

*Mapping the range shifts of
East River Valley caddisflies (Trichoptera)*



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Abstract

Range shifts occur when all individuals of a species or population move from a previously-habitable area to a newly-habitable area in response to changing environmental conditions. Climate-induced range shifts are well-documented for certain regions, biomes, and taxa, but large knowledge gaps exist for the Western Hemisphere and for aquatic macroinvertebrates specifically. There is a need to understand how climate-induced range shifts of aquatic macroinvertebrates are occurring, especially for taxa which have marked effects on ecosystem functioning, such as detritus shredders. Thirty years of aquatic sampling at the Rocky Mountain Biological Laboratory have revealed that Trichoptera species seem to be shifting their ranges, but the details of this observation have not been quantified. My project aimed to map and describe the multidimensional ranges (and later, range shifts) of caddisflies in this region using survey data and GIS technology. I mapped the current ranges of twelve species in the region and found results consistent with previous studies on life histories, predator vulnerability, and pond hydroperiod tolerance. I will continue this project as part of my senior thesis, which will specifically entail investigating previous ranges and describing range shifts through time and space. These results have several broad-scale implications. First, quantifying which new combinations of species are emerging across the landscape provides a jumping point to researchers wanting to study population and community studies focused on the interactions among species of caddisflies. Second, it also allows ecologists to ask new questions: what are the ecosystem functioning consequences of new community structuring with these taxa? What limits ranges and range shifts for these taxa?

Introduction

Range shifts, climate change, and consequences

A species' range is the set of geospatial dimensions in which all individuals of a species or population are located. Ranges are usually described in terms of some combination of three directions: latitude, longitude, and elevation or depth (Lenoir and Svenning, 2013). Although not fully indicative of a species' ecological niche, nor even the full geographic extent which the species could occupy, a species' range is thought to be most shaped by its climatic tolerances (or "climate niche"), particularly at larger scales (Pearson and Dawson, 2003, in Lenoir and Svenning, 2013). Even in stable environments, ranges are dynamic over time due to metapopulation processes such as dispersal, colonization, and sink extinction, especially at the outer peripheries of a range where conditions are less suitable than those in the core or range optimum (Pulliam, 2000, in Lenoir and Svenning, 2013).

Major changes in environmental conditions, such as precipitation patterns or ecological succession stages, can shift the geographic area to which a species is most suited, causing the individuals of that species to move and form a new, persisting distributional range; this is called a range shift and is one of three options afforded to a species when previously-suitable conditions become unfavorable (the other two are adaptation or extinction) (Maginni *et al.*, 2011, in Lenoir and Svenning, 2013). Range shifts can occur by way of changes in multiple distributional parameters, sometimes in combination. For example, a species' optimum may shift while peripheries stay mostly the same; this is called a "lean" shift. Another example is the "march" shift, in which the optimum, leading edge, and trailing edge all shift together in a certain dimension, such as elevation (Lenoir and Svenning, 2013). Each type of range shift tends to be linked to certain species characteristics; for example, march shifts are typical of small-bodied, short-lived, and highly vagile organisms, such as butterflies, while sessile, long-lived, and large-sized organisms, such as trees, tend to exhibit lean shifts (Lenoir and Svenning, 2013). Species can shift their distributions in different ways in different dimensions at the same time. For example, one study

(Grenouillet and Comte, 2013) described the multidimensional shifts of 32 stream fish species in France; many species shifted their ranges by leading-edge expansion along the elevational gradient while simultaneously shifting by trailing-edge retractions along the horizontal gradients (latitude and longitude). Range shifts, especially those under climate change, can lead to severe ecological consequences such as lowland biotic attrition (loss of biodiversity that cannot be replaced by lower species shifting upwards), reorganization into non-analog communities (communities different in composition from any communities present at a selected reference point in time), and trophic cascades (Lenoir and Svenning, 2013).

The knowledge gaps

Since the 1850s, there have been more than 200 peer-reviewed studies published that describe climate-related range shifts under contemporary climate change (Lenoir and Svenning, 2014). As global climate change progresses, many species are displaying range shifts poleward and upward, with few documented shifts in unexpected directions resulting from region-specific differences in temperature and precipitation patterns. Despite the known consequences of range shifts and climate change on ecosystems, several research biases have been identified in this field of study, and thus the general patterns observed may not be wholly representative (Lenoir and Svenning, 2014).

Geographic shortfalls. Most research on range shifts under contemporary climate change has been based in Europe, especially in the United Kingdom. Further, there is a bias towards certain biomes within the most heavily-studied geographic regions; evidence of climate-related range shifts in Europe (as well as in North America) is mainly from Mediterranean woodlands, temperate broad-leaved and mixed forests, temperate conifer forests, boreal forests, and tundra (Lenoir and Svenning, 2014).

Taxonomic shortfalls. Most research on range shifts has been on animals, mostly birds and mammals. Only a handful of papers have been published on shifts in invertebrates, such as butterflies and moths, and even fewer of those papers have been based on invertebrates with aquatic larval and/or adult forms. One study on odonates was based on adult odonate observations in terrestrial transects, not larval sampling in streams or ponds (Hickling et al., 2005). One of the few range-shift studies on lentic invertebrates quantified ranges and range shifts of perlid stoneflies in an Appalachian stream shed (Sheldon, 1985 and Sheldon, 2012), but I know of no similar lentic-focused studies.

Methodological shortfalls. Most research on range shifts has focused on a singular dimension and a singular distributional parameter at a time. In fact, most studies that focused on the latitudinal dimension also focused on changes at distributional margins (trailing and/or leading edges), while most studies that focused on the elevational gradient also focused on shifts of or abundance changes within the range optimum. Only one study (Comte and Grenouillet, 2013) has integrated all major dimensions (latitude, longitude, and elevation) to assess all major distributional parameters (optima, leading edge, and trailing edge), which revealed that species can shift in multiple dimensions in multiple ways (distribution-wise) in tandem.

In summary, there is a need for more research to be conducted on range shifts under contemporary climate change in the Western Hemisphere, focused on understudied taxa such as invertebrates, and that considers multiple dimensions and distributional patterns at the same time. Such research would bolster the current understanding of the effects of contemporary climate change on the distribution of species through time.

Contextualization of this study

Macroinvertebrates contribute to multiple ecosystem functions and services (via pollination, decomposition, burrowing, etc.) and are highly responsive to climate change compared to other organisms (Prather *et al.*, 2013). Despite this knowledge, it is unknown how climate change will affect ecosystem functioning by impacting invertebrate populations. Wetland ecosystems in particular provide a number of unique services, such as carbon sequestration, water filtration and retention, and habitat for economically-important species such as game fowl (Mitsch *et al.*, 2015), and this is due in part to the comparatively high biodiversity supported by wetland systems. Even temporary wetland ponds (those that fill with water from snowmelt or other precipitation and dry completely over the course of several weeks) are beneficial systems because, among other services, they act as havens for organisms (i.e., macroinvertebrates) whose larval forms would otherwise be easily preyed upon by predators in more permanent settings (i.e., fish); in fact, temporary wetlands have been compared to “keystone species” in that their impacts within entire landscapes can be considered disproportionately important compared to what would be assumed by their relatively small size (Calhoun *et al.*, 2017). Similar to macroinvertebrates, small ponds -- especially those at high elevations -- are highly responsive to climate change, with consequences including hydroperiod shifts for the first time in millennia (Smol and Douglas, 2007).

Detritus, or dead organic material, is the major source of energy and nutrients for many wetland taxa (Holgerson *et al.*, 2016), and thus detritus processing is vital to the functioning of these valuable ecosystems. Macroinvertebrate taxa that are classified as “detritus shredders” contribute to the reintroduction of nutrients useable by other trophic levels in aquatic systems by shredding and feeding on plant detritus (colonized by microbes, the actual source of the shredders’ nutrients) (Prather *et al.*, 2013). In certain wetland systems, shredder activity seems to have a positive effect on detritus breakdown rates when compared to decomposer-microbe activity alone; *in situ* studies in montane kettle ponds (Wissinger *et al.*, 2018; 2016) and subalpine ponds (O’Malley, 2018, student paper) in the Rocky Mountains of Colorado have found a positive relationship between shredder presence and detritus breakdown rates. In these systems, Limnephilid caddisfly shredders are the biomass-dominant taxa (Wissinger, unpub. data). Caddisfly species there majorly comprise the same functional guild but differ interspecifically in their life histories (Wissinger *et al.*, 2003), diets (Wissinger *et al.*, 2018), and excretions of nutrients (Balik *et al.*, 2018). Thus, range shifts leading to species gains or losses within pond systems have the potential to have very large effects on ecosystem processes, even in the event of displacement or replacement of a shredder by another shredder.

Since 1989, caddisfly presence throughout the East River Valley have been monitored by Scott Wissinger and students via larval surveys of about 100 ponds. The resulting dataset shows species-level presence/absence as well as abundance across an elevational/latitudinal gradient from Gunnison, CO (2316 m), to the Mexican Cut Nature Preserve in the Gunnison National Forest (3688 m). Throughout these surveys, gradual species movement and persistence upslope have been observed, though the details of these range shifts (type of shift, meters of increase in elevation, etc.) need to be quantified (Table 1). During this time, local temperatures at the Rocky Mountain Biological Laboratory (RMBL) were reported to rise by at least 1.4 °C between 1975 and 1999 (Inouye *et al.*, 2000, in Parmesan, 2006), and hydroperiod shifts of ponds towards more temporary (earlier-drying) conditions have also been observed (see Lund *et al.*, 2016). Thus, the effects of climate change in this region may be causing caddisfly species to shift their ranges, though it is unknown to what degree species are responding spatially.

Research objectives

The goals of my study for this summer were to:

- (a) Identify the most common and/or widespread lentic Trichoptera species from Gunnison to Mexican Cut and to create a species-level key that can be used for identification in the future. Species-level keys are available for adult caddisflies, but not for larvae.
- (b) Complete the 2019 caddisfly survey, which was a quantitative survey (taken every five years) as well as the 30th annual survey overall.
- (c) Develop a model that produces a summary of the current elevational and permanence ranges of the core species in the region, which could then be used with historic survey data to compare change over time.

Further analysis will be performed following this project as part of my senior thesis at Allegheny College; this will be discussed later in this report.

Methods

A total of 89 ponds were sampled in the 2019 caddisfly survey (Fig. 1). The resulting elevational gradient spanned from below Gunnison, CO (min. elev. 2309 m) through Gothic, CO (max. elev. 3482 m). A permanence or hydroperiod gradient spanning from temporary to permanent, with semi-permanent as an intermediary, was also covered by this survey. The ponds had various source characteristics (natural, human-constructed, and beaver-constructed) as well as various types (isolated kettles, riparians, marshes, and vernal/autumnal pools, among others). At ponds for which geospatial data did not already exist, points were taken by the pond's edge using a Trimble Juno 3B GPS unit. Permanence was attributed to each pond using historical data (Wissinger, unpub. data), and elevation was obtained at each point using a 10x10m digital elevation model (DEM) of Gunnison County in ArcMap 10.4.1 (Esri).

Quantitative aquatic surveys were performed at each pond. A 0.3-meter D-frame kick net was swept across the surface of the water at the edge of the pond near microhabitat (vegetated areas). Three sweeps were taken in this manner across a span of approximately 1 meter (forward, back, forward) to collect a sample representing about 1 square-meter. The contents of the net were then dumped into a white sampling tray with pond water. Caddisfly larvae were counted and recorded by species, abundance (number of individuals), and instar (number of moults out of five before pupation). Then, the contents of the tray were returned to the pond. This was repeated four times at each pond to account for differences in microhabitat (especially in the case of beaver ponds and partially-shaded ponds, where thermal variations may exist); samples were taken at the north, south, east, and west ends.

Voucher specimens were selected at various ponds, preserved in ethanol, and brought back to the lab for identification under a dissecting microscope (Wild Heerbrugg M-8). Three dichotomous keys were used to identify individuals to genus: *Freshwater Macroinvertebrates of Northeastern North America* (Peckarsky, 1990), *Larvae of the North American Caddisfly Genera (Trichoptera)* (Wiggins, 1996), and *An Introduction to the Aquatic Insects of North America* (Eds. Merritt, Cummins, and Berg, 2009). Species-level identification was accomplished using a historic reference collection of individuals, which have been previously confirmed by Scott Wissinger and Dave Ruiter (personal correspondence) as well as Wendy Brown (Brown, 2004). Photos of species heads, cases, gills, and legs were taken under the microscope for use in constructing a species-level larval key (Wirebach, unpub. data; Fig. 2.).

Ranges were mapped using RStudio (ver. 1.1.453) (Fig. 4). The abundances from each sample for each species were averaged at each pond. Minimum and maximum elevations for each species were found based on the highest and lowest ponds sampled that had that species. Abundance was scaled for each species using a square-root function; across each species' elevational range, each pond was symbolized based on the proportion of the total abundance occupied by that pond (ponds with greater numbers of

individuals comprised of a larger proportion of the total number of individuals found in the survey this year, and vice-versa). The average elevation of a species' range, weighted by abundance, was found and used as a proxy for elevational range core.

Results

Taxonomy

A total of 16 caddisfly species were observed and identified in the 2019 survey; three of these species are classified as lotic (flowing water) species while the other 13 are classified as lentic (Wissinger, unpub. data; Table 2). One species, given the operational taxonomic unit "Patchwork," has not been identified as of yet; however, live pupal cases have been placed in emergence chambers (mosquito breeders, prod. #1425, *BioQuip Products, Inc.*). Any adults that emerge from these chambers will be matched with voucher larvae and confirmed using an adult key.

Twelve lentic species were identified as main study species; these are species that are abundant across the study region, newly present in the study region, or have been part of the long-term dataset for several years (Fig. 2). The current ranges of these species were mapped for this project and will be compared to the historic dataset as part of my senior thesis.

Current range statuses

Upon the completion of the 2019 survey, the elevational and permanence ranges of 12 caddisfly species were mapped and ordered by lowest-to-highest core of their range (Fig. 3). Based on sampling, *P. quaeris* has the lowest elevational range, while *A. deflata* has the highest. Elevational cores did not always fall in the centers of ranges; some cores fell towards the leading edge (as in "Patchwork," *G. lorettae*, and *A. nigriculus*, for example) while others fell towards the trailing edge (as in *P. quaeris* and *L. picturatus*).

In terms of permanence, species displayed varied occupation patterns across the elevational gradient. Some species maintained similar permanence presence across their ranges (as in *A. bimaculata* occupying permanent beaver ponds and *L. tarsalis* occupying majorly temporary ponds). Other species occupied different permanences depending on the elevation (as in *P. quaeris* occupying more temporary ponds as elevation increases and *L. picturatus* appearing to be a generalist at lower elevations but confined to semi-permanent ponds at higher elevations).

Investigating range shifts

The results of mapping the 2019 survey data were compared to the observations of the 1989 survey in order to document the overall pattern of range stasis or range shifts up until this point in time (Wissinger, personal correspondence; Fig. 4). The species that have not significantly changed their elevational ranges include *L. externus*, *L. secludens*, *L. tarsalis*, *A. nigriculus*, *H. occidentalis*, and *A. deflata*. The species that continued their range shifts (apparent leading edge expansion) into 2019 include *N. hostilis* (1994 - 2019), *A. bimaculata* (1994 - 2019), and *P. quaeris* (2015 - 2019). At the same time, *L. picturatus* has continued an ongoing trailing edge retraction (2015 - 2019), which is more recent than its previous leading-edge expansion (1999 - 2004) that was almost in tandem with the leading-edge expansion of *L. sublunatus* (1999 - 2009). Not shown in this figure is the occupation and extinction of *G. lorettae* at the Mexican Cut Nature Preserve (elev. 3400 m) for seven years (2009-2016).

Mapping caddisfly distribution

For two species, *A. nigriculus* and *L. picturatus*, pond abundance was mapped in a GIS (ArcMap 10.4.1, *Esri*) so that co-occurrence and other distribution patterns could be observed at a large scale (Figure 5). However, due to time constraints and technological issues, no other species could be mapped in this way.

Discussion

I was able to develop a model that mapped the elevational and permanence ranges of twelve species of caddisfly in the East River Valley region of the Rocky Mountains, Colorado. The script used to plot ranges in RStudio showed minimum and maximum elevations, permanences, cores, and pond-specific characteristics (exact elevation and permanence as well as caddisfly abundance and co-occurrence) simultaneously (Fig. 3). My results were consistent with previous reports of caddisfly species-specific life histories, predator vulnerability, and hydroperiod occupation (Wissinger *et al.*, 2003). For example, *A. deflata*, a desiccation-intolerant species, was found in only permanent and semi-permanent ponds across its narrow elevational range, whereas rapid-growing and desiccation-tolerant species (*A. nigriculus*, *L. externus*, and *L. picturatus*) were “permanence generalists” across their elevational ranges, with *A. nigriculus* occupying more temporary ponds and the latter two species occupying more permanent ponds in similar patterns regardless of elevation. This is likely due to their varied abilities to avoid predators, as permanent ponds support salamanders while temporary ponds do not (Wissinger *et al.*, 2003).

The data I collected this summer will be combined with previous surveys during my senior year at Allegheny to estimate the type and precise elevational shifts of species. Using a GIS to map species abundance would add nuance to range descriptions, especially if analysis tools are used beyond simple symbology choices. For example, a full range “shape” can be created across the landscape (i.e., the terrestrial environment between ponds) in a GIS using interpolation tools, such as kriging, which estimate values for missing spaces in geospatial data based on known values and guiding parameters (in this case, dispersal distances of adult caddisflies) (Gimond, 2019). Through this method, I will map estimated terrestrial adult ranges in addition to aquatic larval ranges and report the total geographic area covered by each species’s range. Doing so will have the added benefits of not only displaying clearer range cores and peripheries but also, in the case of change over time, allowing me to track the paths and rates of core and periphery shifts. This could make the process of defining the type of shift (lean, march, expansion, etc.) more refined (Lenoir and Svenning, 2014).

Several observed patterns in the results could be explained by further analysis. For one, I used average elevation weighted by abundance as a proxy for range core, and the positioning of the core was not consistently positioned in the approximate center of the elevational range (Figs. 3, 4). Indeed, a species’s core does not necessarily always exist in the geographic center of its range (Lenoir and Svenning, 2014). However, in mapping ranges through time, the positioning of the core may be indicative of the direction and/or rate of a range shift. Another observed pattern was that *L. picturatus* exhibited an apparent trailing-edge retraction shortly after *L. sublunatus* made an apparent leading-edge expansion through the upper montane elevations, leading to the question of whether the former shift was initiated by competition in ponds of co-occurrence (Fig. 4; Wissinger, personal correspondence). Investigating patterns and timings of new community compositions in tandem with tracking species-level range shifts could allow me to answer that question.

The next steps for this project will be completed in fulfillment of my senior thesis at Allegheny College. I will fit the historic dataset -- the quantitative surveys taken every five years -- to my models in

order to meet several further objectives: (1) quantify the details of range shifts made by species over time (specifically, the distances, rates, projections, and type(s)), and (2) summarize the status of new communities across elevations as well as across permanences within elevations, namely the locations and number of new community compositions. Meeting these objectives will provide the basis for modelling how changes in communities affects ecosystem function; allow us to ask the questions, “what are the ecosystem functioning consequences of new community structuring with these taxa? What factors limit ranges and range shifts for these taxa?”

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Tables and Figures

Table 1. Distributions of caddisflies (Trichoptera: Limnephilidae) near RMBL in central Colorado. *L.* = *Limnephilus*; *A.* = *Asynarchus*; *G.* = *Grammotaulis*, *H.* = *Hesperophylax*, and *N.* = *Nemotaulius*. Ranges based on survey data from 1990 – 2018 (Wissinger *et al.* 2003; 2015; unpub. data). **Bold indicates dominant species.** * indicates upslope range shift in elevation since 1990, and dates represent the first time that species was encountered in temporary and permanent ponds annually surveyed at that elevation. From Wissinger *et al.*, 2016. *Agrypnia deflata* (Trichoptera: Phryganeidae) is absent from this graph but was included in the present analysis because it is included in the historic dataset.

Lower Montane (2500-2750 m)		Upper Montane (2750-3000 m)		Subalpine (3000-3500 m)	
Temporary	Permanent	Temporary	Permanent	Temporary	Permanent
<i>L. externus</i>	<i>L. externus</i>	<i>L. externus</i>	<i>L. externus</i>	<i>L. externus</i>	<i>L. externus</i>
<i>G. lorretae</i>	<i>G. lorretae</i>	<i>L. picturatus</i>	<i>L. picturatus</i>	<i>A. nigriculus</i>	<i>A. nigriculus</i>
<i>L. secludens</i>	<i>N. hostilis</i>	<i>G. lorretae</i>	<i>G. lorretae</i>	<i>H. occidentalis</i>	<i>H. occidentalis</i>
<i>L. sublunatus</i>		<i>L. secludens</i>	<i>N. hostilis</i>	* <i>L. picturatus</i> (1998)	* <i>L. picturatus</i> (1998)
<i>L. abbreviatus</i>		<i>L. tarsalis</i>		* <i>G. lorretae</i> (2009)	* <i>G. lorretae</i> (2009)
		* <i>L. sublunatus</i> (2000)	* <i>L. sublunatus</i> (2000)	* <i>L. abbreviatus</i> (2018)	* <i>N. hostilis</i> (2015)
		* <i>L. abbreviatus</i> (2015)			

Table 2. Species identified in the 2019 survey. Species in gray cells are lotic (present in several beaver flow-through beaver ponds, while species in white cells are lentic.

<i>Limnephilus externus</i>	<i>L. picturatus</i>	<i>L. sublunatus</i>	<i>L. secludens</i>
<i>L. tarsalis</i>	<i>Grammotaulius lorettae</i>	<i>Anabolia bimaculata</i>	<i>Nemotaulius hostilis</i>
<i>Agrypnia deflata</i>	<i>Philarctus quaeris</i>	<i>Asynarchus nigriculus</i>	<i>Lenarchus brevipennis</i>
<i>Ecclisomyia conspersa</i>	<i>Onocosmoecus unicolor</i>	<i>Psychoglypha subborealis</i>	"Patchwork sp."

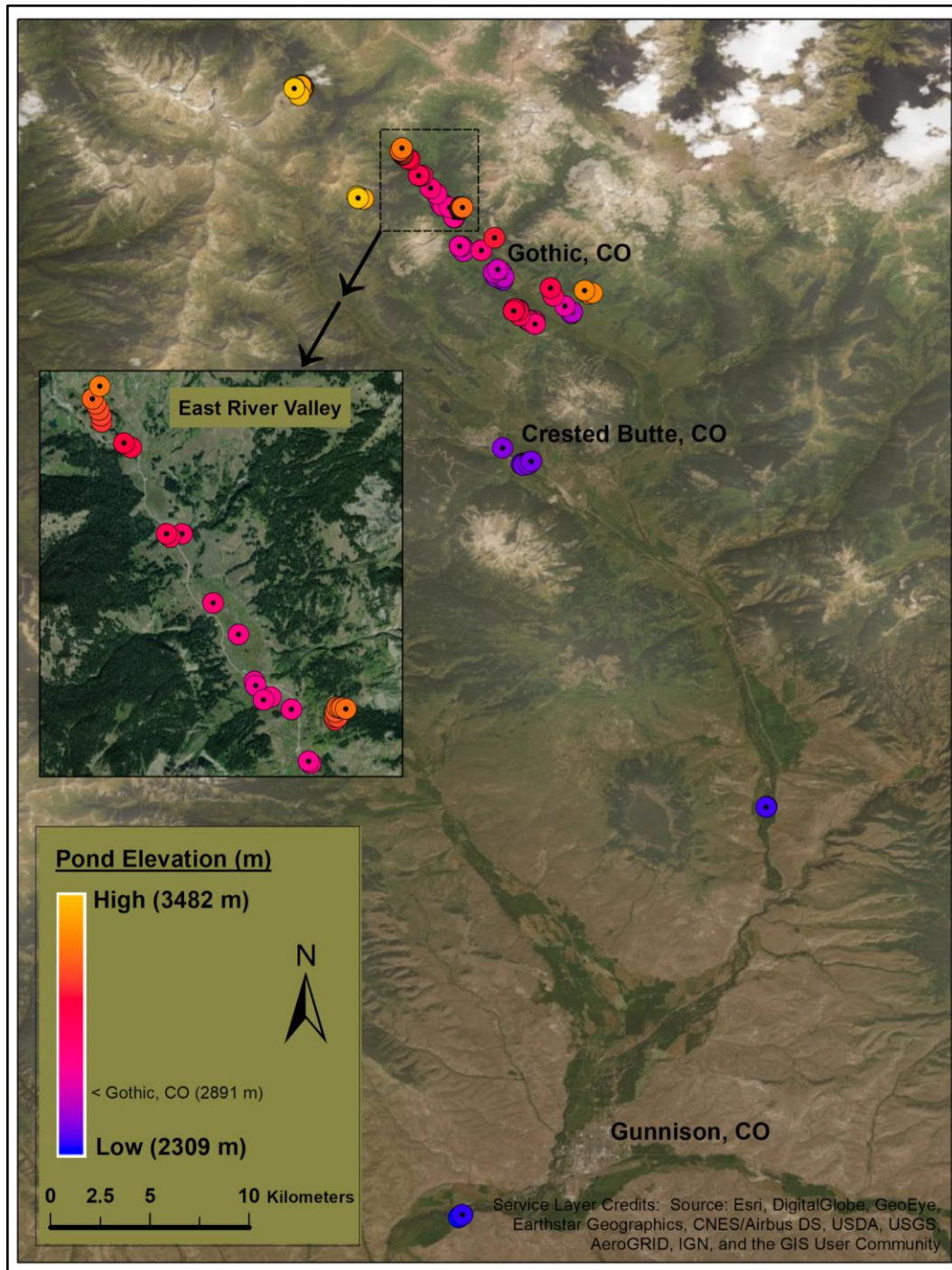


Figure 1. Pond survey sample sites along an elevational gradient from below Gunnison, CO (min. elev. 2309 m) through Gothic, CO (max. elev. 3482 m). Inset shows ponds within the East River Valley. n = 89.



Figure 2. Head photos of the most common Trichoptera species in the East River Valley region. *A. nigriculus* is also a core species, but no head photos were retrieved; thus, it was not included here but was included in the analysis. *L.* = *Limnephilus*; *G.* = *Grammotaulius*; *N.* = *Nemotaulius*; *A. (bimaculata)* = *Anabolia*; *A. (deflata)* = *Agrypnia* (Phryganeidae); *P.* = *Philarctus*.

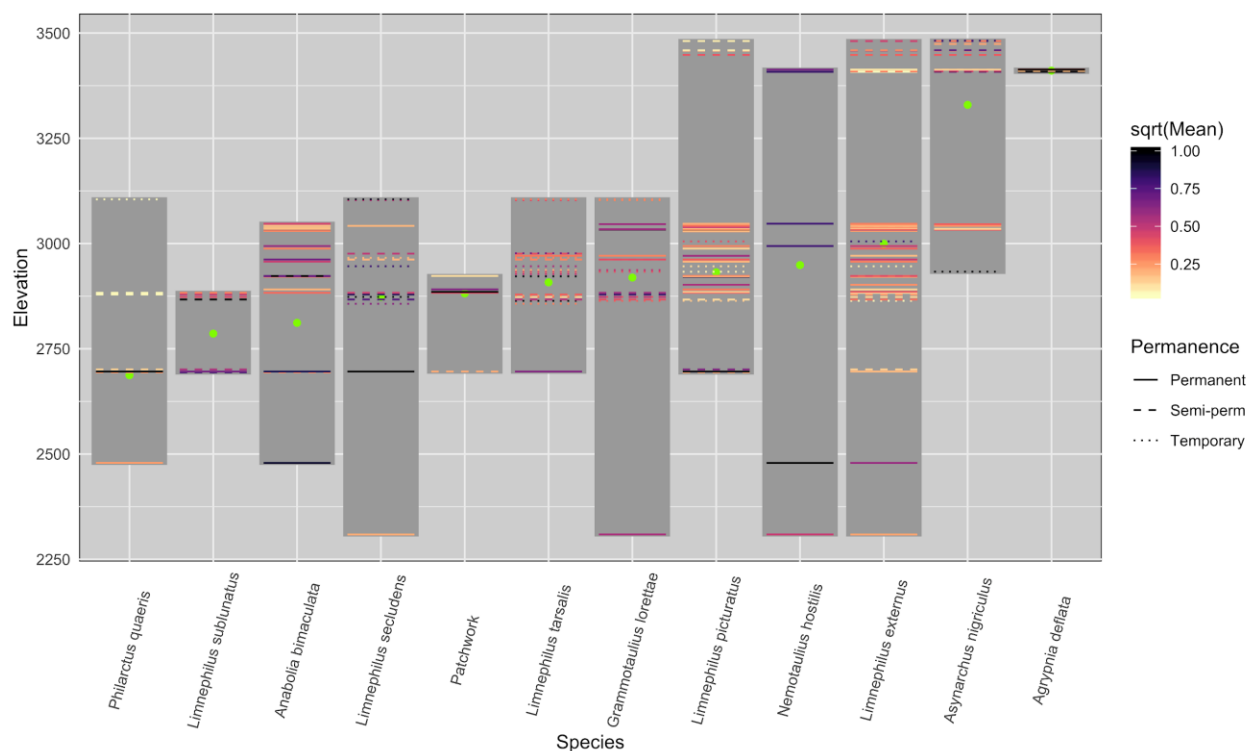
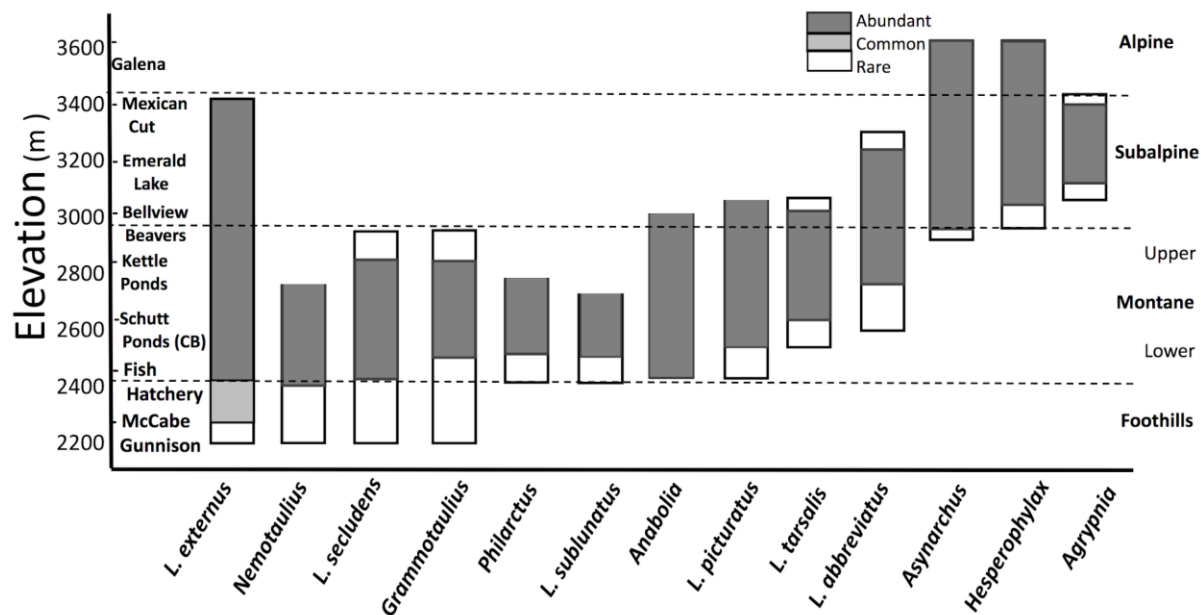


Figure 3. Abundance across the elevational gradient for East River valley caddisfly species. Each bar shows the elevational range of each species based on sample results. The horizontal lines in the bars show the elevation of each pond sampled; the hatching of the bar denotes the pond's permanence or hydroperiod (solid = permanent, dashed = semipermanent, and dotted = temporary). The color of the bar shows the proportion of the species's total abundance across the elevational gradient for that particular

pond (the totals were square-rooted to create a smaller scale); lighter colors indicate a smaller proportion of the total, while darker colors denote a larger proportion of the total. The green dot in each bar represents the mean elevation weighted by abundance for that species, serving as a proxy for range core.

(a) 1989



(b) 2019

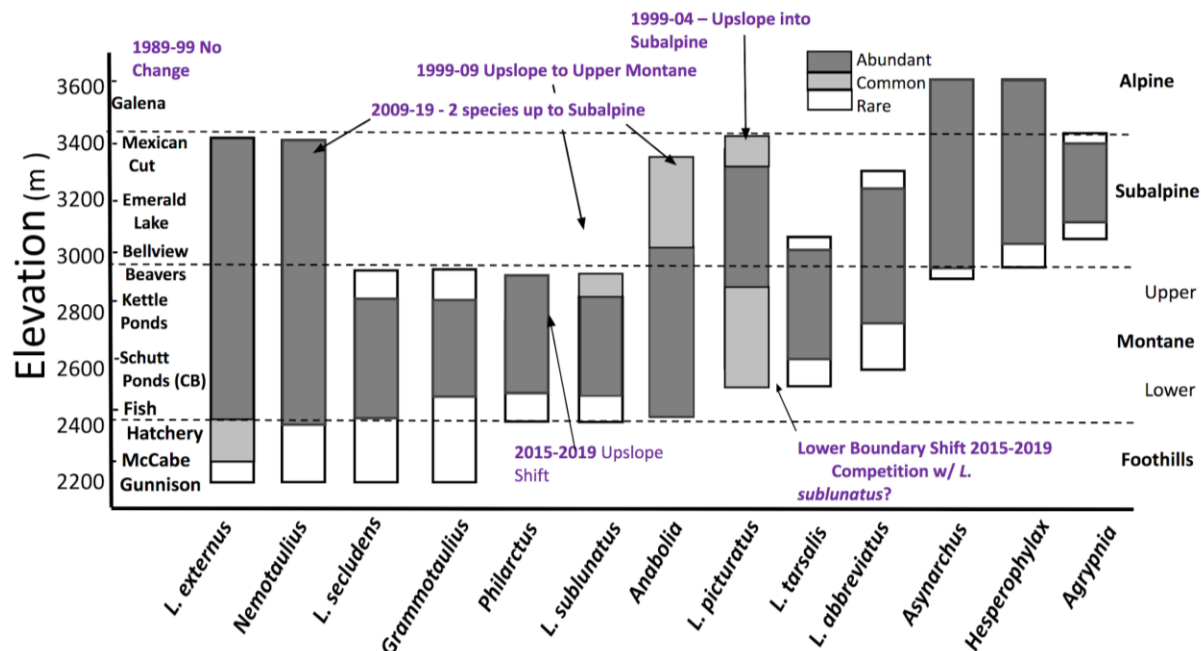


Figure 4. Brief overview of observed range shifts (or lack thereof) for common species (incl. the lotic species *Hesperophylax occidentalis*, which was not included elsewhere in the analysis) between 1989 (a) and 2019 (b). Note that these graphs are ordered by minimum elevation, not core ranges, as is the case in Fig. 2.

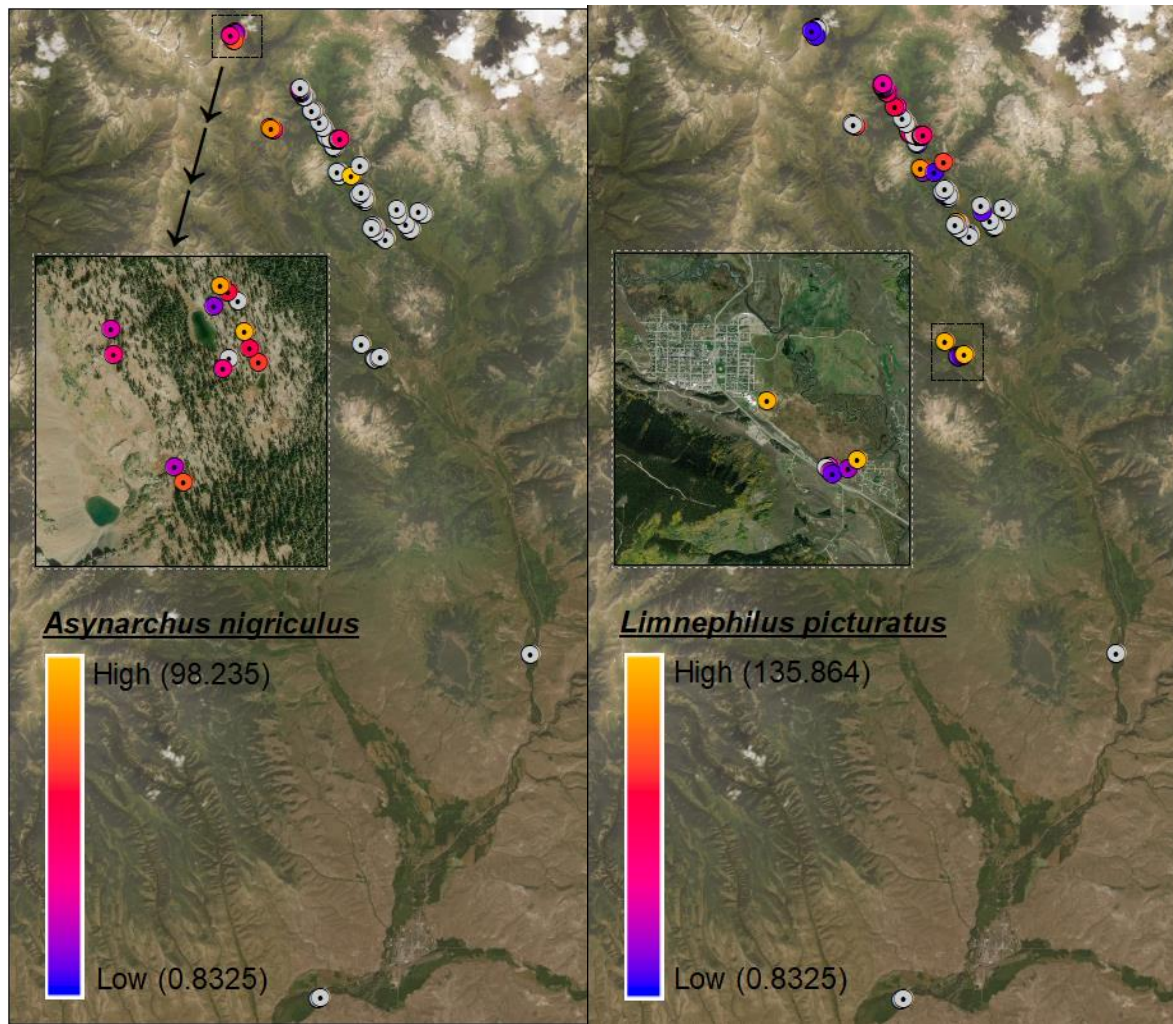


Figure 5. Variations in pond presence/absence and abundance (no. m⁻²) between *A. nigriculus* and *L. picturatus*. Gray-symbolized ponds denote species absence from that pond. Insets show details of highly-clustered and abundantly-populated ponds.