidae	Ameletus	suffusus	16	86.26	4.21	19.02	32.36	14.82
Ephemerellidae	Drunella	coloradensis	51	93.65	3.89	19.41	27.79	19.90
		doddsii	13	96.73	-0.06	16.24	13.29	16.67

Table 1. Established ranges of each Ephemeropteran genus, by environmental parameter.

*Annual averages. **Monthly mean, in millimeters

This parameter demonstrated the highest percent contribution to the species' current distribution model

Projected distribution with 2°C increase in Temperature

For the projected distribution of the family *Baetidae*, under the CalAdapt (2-degree 40-year) climate change scenario, I found a distribution covering a 3580km² range. The boundaries of this range are very similar to the current scenario, but with universal contractions coupled with fragmentation for two species (*pictus* and *californicus*). However, species persistence was still observable in the Central Valley. In this future scenario, every parameter increased in percent contribution except for precipitation, which actually decreased (Table 2).

For the projected distribution of the family *Ephemerellidae*, I found a distribution covering a 920km² range. The range contraction is characterized by a fragmentation of observed distributions, with nearly a clean split away from the Central Valley. Precipitation, with minimum temperature as a close second, were of greatest contribution to the model.

For the projected distribution of the family *Ameletidae*, I found a distribution covering a highly fragmented 200km² range. The parameters precipitation and runoff were of greatest contribution to the model. However, parameters such as temperature and snowmelt produced percent-contribution values of zero, which is possibly a software anomaly (Figure 3). The quantitative comparison of the current and projected maps indicate a projected aversion to areas where precipitation is expected to decline most sharply.

	Percent Contribution							
Baetidae	precip*	t_min*	t_max*	snowmelt**	runoff**			
Current (1980-2010)	33.23	22.53	10.27	15.63	15.00			
Projected (2050)	26.20	30.47	13.13	16.10	21.03			
Ephemerellidae								
Current (1980-2010)	68.45	19.2	13.7	7.4	6.05			
Projected (2050)	54.55	32.6	23.2	2.3	10			
Ameletidae								
Current (1980-2010)	52.6	1.1	0	0	46.3			
Projected (2050)	52.8	1.7	0	0	9.5			

 Table 2. Quantitative comparison, by family, of environmental parameters under current and projected (50-year) climate conditions.

 Parameters exhibiting a high decrease in percent contribution [>25%] are highlighted.

*Annual averages.

**Monthly mean, in millimeters

□ This parameter demonstrated decreased % contribution to the taxa's distribution model under future climate scenarios.



Figure 3. Graphical representation of changes in percent contribution

of each environmental parameter, by family.



Figures 4a, 4b, 4c. Current (top row) and projected (bottom row) distributions of (a)Baetidae, (b)Ephemerellidae, and (c)Ameletidae.

DISCUSSION

In the context of climate change, species distribution models for aquatic taxa have almost universally indicated habitat contractions or local extinctions for those most sensitive to precipitation and temperature (Lawrence et al. 2010, Bonada et al. 2006a, Heino et al. 2009). This study of Ephemeroptera indicates significant contractions and large dispersal events for all taxa examined. Precipitation and temperature were the greatest drivers of range transformation, with additional contribution from runoff and snowmelt, especially for the Baetids. Although future studies would benefit from a more robust set of parameters, this study provides evidence that climate change will greatly reconfigure the distribution of the three considered Ephemeropteran families within the next forty years.

Present Climate Model

Maxent's predicted distributions for current distribution of all families were highly consistent with observed samples. Upon visual inspection, both maps suggested high presence of all families in north-coast and montane regions; as expected, the model suggests presence in regions that were not sampled, but shared similar habitat conditions to sampled areas, namely along the central coast. It is difficult to contextualize this within the literature from a modeling perspective, as no other study has used only this specific dataset and only these parameters. However, consistent with taxonomic literature, areas indicated for the presence of Baetidae were well-distributed throughout the north and central coast, with presence across the central valley and into the Sierran foothills (McElravy et al. 1989).

Present distributions of the Baetidae, Ameletidae, and Ephemerellidae in California differ from each other. Baetidae is cosmopolitan, generally considered particularly sensitive to precipitation (Brittain 1982), which is emphasized in their reliance on snowmelt and runoff. Although the Baetids are a widely dispersed group, present species distributions cluster into montane (*Callibaetis pictus*) and coastal (*Baetis tricaudatus*) species. Percent contribution of precipitation to the present model was wildly different between species, with nearly 80% higher sensitivity in the coastal taxa. This pattern, wherein coastal species exhibited elevated sensitivity to precipitation, held for both Ameletidae and Ephemerellidae.

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Two significant regions of overlap were found from the Marin Headlands through the northern coast, as well as the lower Sierra Nevadas, with present distributions indicated by 3 highland and 4 montane species, with representatives from every family studied. The first area is characterized by high precipitation in a coastal zone. The latter is characterized by cooler temperatures, with slightly less precipitation yet high levels of snowmelt and subsequent runoff. These suggest that populations across genera exhibit profiles of preferred habitat within biomes, which are principally driven by precipitation, snowmelt and temperature.

Projected Climate Model and Percent Contraction

The projected climate model indicates significant changes in habitat range for all species, which indicates that the effects of climate change will strongly influence future taxa distributions. This finding provides unique insight because snowmelt and subsequent runoff made high contributions to the model (Bonada et al. 2006). Notably, the variation in magnitude and direction of habitat shifts suggests that sensitivities vary across species. Although ranges of coastal species were more likely to contract, inland populations exhibited a tendency to move to higher elevations and, in some cases, northward in latitude. For example, *Callibaetis pictus* (a highland species) experienced less than 1% range contraction in terms of square kilometers, but the projected range overlaps with only 40% of the current distribution. It is difficult to speculate whether, in reality, inland taxa would have greater dispersal capacity than those on the coast, yet it is sensible to foresee inland taxa making the shorter journey to higher elevations than for coastal species to expand through the ever-warmer central plains to reach the inland mountains. Effectively, the Central Valley may act as a barrier to dispersal for coastal species.

In similar studies of climate-responses of terrestrial megafauna, Maxent models less frequently demonstrate large habitat contractions in favor of range shifts (Laliberte & Ripple 2004). Intuitively, this is because land-based fauna have a higher dispersal capacity, whereas stream networks are not uniformly sized nor accessible to accommodate movement of threatened taxa (Reiss et al. 2011, Taft et al. 2008). This "choke effect" is central to the argument for examining aquatic taxa as uniquely sensitive to climate change, exhibiting responses in both the size and location of populations.

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Model considerations

The question addressed in this study was what changes might occur to Ephemeropterans under the climate scenarios delineated under the CalAdapt® climate model. Clearly, although Ephmeroptera are predicted to respond to of environmental conditions, these are not the only important aquatic taxa in California. Examination of other groups may reveal entirely different responses to a changing environment, with the potential for emergent niches and territorial expansion, neither of which were indicated in Ephemeroptera. I did not project any regional extinction, which is suspect in light of the taxa's known sensitivity and the unforeseen effects of climate change and human activity in the century to come (Buss and Salles 2007). Repeating this study while involving projected land-use change, urbanization and stream diversion may have given such results.

A separate consideration of spatial extent is worth discussion, alongside the matter of lifehistory strategies (Schmidt-Kloiber et al. 2004). A similar climate-response study took advantage of Trichopteran sensitivity in European ecoregions. Hering et al. (2009) evaluated the sensitivity of caddisflies to climate change by their realized niche and coded "environmental preference" parameters, which accounted for over twenty biotic and abiotic factors as well as life-cycle strategies. Importantly, this study's findings were directly at odds with those of Bonada et al. (2006c), the former projecting that most occurring benthic species in northern Europe will indeed survive climate change effects, the latter predicting a disappearance of many Trichopteran orders to be replaced by more resilient taxa from the south (Bonada et al. 2006c). The authors attribute this disparity to the difference in scale between the two studies: Bonada's study did not distinguish between the adaptability potential of specialist versus generalist species within the genera, though their geographic study scale was markedly smaller (Hering et al. 2009).

Understandably, Bonada projected a disappearance in EPT orders, especially those with low dispersal capacity (such as those living in springs), corresponding to a northward expansion of Mediterranean taxa. Hering's parametric estimation was tailored for a larger spatial scale, disaggregating specialist and generalists into subgroups but further parsing each into even smaller categories. It is important to note that one of the factors deemed "sensitive" and weighted accordingly was "endemism", which indicated the taxa only inhabited a single predetermined ecoregion. Although not arbitrary, this factor may have artificially sensitized taxa present in a relatively large range. In short, the more variable-dense study predicted less regional extinction. Thus, the trade-off between geographic scale and measure of environmental sensitivity seems a defining challenge in climate change adaptation modeling. My study emphasized the former, and as expected more closely matched Hering's prediction that, while ranges will contract, there will not be large extinction events under the model's time frame.

Species interactions, habitat connectivity, and genetic dynamics (Monaghan et al. 2009) are important considerations for any model of species distributions. Similarly, community resilience may deteriorate when conditions no longer match adaptive disturbance-resistance schemes, or when recovery outpaces community turnover (Hershkovitz et al. 2013). Such analysis may have provided more nuances to the projection, and showed complete extinction in certain locales. Within this order, gaps still exist where these parameters haven't been addressed. Ultimately, a complete picture of aquatic streams' response to climate change must include other aquatic taxa and a requisite assessment of all dynamics central to community persistence.

Limitations

The size of the dataset and the parameters I examined were limiting factors to characterizing habitat and predicting future habitats. Because most studies have to rely on collection events alone, many SDM software packages are designed to work with presence-only datasets, which poses an advantage for researchers working with museum and bio-monitoring databases (Lee et al. 2008). My observations were entirely sourced from the collection records of the Essig Museum and the labs of Resh and O'Grady, all marked by temporal gaps in the record and uneven representation of genera. In some cases, there were only 25 observations for a given species (e.g. *Ameletidae suffussus*), which barely reaches the threshold for Maxent's validity indices (Phillips et al. 2006). Though there were records for over 30 Ameletidae species, some only had 1 or 2 observations and could not be modeled at all. This resulted in the family having a much lesser representation than Baetidae, where four species had at least 25 records each. This alone could have contributed to the greater percent-contraction witnessed in the former, while the later family appeared more resilient. In addition, non-systematic sampling approaches are riddled with inequalities in site frequency, sampling technique, and environmental conditions at the time of collection.

An additional concern when working in Mediterranean climates is the possible mismatch between large-scale environmental data for the year sampled and the local climactic variability at the stream level. These concerns have not hindered successful SDM development, but are points of caution to those working with punctuated datasets. In light of the discrepancies mentioned earlier between small-scale, high-resolution and large-scale modeling efforts, efforts would be best spent filling in the sampling record with more dense and diverse collections (Schmidt-Kloiber 2004, Lenat et al. 2001). An emphasis on fleshing out datasets for specific ecoregions, such as those within California, would prove more useful for modeling efforts than a less-complete sampling regime across the entire country (Bonada et al. 2006, Schmidt-Kloiber 2004).

Conclusions

Ranges of Ephemeroptera in California will shrink, although they are not predicted to be regionally extirpated. The greatest threat to community persistence, especially in coastal zones, is the well-supported prediction of precipitation loss, which covaries with annual snowmelt. Decreased precipitation along massive swaths of inland habitat appears directly correlated with northward population shifts. Considering projected increases in other compounding factors such as temperature, the projected outcomes may be even exacerbated. For researchers and policymakers, the best actions are to acknowledge the projected changes as inevitable and evaluate how this will refigure food webs and other ecological services. Macroinvertebrates can and will continue to be useful indicators of climactic conditions and the health of streams (McElravy 1989).

In a changing climate, the monitoring and protection of aquatic taxa will be of increasing importance. Although climate change is inevitable, we can control activities and practices such as land use, which does directly affect presence and resilience of EPT taxa. Ultimately, it will be habitat and changes in *other* species that humans will notice first, such as decline in fishery populations, or absence of migratory songbirds in the spring. A wise plan of action is to use this data, and the finer models that build upon it, to make management strategies for the greater network of species upon which we rely.

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APPENDIX A: Maxent-modeled Outputs for Studied Species

Figure A1. Representation of the current (1980-2010) Maxent model for Baetis_tricaudatus. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations. (This description holds for the entirety of Appendix A).



Figure A2. Baetis_tricaudatus, 2010-2050. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations.



Figure A3. Representation of the current (1980-2010) Maxent model for Callibaetis_californicus. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations. (This description holds for the entirety of Appendix A).



Figure A4. Callibaetis_californicus, 2010-2050. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations. (This description holds for the entirety of Appendix A).



Figure A5. Representation of the current (1980-2010) Maxent model for Callibaetis_ferrugineus. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations. (This description holds for the entirety of Appendix A).



Figure A6. Callibaetis_ferrugineus, 2010-2050. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations. (This description holds for the entirety of Appendix A).



Figure A7. Representation of the current (1980-2010) Maxent model for Callibaetis_pictus. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations. (This description holds for the entirety of Appendix A).



Figure A8. Callibaetis_pictus, 2010-2050. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations. (This description holds for the entirety of Appendix A).



Figure A9. Representation of the current (1980-2010) Maxent model for Ameletus_suffusus. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations. (This description holds for the entirety of Appendix A).



Figure A10. Ameletus_suffusus, 2010-2050. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations. (This description holds for the entirety of Appendix A).



Figure A11. Representation of the current (1980-2010) Maxent model for Drunella_coloradensis. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations. (This description holds for the entirety of Appendix A).



Figure A12. Drunella_coloradensis, 2010-2050. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations. (This description holds for the entirety of Appendix A).



Figure A13. Representation of the current (1980-2010) Maxent model for Drunella_doddsii. Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations. (This description holds for the entirety of Appendix A).



Figure A14. Drunella_doddsii, 2010-2050 Warmer colors show areas with better predicted conditions. White dots show the presence locations used for training, while violet dots show test locations. (This description holds for the entirety of Appendix A).