Predicting Climate Change Effects on Riverine Mayfly (Ephemeroptera), Stonefly (Plecoptera),
and Caddisfly (Trichoptera) Species in the Upper Midwest

By

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Abstract. Mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera) (a.k.a. EPT taxa) are the most environmentally sensitive of freshwater insects. They are utilized the world over as indicators of water quality in flowing waters. Their decline has been documented in Asia, Europe, and North America. A 220,321 record dataset of new and museum EPT specimen records covering much of the Midwest and Maximum Entropy (Maxent) software were used to construct current and future, climate influenced distribution models. Nearly 100 physical and historic vegetation variables and 9 BIOCLIM variables derived from downscaled climate data for the region were employed in this process. A total of 426 EPT species were modeled across Illinois, Indiana, Iowa, Michigan, Minnesota, Ohio, and Wisconsin (117 Ephemeroptera, 95 Plecoptera and 214 Trichoptera species). Mayflies and stoneflies were predicted to increase in range and in species richness throughout the region. Caddisflies were predicted to lose range on average, decreasing in richness. Generally, areas of low to moderate richness are predicted to gain species by the end of the century. Much variation in predicted change of species range and species richness patterns were due to which climate model was used to calculate the prediction. Effort must take place to understand which climate models produce the most accurate results. Future work should center on identifying and rehabilitating pathways and barriers to dispersal of EPT taxa.

INTRODUCTION

Freshwater ecosystems have been more severely altered by human activities and are more vulnerable to climate change than terrestrial ecosystems (Ricciardi & Rasmussen 1999, Vitousek et al. 1997, Vörösmarty et al. 2010). There is a clear and urgent need to understand spatial distributions and diversity patterns of aquatic species in order to maintain and restore aquatic biodiversity and to assess the impact of climate change and future land-use on species distributions. Species distribution modeling (SDM) is of great value for ecologists to serve these needs (Pearson et al. 2007, Newbold 2010, Peterson et al. 2011).

The Upper Midwest Great Lakes Landscape Conservation Cooperative (UMGLLCC) (US Department of the Interior 2013) is home to many cool- and coldwater inhabiting species due to it encompassing several ecotones (prairie, eastern deciduous forest, boreal forest, Great Lakes). These species are at risk for changes in their distribution related to a warming climate. By the end of the century, USA and Canada mean annual temperature is expected to rise by 2-3°C and be accompanied by changing precipitation patterns and increase in storm severity. Northern North American minimum winter temperatures are expected to increase more than the global average (IPCC 2007). Midwest regional climate predictions by the end of the century suggest that the spring season will commence earlier, heat waves will be more frequent and of longer duration, storms will be of greater severity, and stream flows will become more variable (Hayhoe et al. 2010).

The effects of climate change on aquatic insects has been relatively poorly studied, despite their being extremely abundant in most freshwater systems, their importance to the
nutrient and energy economy of streams and adjacent riparian habitat, and their demonstrated sensitivity to changes in temperature and water quality (Surdick & Gaufin 1978, Barbour et. al. 1999). Recent work in Europe (Balint et al. 2011, Domisch et al. 2011, 2013) and in western Asia (Shah et al. 2012) have predicted vast changes in aquatic insect distributions due to climate change. Balint et al. (2011) have also found that many evolutionarily significant units would be lost from refugial habitats in the mountains of Europe due to climate change. In North America, much less is known of the consequences of climate change on aquatic insect distributions. One continent-wide study predicted that the average locations of climatically suitable areas (CSAs) for genera of the most sensitive aquatic insect orders would be located between latitudes 44°-47° latitude. Projections by the end of the century suggested that these CSA averages would shift northward by 4°-5° latitude (276-425 miles) (Shah et al. 2014). Brooks (2009) strongly suggests that climate change will be overwhelmingly negative for ephemeral wetlands and intermittent streams in northeastern North America, reducing the length of time and phenology of wetting of these habitat so critical for harboring endangered species and for the functioning of forest ecosystems. These sorts of changes are also likely to occur in the UMGLLCC.

Predictions concerning future distributions of aquatic insects and their relationships to food webs and nutrient dynamics are dire, but the certainty about these predictions must be scrutinized carefully. Recent predictions rely on relatively small amounts of specimen data, often at the genus level (Shah et al. 2014) and are based on models that utilize predictors that include climate data only (Balint et al. 2011, Domisch et al. 2011, 2013, Shah et al. 2012). Use of climate only predictors will represent maximum potential change or worst-case scenarios. We expect that the inclusion of other variables in model building would provide predictions that were less dire, that vegetation cover, geology, surficial deposits, slope, etc. would ameliorate the predicted impacts of climate alone on model results. It is extremely important that the predictions for future CSAs be based on the very best data available since meeting conservation and management objectives for the next century will depend upon the severity of predictions of change.

The aquatic insects most sensitive to human-caused disturbance and climate change are in the orders Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies) (a.k.a. EPT species) (Fig. 1). Immatures of these insects are used the world over as indicators of water quality (Barbour et al. 1999). The EPT of the Midwest have been studied intensively for nearly a century (Armitage et al. 2011, Burks 1957, Frison 1935, Randolph & McCafferty 1998, DeWalt et al. 2005, DeWalt & Grubbs 2011, DeWalt et al. 2012, Grubbs et al. 2012, Harden & Mickel 1952, Hilsenhoff 1995, Houghton 2012, Leonard & Leonard 1962, Ross 1944, and many others). The USA portion of the UMGLLCC is home to at least 800 species of EPT (Randolph & McCafferty, DeWalt et al. 2012, Ross 1944, Houghton 2012). These run the gamut of sensitivity to various forms of water pollution, dissolved oxygen levels, thermal requirements, and habitat quality. The response of this fauna may be similar to that of other freshwater aquatic groups in the region. In addition, loss of many of these species may be detrimental to sustaining desired sport fisheries and could also drastically change the nutrient and energy dynamics in streams of
the region. Since many state and federal agencies use EPT species are indicators of stream health, using EPT metrics in indices of biological condition, the loss of large numbers of species will necessitate updating of numerical criteria for water quality assessment. This may require large-scale resampling of reference streams in the region and reassessment of expectations for high quality streams in the Midwest.

EPT species have been lost from large, European rivers due to the impacts of organic enrichment and the concomitant decrease in dissolved oxygen levels (Zwick 1992). Streams at lower altitudes in Europe have experienced dramatic losses by mid-20th century and have never recovered their species (Bojkov et al. 2012). We believe these same losses of diversity are occurring within various regions of North America. Master et al. (2000), using NatureServe data, listed stoneflies as the third most imperiled assemblage (across both aquatic and terrestrial systems) in the United States. Only freshwater mussels and crayfish were listed as more imperiled than stoneflies. DeWalt et al. (2005), working in Illinois, concluded that 28.6% of stonefly species had been either extirpated or extinguished from Illinois streams over the course of the 20th century. This rate of species loss surpassed that of both fish and mussels in the state. Adjacent states have experienced similar losses of within agricultural and urban areas (DeWalt & Grubbs 2011, DeWalt et al. 2012, Grubbs et al., 2012). We feel that mayflies and caddisflies are similarly imperiled within the region.

A National Science Foundation funded project (DEB 09-18805 ARRA) enabled the compilation of a large stonefly specimen database from museums and new sampling for a large proportion of the UMGLLCC geography. Department of Interior grant INT X-1-R-1 enabled the compilation of large mayfly and caddisfly databases from museums, new samples, literature, colleagues, and state water quality agencies.

The current project predicts historic and future range for species and species richness pattern for over 400 EPT species over much of the USA portion of the UMGLLCC and a large portion of the Eastern Tallgrass Prairie and Big Rivers LCC (ETPBRLCC) attributable to climate change.

**Objectives.** Our objectives are the following:

1. Derive 19 BIOCLIM variables from Vimont, University of Wisconsin downscaled climate data set and briefly compare temperature and rainfall changes across the region.
2. Compile EPT specimen data from throughout the UMGLLCC within the USA, excluding Pennsylvania and New York.
3. Construct pre-European settlement SDMs and species richness index patterns for over EPT species in the region.
4. Construct future SDMs and species richness indices for EPT species using physical and derived BIOCLIM variables for emission scenario a1b through the end of the century.
5. Compare current and future ranges and species richness patterns to determine patterns of predicted change.
   a. examine proportional range change of EPT species.
   b. examine change in species richness
**Methodology**

*EPT Specimen Data.* Specimen data were gathered from museum records, new records, from trusted literature sources, and from data provided by the Iowa Hygenics Laboratory and the Ohio Environmental Protection Agency for seven states: Iowa, Illinois, Indiana, Michigan, Ohio, and Wisconsin. The total number of raw data records used for model construction now stands at 220,321. All records were scrutinized for use of synonyms and corrected to current valid usage.

These data were skewed by a high number of records/km² for mayflies and caddisflies within Ohio (Fig. 2). We expected that this bias would significantly impact model development; hence, we partitioned the Ohio records from the dataset, then subsampled the records to achieve densities equivalent to the next most intensively sampled state (Illinois for mayflies, Minnesota for caddisflies), then recombined the records with the dataset from the other states. No such bias was present in the stonefly data set.

*Bioclimatic variable derivation and comparison.* Regionally downscaled climate predictions were obtained from the laboratory of Dr. Dan Vimont at the University of Wisconsin-Madison, a project funded by the UMGLLCC (Upper Midwest Great Lakes Landscape Conservation Cooperative 2013). This dataset is stored as annual netCDF files, each containing a 366 band raster of daily temperature maximum (tmax), temperature minimum (tmin), and precipitation predictions. A total of 13 climate model scenarios were generated by Vimont for current conditions and for three future emissions scenarios where the two coincided (Table 1). For each of the climate variable/emission scenario combinations, all 19 BIOCLIM variables were derived (Table 2).

In order to derive values for these variables from the Vimont data, we collaborated with Mr. Andrew Bartley M.Sc., formerly of the Geospatial Information Science and Technology Department at North Carolina State University, Raleigh. His is now employed by Camden County, NC as a GIS specialist.

We have also accepted as a useful objective the comparison of differences in BIOCLIM variables across the different model/scenario combinations, not only to quantify the difference in the patterns predicted by models, but also as a valuable heuristic tool to summarize the anticipated direction and magnitude of changes in temperature and precipitation experienced in any region. Although a full account of the variation among models and the geographic patterns of trends in bioclimatic variables is beyond the scope of our contract, we provide some detail on provisional patterns we have identified in the BIOCLIM variables created for modeling. These changes in temperature and precipitation patterns are easily communicated by maps of the change in the variable between current conditions and future (average response during 2046-2100) scenario predictions for each scenario.

*Natural Variable Derivation.* We previously used a large set of geology, pre-European settlement land cover, temperature, precipitation, hydrology and watershed variables as
predictors of pre-European settlement species distributions (Cao et al. 2012). To improve the interpretation of models of the potential future distribution of aquatic insects, we used cluster analyses to reduce the total number of predictors. We chose temperature or precipitation variables from clusters of highly correlated variables, instead of non-climate variables, to maximize the potential change in future distributions and updated these variables with values derived from Vimont’s data, averaged or aggregated to the scale of HUC12 watersheds. The resulting product, for each climate model, is a natural variables layer for future conditions of temperature and precipitation but constrained by natural factors unlikely to change as a consequence of changing climate (e.g., bedrock geology, soil types). These natural variables scaled, to the HUC12 level, have been provided as a supplemental data deliverable.

**Distribution Modeling.** Future predictions of stonefly distributions conducted in the previous phase of this research employed Maxent modeling using climate variables only (DeWalt et al. 2013). The predictions strongly suggested that suitable range for stoneflies in the region would be dramatically reduced and historical species richness patterns would be altered by the end of the century. Our expectation is that models built for species using climate data alone provide estimates of maximum potential change to the distribution of species that present worst-case scenarios. However, models that additionally use geological, hydrological, and land cover variables (which do not change at the rate of climate) provide a more realistic estimate of the realized change of aquatic insect species distributions than that obtained from change in patterns of temperature and precipitation alone. In this final phase of our research, we have analyzed current vs. future distributions and richness patterns using these vegetation, land use, geological, and soils data along with climate. Several of the derived BIOCLIM variables are known to be correlated (Elith et al. 2006), therefore we used a subset of 9 of these variables for distribution modeling (Table 2) which have previously been used to reconstruct large scale patterns of species richness (Vasconcelos et al. 2011). Construction of SDMs was completed using Maximum Entropy (Maxent) (Elith et al. 2011) using standard settings; cumulative outputs were transformed to presence/absence using the maximum training specificity and sensitivity (MTSS) criterion as suggested by Cao et al. (2013). These models were built for both current conditions and future scenarios, by projecting current models on to future climate scenarios. Changes in richness were calculated as future values minus current values.

These comparisons have been conducted for a large proportion of the EPT fauna found in the Midwest for seven of Vimont’s climate models (Table 3) for the a1b emission scenario. This methodology should yield a powerful prediction for EPT distributions and species richness patterns.

**RESULTS**
Comparison of current and future temperature and rainfall. As an example of how conditions may change under future climate models (ccma and giss) and under a single climate scenario (a2), we present an examination of maximum temperatures in the warmest month, precipitation in the driest month, and precipitation in the wettest month for the eastern USA and adjacent Canada (Figs. 3-5). Current maximum temperature in the warmest month under the climate models examined within the UMGLLCC are nearly indistinguishable (Fig. 3A, B). Under ccma, temperatures within upper WI, northeastern MN, and the upper and lower peninsulas of MI are predicted to increase in maximum temperature during the warmest month by up to \(4^\circ\text{C}\). The predicted increases under the giss model appear to be ameliorated over the ccma model. In both models, areas of the UMGLLCC with highest predicted increases in highs for the warmest month include regions that currently support rich EPT assemblages. Precipitation in the driest month appears to remain relatively constant or increase slightly under the ccma model within the UMGLLCC (Fig. 4C). Under the giss model, rainfall during the driest month is predicted to increase, but again, only slightly (Fig. 4D). Precipitation in the wettest month under ccma appears to be slightly higher in western WI and much of MN (Fig. 5C). The eastern portions of WI and MI are predicted to have little change in rainfall. Under the GISS model, these same patterns are predicted (Fig. 5D).

Specimen Data Accumulation. Specimen data were accumulated from 25 regional institutions and from individuals across the region. In addition, new sampling, especially in poorly sampled Michigan, yielded many new specimens. The number of records accumulated for this project tallied 220,321 (Fig. 6).

Current and Future EPT Species Distributions in the Midwest. A total of 427 species of EPT were model in current and future space (Table 4). There are too many species to examine individually, but both incidence and proportion range change has been recorded in Appendix 1. Most climate models for the a1b emission scenario for EPT species were predicted to increase the range of EPT species over the century (Fig. 7-9). This was especially evident for mayflies (Fig. 7) and stoneflies (Fig. 8). However, most caddisfly species distributions appeared to either remain the same or shrink in distribution (Fig. 9). Examination of histograms of proportional range change averaged across all climate models for each species demonstrated a similar outcome, the mayflies (loss 30.8%, gain 69.2%) and stoneflies (loss 24.2%, gain 75.8%) were mostly predicted to gain ranged, while a slight plurality of caddisfly species (loss 54.7%, gain 45.3%) lost range (Fig. 10A-C).

It appears that the response to climate change for EPT has some phylogenetic basis, e.g., the members of families often share a similar response (Figs. 11-13). Proportional range change as an average across climate models and families demonstrated that within mayflies, the well represented families Baetidae, Caenidae, Ephemeridae, Ephemeroellidae, and Leptophlebiidae demonstrated the same directional response with relatively low standard error (Fig. 11). Within stoneflies, the families Capniidae, Chloroperlidae, Leuctridae, Perlidae, and Taeniopterygidae clearly would increase in range due to climate change (Fig. 12). Fewer caddisfly families show
clear trends related to climate change. Brachycentridae, Hydropsychidae, and Leptoceridae show clear responses to climate change (Fig. 13).

Examining closely the response of many individual species is not possible in this venue, but it is instructive on how much variation there is about predictions of range loss. To this end, we have produced maps of range change that utilize the predictions of all seven climate models vs. the current distribution for one species in each of the orders. *Baetis brunneicolor* is a cool- to coldwater mayfly that is most common in the northern part of the UMGLLLCC, especially in springbrooks. The current prediction follow our point data and the distribution proposed by Randolph & McCafferty (1998). The average future response is a decrease in range by 64% (Fig. 14). In this instance, six of the seven models agreed that the change in range would be negative, all six being of substantial loss. The stonefly *Perlesta decipiens* inhabits medium to large, warm rivers throughout the region (DeWalt et al. 2001) (Fig. 15). This species is projected to increase its range by 7%. Five models predicted substantial range loss, one predicted a 103% gain, calling into question the average change value. The major projected increase is in the northern part of Wisconsin and in drainages that lead into the Ohio River where several large rivers may warm sufficiently to support the species by the end of the century. The caddisfly *Dolophilodes distinctus* inhabits ravine streams and larger cool- to coldwater streams in the unglaciated section of Indiana and Ohio and again in northern Michigan, Wisconsin, and Michigan (Armitage 1991) (Fig. 16). This species is expected to increase range by 8%. Models were evenly split in the direction of change. It is quite possible that species whose habitat is scattered, such as in ravine streams and springbrooks, pose significant difficulties in predicting distributions; although, our current model seems to represent the observed distribution fairly well.

**Current Predicted EPT Species Richness in the Midwest.** Models of current species richness for mayflies predicts the richest assemblages in HUC12s associated with the Illinois, Kankakee, upper Mississippi, St. Croix, Wabash, Rock (IL), and Wisconsin rivers (Fig. 17). Other areas of high richness include the Lake Superior Highlands of northern Wisconsin. Unglaciated are not predicted to be nearly as diverse. Areas of low richness include the Lake Huron/Erie Lake Plain in eastern Michigan and northwestern Ohio and the Illinoisan age glaciated southern half of Illinois and adjacent Indiana. Western Minnesota appears to be depauperate of mayflies, but our occurrence data are confined to areas east of a north/south line through Minneapolis. Minnesota is one of the most poorly collected of the Midwest states for mayflies (L. Jacobus, pers. comm.). It appears that mayflies moved from surmised refugia (no studies for mayflies exist) south of the Ohio River straight through the till plain into the north reaches of the UMGLLCC, through drainage connections of the Ohio, Wabash, and Mississippi rivers.

Plecoptera richness was overall lower than that of mayflies and concentrated in two principal areas: the unglaciated, rugged terrain of southern Ohio, Indiana, and Illinois and the forested drift plain habitat of northeastern Ohio and the Lake Superior Highlands of northern Wisconsin and Minnesota (Fig. 18). Secondary areas of moderate richness existed in the Wabash and Rock (IL) river drainages and the upper third of Michigan's Lower Peninsula. Low richness was predicted for much of the Wisconsinan and Illinoisan till plain and lake plain that stretches
from western Lake Erie to near St. Louis, Missouri. The predicted distribution of stoneflies suggests the till and lake plain of the central Midwest was a barrier to dispersal. It is presumed that many species must have used more suitable drainage routes northward such as drainages on the north shores of the Great Lakes and bluff streams along the Mississippi River (Ross & Ricker 1971).

Caddisflies are far richer in species in the Midwest than either mayflies or stoneflies. The prediction for current species richness pattern supports this assertion (Fig. 19). The caddisfly pattern is similar to that of stoneflies in that it appears that caddisflies have on average a Laurentian distribution—many species having migrated north of the Great Lakes from the east, then westward. Currently, caddisfly species richness is predicted to be highest in unglaciated areas of the south, and increasing in the upper part of lower Michigan, parts of northern Wisconsin and Minnesota especially in Lake Superior drainages, and in the high elevation areas of northern Minnesota. Areas of low richness included the till and lake plain from Ohio to St. Louis.

*Future Predicted Richness in the Midwest.* Generally, mayfly species richness is predicted to increase in the Midwest (Figs. 20, 21). The seven models, however, respond somewhat differently. Two models produce similar results, that of cnrm (Fig. 20A, 21A) and giss_e_r (Fig. 20E, 21E). These models increase richness in the Lake Superior Highlands of Wisconsin, the unglaciated areas in the south, and the eastern Lake Michigan shoreline. The scatterplots of richness values in the same HUC12s for both demonstrate that there are many more points above slope of one, indicating greater future richness. The other models tend to maintain similar levels of richness (Fig. 20B, D, F, G, 21 B, D, F, G).

Stonefly richness is also predicted to increase across the region. As with mayflies, the models cnmr and giss_e_r increase richness in the far northern and southern areas of the Midwest (Fig. 22A, E). They also increase richness along the eastern shore of Lake Michigan. Scatterplots for these models also demonstrate richness to increase in the future (Fig. 23A, E). An interesting outcome of the giss model is that drainages to Lake Superior in the Upper Peninsula and Arrowhead region of Minnesota are predicted to dramatically increase in stonefly richness (Fig. 22E). Other models predict little change in the future (Figs. 22B, C, D, F, 23 B, C, D, F).

Caddisfly richness, on average, is predicted to slightly decrease across the region. Decrease in richness is predicted by the cnrm, csiro_mk_0, csiro_mk3_5, mpi_echam5, and the mri_cgcm models (Fig. 24A, B, C, F, G). Scatterplots of current versus future richness all demonstrate lower richness in the future (Fig. 25A, B, C, F, G). Many of these models demonstrate loss in the HUC12s with currently high richness and an increase in current drainages with low to moderate richness. Two models suggest increases of richness in the future, gfdl_cm2_0 and giss_e_r (Figs. 24D, E, 25D, E). Areas that would increase in richness are southern Indiana, southwestern Michigan, and northern Illinois (Fig. 24D) and northern Wisconsin/Upper Peninsula of Michigan (24E).
In an attempt to produce a broad scale depiction of the change to be expected in the Midwest region, the average change in richness across the seven models was compared to current richness, and a map produced of change (current-future) produced. Ephemoptera will experience the greatest loss of richness from western Ohio, across the till plain of Illinois, west and north into Iowa and central Wisconsin. Areas that will gain species are in the far north, the unglaciated sections of the south, and in much of Michigan (Fig. 26). For stoneflies, losses will occur in northern Wisconsin, in the Wabash drainage of Illinois and Indiana, and in the unglaciated areas of Indiana and Ohio. Other areas look to gain species (Fig. 27). Caddisflies appear to be the big losers among EPT. Losses are expected to be highest in Ohio, central Wisconsin and Iowa, northeastern Minnesota, and parts of the lower peninsula of Michigan (Fig. 28). It appears that the southern portion of the Midwest, excepting Ohio, will gain species.

DISCUSSION

Little work has been done to measure the effects of climate change on aquatic insects. What has been done has occurred in Europe (Balint et al. 2011, Domisch et al. 2011, 2013) and in western Asia (Shah et al. 2012). In North America, Shah et al. (2014) predicted changes in the average distribution of genera of EPT due to climate. These authors have presented the worst-case scenario by employing climate-only distribution modeling, predicting large losses in aquatic insect distributions as a result. We feel that by employing many additional variables such as pre-European settlement vegetation, a wealth of geological, soils, topography, and other variables that we would ameliorate the predictions of our colleagues. In addition, we have employed a nested, hierarchical drainage approach that allows us to examine model results in a network and take advantage of a wealth of information that is available about the watersheds. Other authors have employed a grid system to model responses to climate. Using multiple climate models derived from the Vimont, University of Wisconsin downscaled climate data set permits us to replicate model runs for each species, thereby improving our understanding of the variability of forecasts. Lastly, we have chosen to work at the species level, where evolution and ecology take place. Construction of models from a large set of vetted records should yield more informative results.

Climate in the region is predicted to change and we have demonstrated that for three BIOCLIM variables for two climate models and one emission scenario. Downscaled climate data derive to BIOCLIM variables have been provided to the Dana Infante laboratory and to UMGLLCC officials so that other can use the data we have derived. Using multiple climate models for distribution modeling into the future has been extremely illuminating. Each model produces unique results, some similar to each other, but some quite different (see Figs. 7-9). Models cnrm, gdfl_cm2_0, and giss_e_r often produced results that were extreme to the other models, sometimes to the point of driving averages across the models. More work should be done to investigate whether it is better to use all models or decide that some are too extreme to be useful.
A cascade of information about EPT response came to light as the scale of the investigation developed. Responses at the order level differed. Mayflies and stoneflies clearly are predicted to increase in range through the end of the century (Fig. 7, 8). However, proportional caddisflies are expected to lose range (Fig. 9). An examination at the species level within orders supported this contention, with most species of mayflies and stoneflies gaining range (Fig. 10A, B), while a slight plurality of species of caddisflies were expected to lose range (Fig. 10C).

Family assignment was found to be useful in predicting the direct of range change such that several families in each order, for which a large number of species were available, demonstrated relatively narrow ranges of responses (Figs. 11-13). Responses of individual species were illuminating. Usually, the current distribution model agreed well with the known distribution of the species. However, there were wide differences in the predicted future range of species based on which model was used (Fig. 14). Average range change of some species frequently had large standard errors and statistical ranges. At some point we may well wish to minimize the models used to build future distributions, finding a more conservative balance.

Overall, current models of species richness index produced maps that represent observed values quite well. All recovered known areas of high richness for each order (Fig. 17-19). High richness was generally in the forested, unglaciated areas of the south, and in the Lake Superior Highlands of northern Wisconsin, Minnesota, and the Upper Peninsula of Michigan. Mayflies are also rich in the large river systems of the Wabash, Illinois, Rock, and Wisconsin rivers. Current models also recovered areas of low richness, often the till and lake plain that runs from northwestern Ohio to opposite of St. Louis, Missouri. Richness for stoneflies and mayflies was predicted to increase, often in areas where the richness is low to moderate currently. The models cnrm and giss_e_r drove this outcome for both orders. Caddisfly richness was expected to decrease in general. However, the models gfdl_cm2_0 and giss_e_r were important in shifting the loss to a less severe overall prediction. Large scale richness losses were mostly likely to occur in areas of the Midwest that are currently the richest in species (Figs. 26-28). Gains are predicted to occur for all orders in southern Illinois and Indiana, and for mayflies and stoneflies much of the east shore of Lake Michigan and along the Lake Superior coastline. Losses for caddisflies are mostly limited to Ohio and the Arrowhead region of Minnesota.

Future work should be concentrated on determining if some climate models are functioning poorly. The standard error of proportional range change for most species would be dramatically lowered if the models cnrm and giss_e_r were eliminated. Once a more conservative estimation of future range was developed, model output for both current and future models to run least-cost path analyses to determine if pathways and barriers to dispersal exist to accommodate the movement of these species. The current analysis suggests that many species will be moving into the till plain areas from the south. Most EPT species require corridors intact riparian vegetation and good water quality to migrate (DeWalt et al. 2005). However, it is highly probably that these corridors leading north to south are compromised by poor water and habitat quality. The till plain of Illinois, Indiana, and Ohio has been heavily modified for agriculture where removal of riparian vegetation, straightening of stream channels, and tiling of fields has
changed the thermal regime and hydrology of streams such that normal migration is not possible. Use of a cost-path analysis would suggest potential pathways that need to be rehabilitated—remeandered, riparian replanted, easements and land purchased—in order to improve the corridor for migration.

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LITERATURE CITED


Table 1. Climate models and emission scenarios represented in the Vimont, University of Wisconsin data set.

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<td></td>
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<tr>
<td>giss_model_e_r</td>
<td>x</td>
<td>x</td>
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<tr>
<td>iap_fgoals1_0_g</td>
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<tr>
<td>miroc3_2_hires</td>
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<tr>
<td>miub_echog_g</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>mpi_echam5</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>mri_cgcm2_3_2a</td>
<td>x</td>
<td>x</td>
<td>x</td>
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Table 2. BIOCLIM variables list derived from Vimont models (see Table 1). Nine variables are in bold face, denoting their use in UMGLLCC modeling of EPT species distributions and species richness patterns.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
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<tbody>
<tr>
<td>BIO1</td>
<td>Annual Mean Temperature</td>
</tr>
<tr>
<td><strong>BIO2</strong></td>
<td><strong>Mean Diurnal Range (Mean of monthly (max temp - min temp))</strong></td>
</tr>
<tr>
<td><strong>BIO3</strong></td>
<td><em><em>Isothermality (BIO2/BIO7) (</em> 100)</em>*</td>
</tr>
<tr>
<td>BIO4</td>
<td>Temperature Seasonality (standard deviation *100)</td>
</tr>
<tr>
<td><strong>BIO5</strong></td>
<td><strong>Max Temperature of Warmest Month</strong></td>
</tr>
<tr>
<td><strong>BIO6</strong></td>
<td><strong>Min Temperature of Coldest Month</strong></td>
</tr>
<tr>
<td><strong>BIO7</strong></td>
<td><strong>Temperature Annual Range (BIO5-BIO6)</strong></td>
</tr>
<tr>
<td>BIO8</td>
<td>Mean Temperature of Wettest Quarter</td>
</tr>
<tr>
<td>BIO9</td>
<td>Mean Temperature of Driest Quarter</td>
</tr>
<tr>
<td>BIO10</td>
<td>Mean Temperature of Warmest Quarter</td>
</tr>
<tr>
<td>BIO11</td>
<td>Mean Temperature of Coldest Quarter</td>
</tr>
<tr>
<td>BIO12</td>
<td>Annual Precipitation</td>
</tr>
<tr>
<td><strong>BIO13</strong></td>
<td><strong>Precipitation of Wettest Month</strong></td>
</tr>
<tr>
<td><strong>BIO14</strong></td>
<td><strong>Precipitation of Driest Month</strong></td>
</tr>
<tr>
<td><strong>BIO15</strong></td>
<td><strong>Precipitation Seasonality (Coefficient of Variation)</strong></td>
</tr>
<tr>
<td>BIO16</td>
<td>Precipitation of Wettest Quarter</td>
</tr>
<tr>
<td>BIO17</td>
<td>Precipitation of Driest Quarter</td>
</tr>
<tr>
<td><strong>BIO18</strong></td>
<td><strong>Precipitation of Warmest Quarter</strong></td>
</tr>
<tr>
<td>BIO19</td>
<td>Precipitation of Coldest Quarter</td>
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<tr>
<td>Climate models used in future SDMs</td>
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<td>mri_cgcm_2.3.29</td>
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Table 4. Summary of number of models conducted for EPT species in the UMGLLCC. Future models are for 7 climate models and for the emission scenario A1b.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Species Modeled</th>
<th>Current Models</th>
<th>Future Models</th>
<th>Total Models</th>
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<tbody>
<tr>
<td>Ephemeroptera</td>
<td>117</td>
<td>1</td>
<td>7</td>
<td>936</td>
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<tr>
<td>Plecoptera</td>
<td>95</td>
<td>1</td>
<td>7</td>
<td>760</td>
</tr>
<tr>
<td>Trichoptera</td>
<td>214</td>
<td>1</td>
<td>7</td>
<td>1712</td>
</tr>
<tr>
<td>Total</td>
<td>426</td>
<td></td>
<td></td>
<td>3408</td>
</tr>
</tbody>
</table>
Fig. 1. Immatures of Ephemeroptera (mayfly, left), Plecoptera (stonefly, center), and Trichoptera (caddisfly, right).
Fig. 2. Density of records for mayflies (A, Ephemeroptera) and caddisflies (B, Trichoptera) by state. Note that Ohio records are much more dense due the large amount of specimen data contributed by the Ohio EPA and Ohio Biological Survey.
Fig. 3. Comparison of maximum temperatures of warmest month (°C) under current conditions, (A) model ccma and (B) giss_e_r climate models. Future predictions for the a2 emission scenario (2046-2100) for (C) ccma and (D) giss climate models. The color panels detail predicted warming (Future – Current) for each model. Area of UMGLLCC indicated in orange (current conditions) or aqua marine (future conditions).
Fig. 4. Change in total precipitation (mm) predicted for the driest calendar month, in current (A & B) and future conditions (C & D) for climate models (ccma and giss_e_r) and climate scenario a2. Area of UMGLLCC indicated in orange.
Fig. 5. Change in total precipitation (mm) predicted for the wettest calendar month, in current (A & B) and future conditions (C & D) for models (ccma and giss_e_r) and climate scenarios a2. Area of UMGLLC indicated in orange.
Fig. 6. Number of Ephemeroptera, Plecoptera, and Trichoptera specimen records compiled for the UMGLLCC past and future distribution modeling project. Total number of records prior to data reduction is 220,321.
Fig 7. Box plot of proportional range change in Midwest mayflies (Ephemeroptera) calculated across all species for each of 7 climate models and the future emission scenario a1b. Box plots indicate mean, 10th, 25th, 75th, and 90th percentiles. The extremes values are indicated above the 90th percentile. The line at zero indicates no range change.
Fig. 8. Box plot of proportional range change in Midwest stoneflies (Plecoptera) calculated across all species for each of 7 climate models and the future emission scenario a1b. Box plots indicate mean, 10th, 25th, 75th, and 90th percentiles. The extremes values are indicated above the 90th percentile. The line at zero indicates no range change.
Fig. 9. Box plot of proportional range change in Midwest stoneflies (Trichoptera) calculated across all species for each of 7 climate models and the future emission scenario a1b. Box plots indicate mean, 10th, 25th, 75th, and 90th percentiles. The extremes values are indicated above the 90th percentile. The line at zero indicates no range change.
Fig. 10. Frequency histogram of proportional range change for future distributions of mayflies (A, Ephemeroptera), stoneflies (B, Plecoptera), and caddisflies (C, Trichoptera) across the Midwest, USA. Values were averages across seven climate models for the a1b emission scenario for each species. Change by the end of the 20th century. Numbers indicate the number species modeled within the order.
Fig. 11. Proportional range change for mayfly (Ephemeroptera) families across the Midwest, USA, averaged across seven climate models for the a1b emission scenario by the end of the 20th century. Bars and error bars represent mean and standard error. Numbers below bars indicate the number species within the family.
Fig. 12. Proportional range change for stonefly (Plecoptera) families across the Midwest, USA, averaged across seven climate models for the a1b emission scenario by the end of the 20th century. Bars and error bars represent mean and standard error. Numbers below bars indicate the number species within the family.
Fig. 13. Proportional range change for caddisflies (Trichoptera) families across the Midwest, USA, averaged across seven climate models for the a1b emission scenario by the end of the 20th century. Bars and error bars represent mean and standard error. Numbers below bars indicate the number species within the family.
Fig. 14. Species distribution model for the Midwest, USA for the mayfly *Baetis brunneicolor* (Ephemeroptera), a cool- coldwater obligate species. Seven future models (a1b emission scenario) and current distribution model depicted for the end of the 20th century. Response is range loss at an average of 64% of current. Inset is a nymph of the species, image used under an open access, share-like license from BOLD (2014).
Fig. 15. Species distribution model for the Midwest, USA for the stonefly *Perlesta decipiens* (Plecoptera), a warmwater species. Seven future models (a1b emission scenario) and current distribution model depicted for the end of the 20th century. Response is range gain at an average of 7% of current. Inset is a copulating pair, image is from DeWalt.
Fig. 16. Species distribution model for the Midwest, USA for the caddisfly *Dolophilodes distinctus* (Trichoptera), a cool- coldwater species. Seven future models (a1b emission scenario) and current distribution model depicted for the end of the 20th century. Response is range gain at an average of 8% of current. Inset is an adult male of the species © Tom Murray (BugGuide.net).
Fig. 17. Current index of species richness for mayflies (Ephemeroptera) occurring in the Midwest, USA. Yellow and red shades indicate higher predicted species richness based on a total 117 species modeled.
Fig. 18. Current index of species richness for stoneflies (Plecoptera) occurring in the Midwest, USA. Yellow and red shades indicate higher predicted species richness based a total 95 species modeled.
Fig. 19. Current index of species richness for caddisflies (Trichoptera) occurring in the Midwest, USA. Yellow and red shades indicate higher predicted species richness based on a total 214 species modeled.
Fig. 20. Future mayfly (Ephemeroptera) index of species richness in HUC12s under several climate models and the emission scenario a1b by the end of the 20th century in Midwest, USA. (A) cnrm, (B) csiro_mk3_0, (C) csir_mk3_5, and (D) gfdl_cm2_0.
Fig. 20. Future mayfly (Ephemeroptera) index of species richness in HUC12s under several climate models and the emission scenario a1b by the end of the 20th century in Midwest, USA. (E) giss_e_r, (F) mpi_echam5, (G) mri_cgcm.
Fig. 21. Scatterplots of mayfly (Ephemeroptera) future vs current richness in HUC12s under several climate models and the emission scenario a1b by the end of the 20th century in Midwest, USA. (A) cnrm, (B) csiro_mk3_0, (C) csir_mk3_5, and (D) gfdl_cm2_0.
Fig. 21. Scatterplots of mayfly (Ephemeroptera) future vs current richness in HUC12s under several climate models and the emission scenario a1b by the end of the 20th century in Midwest, USA. (E) gis_e_r, (F) mpi_echam5, (G) mri_cgm.
Fig. 22. Future stonefly (Plecoptera) index of species richness in HUC12s under several climate models and the emission scenario a1b by the end of the 20th century in Midwest, USA. (A) cnrm, (B) csiro_mk3_0, (C) csir_mk3_5, and (D) gfdl_cm2_0.
Fig. 22. Future stonefly (Plecoptera) index of species richness in HUC12s under several climate models and the emission scenario a1b by the end of the 20th century in Midwest, USA. (E) gis_e_r, (F) mpi_echam5, (G) mri_cgm.
Fig. 23. Scatterplots of stonefly (Plecoptera) future vs current richness in HUC12s under several climate models and the emission scenario a1b by the end of the 20th century in Midwest, USA. (A) cnrm, (B) csiro_mk3_0, (C) csir_mk3_5, and (D) gfdl_cm2_0.
Fig. 23. Scatterplots of stonefly (Plecoptera) future vs current richness in HUC12s under several climate models and the emission scenario a1b by the end of the 20th century in Midwest, USA. (E) gis_e_r, (F) mpi_echam5, (G) mri_cgerm.
Fig. 24. Future caddisfly (Trichoptera) index of species richness in HUC12s under several climate models and the emission scenario a1b by the end of the 20th century in Midwest, USA. (A) cnrm, (B) csiro_mk3_0, (C) csiro_mk3_5, and (D) gfdl_cm2_0.
Fig. 24. Future caddisfly (Trichoptera) index of species richness in HUC12s under several climate models and the emission scenario a1b by the end of the 20th century in Midwest, USA. (E) gis_e_r, (F) mpi_echam5, (G) mri_cgm.
Fig. 25. Scatterplots of caddisfly (Trichoptera) future vs current richness in HUC12s under several climate models and the emission scenario a1b by the end of the 20th century in Midwest, USA. (A) cnrm, (B) csiro_mk3_0, (C) csir_mk3_5, and (D) gfdl_cm2_0.
Fig. 25. Scatterplots of caddisfly (Trichoptera) future vs current richness in HUC12s under several climate models and the emission scenario a1b by the end of the 20th century in Midwest, USA. (E) giss_e_r, (F) mpi_echam5, (G) mri_cgcm.
Fig. 26. Average change in richness across seven climate models for Ephemeroptera assemblage in Midwest.
Fig. 27. Average change in richness across seven climate models for Plecoptera assemblage in Midwest.
Fig. 28. Average change in richness across seven climate models for Trichoptera assemblage in Midwest.