

FINE-SCALE MODELING OF RIVERINE ODONATA DISTRIBUTIONS IN THE  
NORTHEASTERN UNITED STATES

by

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## **ABSTRACT**

The distributions of riverine dragonflies and damselflies (Insecta: Odonata) were modeled at the scale of individual river segments across the northeastern United States, a 784,982 km<sup>2</sup> region spanning from Ohio, West Virginia, and Virginia northeast to Maine. The species distribution modeling approach was reviewed with respect to Odonata, and several modeling techniques were compared. Species locality data assigned only to U.S. county is prevalent in invertebrate databases, and it was found that using these data for modeling tends to overpredict the geographic distributions of species. Several techniques to compensate for geographic sampling bias, which is also a characteristic of these largely opportunistically collected databases, were compared, though the optimum method (thinning data, biased background sampling, or no treatment) depended on the dataset. Watersheds and riparian zones are ecologically relevant for riverine organisms, and models with catchment- and local-scale predictors outperformed models based only on climate. This fine-scale modeling approach is appropriate for the conservation of freshwater diversity, because individual river segments containing suitable species habitat can be identified and prioritized. Climate change is expected to reduce the available habitat for riverine Odonata within the northeastern U.S., though some rivers may serve as climatic refugia, and conservation of these rivers and their watersheds is essential.

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## **CHAPTER I**

### **INTRODUCTION**

As a relatively well-known amphibious order of insects, Odonata, the dragonflies and damselflies, are heralded as the charismatic poster child representing a suite of unique aquatic habitats including rivers. The sensitivity of odonate larvae to human disturbance has lent to their usefulness as indicators of aquatic health (Watson et al. 1982, Bulankova 1997, Catling 2005, Foote and Hornung 2005, Silva et al. 2010). The habitat requirements of riverine dragonflies are an integration of riparian quality and local river conditions, which are a function of the upstream watershed. They are dependent on both the aquatic environment and the terrestrial one, so they are an ideal indicator group of river health. Rivers and riparian areas encompass a small proportion of Earth's surface (0.8%), yet they contain a disproportionately high number of known species (> 6%) (Vorosmarty et al. 2010). Additionally, 65% of global water discharge and the habitats it supports is under a moderate to high threat (Vorosmarty et al. 2010). As many as 10,000 freshwater invertebrates are extinct or highly imperiled because of human activities (Strayer 2006, Kalkman et al. 2008, Clausnitzer et al. 2009).

Stream-obligate species do not dominate U.S. diversity, but 18 of the 37 most imperiled U.S. odonates require flowing streams (Bick 2003, Dunkle 2004). This is not only an indication of the status of these organisms, it is also a reflection of the status of our rivers. Society needs healthy rivers, yet these systems are undergoing stresses, such as upstream land conversion, nutrient enrichment, inputs of sediment and other pollutants from runoff, flow alteration and damming, invasive species introduction, and potential impacts of climate change. As representatives of freshwater biodiversity (Simaika and Samways 2009, Darwall et al. 2011), the distribution of Odonata may be used as a tool to identify and protect our most important river resources.

Our knowledge of the distribution of Odonata is becoming more precise through state-sponsored surveys and citizen science, new populations of dragonflies are regularly found (e.g. Reece and McIntyre 2009), and new species are still being discovered (e.g. Abbott and Hibbitts 2011). Because of the myriad of threats aquatic organisms face, it is also likely that some populations are extirpated before they are documented. The first step toward effective species conservation is quantifying a species' geographic distribution. The distribution of most invertebrate species is imperfectly known, so using existing limited information on species presence to inform habitat models is an important and cost-effective technique.

Joseph Grinnell was the first to use the spatial distribution of occurrences of a species to infer factors limiting its distribution (Grinnell 1917, 1924). In Grinnell (1917), it was suggested that the narrow geographic range of the California Thrasher could be explained by a narrow tolerance to environmental conditions. He further postulated that the range of acceptable conditions could be determined by examining the “elements common to all [locations within the range of the species] and of these the ones not in evidence beyond the bird's range.” More importantly, he noted that “no two species regularly established in a single fauna have precisely the same niche relationships.” This is an underlying principle of the ecological niche. In Grinnell (1924), the ecological or environmental niche is considered the “ultimate unit” of geographical distribution. Grinnell added that a niche “is occupied by just one species or subspecies; if a new ecologic niche arises, or if a niche is vacated, nature hastens to supply an occupant, from whatever material may be available.”

George Evelyn Hutchinson defined the fundamental niche of a species, a term first published by Robert H. MacArthur (MacArthur 1957), as an  $n$ -dimensional hypervolume, where  $n$  are environmental variables, every point in which corresponds to the set of environmental variables permitting the species to survive indefinitely (Hutchinson 1958). Hutchinson notes that Volterra (1926) and Lotka (1932) first demonstrated that two species with identical niches cannot coexist in a limited system indefinitely. Environmental space is often not the same as geographic space, and a

scattered species distribution may represent a fairly compact distribution in environmental space (Stockwell 2007). An  $n$ -dimensional hypervolume may be a useful concept, but its utility is limited. Even Hutchinson pointed out some of its limitations, such as the idea of equal probability of species occurrence within the hypervolume. A species is generally most abundant at the center of the range of environmental conditions along which the species occurs (Grinnell 1924, Hochberg and Ives 1999). Additionally, the ability to quantify all  $n$  dimensions is not practical.

A modeling approach based on the concept of the species niche is now commonly referred to as species distribution modeling, which compares known species occurrences to ecologically relevant environmental predictors to determine which environmental variables are the best predictors of the species' distribution and to develop relations between those environmental variables and species occurrence. Dense, representative sampling of a species will usually reveal these environmental relations handily which is helpful when the basic ecological dimensions relevant to the distribution of a species is poorly known (Peterson 2006). These relations can be projected to unsurveyed regions to generate predictive maps of potentially suitable habitat for a given species. The selected environmental predictors may not be exhaustive or the most proximate drivers of species occurrence, but they can be useful surrogates for these drivers (Elith and Leathwick 2009).

Species distribution models (SDMs) are useful for understanding species' ecological requirements and biogeography, for identifying hierarchies of environmental drivers, for predicting unknown populations and identifying areas for conservation or for potential translocations and reintroductions, for testing or generating specific hypothesis about habitat selection, and for forecasting the effects of environmental change (Peterson 2006, Dormann 2007).

The intent of this dissertation is to advance the body of knowledge of species distribution modeling especially with respect to riverine species, to provide realistic and useful predictions of the distribution of riverine Odonata, and to assess the threat climate change may have on these species. The fine-scale species distribution

modeling framework presented here is a valuable tool that can be extended to nearly any riverine organism and can be used to identify biologically important rivers for conservation and water quality improvement.

Chapters 2 through 6 have been prepared independently, and each is intended for stand-alone publication. Chapter 2 summarizes what is currently known about modeling the distribution of Odonata and provides recommendations for model development. Data availability is a major obstacle limiting effective SDM development for many invertebrates, including Odonata. Unfortunately, considerable data are presently recorded only to U.S. county as opposed to precise geographic coordinates, so Chapter 3 assesses the impact of using this type of spatially imprecise data on SDMs. Furthermore, species locality data are often collected opportunistically such that considerable sampling bias is present in existing databases. Chapter 5 compares several techniques for compensating for this spatial bias with respect to geographically segregated testing data.

Bioclimatic niche modeling, or developing models using metrics derived from historical temperature and precipitation data, may not fully capture important processes controlling the distribution of riverine taxa. The distribution of river organisms is also dependent on watershed and local conditions, so it is appropriate to incorporate these variables into SDMs (Hopkins and Burr 2009). Environmental data layers were developed that describe the local hydrology, topography, climate, and upstream soils, geology, and landuse of all streams in the northeastern U.S. Chapter 4 explores which scale of environmental predictor (climatic, watershed, or local) is most effective at discriminating habitat for riverine Odonata.

Although future climate change will be a global phenomenon, impacts on a regional scale, such as on river catchments, will be those most noticeable from a human perspective and from the perspective of organisms. Additionally, temperature is one of the most important factors affecting the life-histories, bioenergetics, physiological, developmental, and behavioral mechanisms, and distribution of stream macroinvertebrates (Ward and Stanford 1982). Some species may be able to respond

to increased temperatures by shifting their distribution, but other species may not, and some river reaches may act as important refugia. Chapter 6 explores the effect of future climates on fine-scale distribution of riverine Odonata in the northeastern United States in an attempt to locate climatic refugia for these indicator species.

## CHAPTER II

### MODELING THE DISTRIBUTION OF ODONATA: A REVIEW

#### Abstract

Species distribution models (SDMs) have been used to relate species' presence to environmental characteristics. Because of the ready availability of Odonata (dragonfly and damselfly) records identified to species, this tool has been applied to answer a variety of ecological questions about odonate distributions. This review of those studies provides guidance on developing SDMs for Odonata. Questions that have been posed relate to the determination of the potential geographic distribution of a species based on scattered records, quantifying hotspots for biodiversity and regionally rare species and identifying reserve gaps, assessing species' environmental requirements and limitations, quantifying dispersal abilities of species with different life histories, studying niche conservatism among sympatric species, modeling the impact of forecasted climate change on species distributions, and the efficacy of different modeling approaches. Although SDMs are powerful and relatively easy to use, there are many items to consider in order to make reasonable inferences and optimize the use of data. Few papers used *a priori* knowledge of individual Odonata species' natural history to select background environmental variables other than climate. Odonata occupy a variety of aquatic habitats, so it is important to consider what constitutes a species' niche before attempting to model it. Fewer than 25% of all Odonata species have been modeled. Out of 26 studies, the median resolution for modeling was 2.5 arcminutes ( $\sim 5 \text{ km}^2$ ), though resolutions as large as 2 degrees were also used to capture imprecision in locality data. Only 17 species have been modeled at resolutions finer than  $1 \text{ km}^2$ . The lack of readily available fine-scale locality data have limited the inferences that can be drawn from modeling and have overestimated odonate distributions in some cases, highlighting the need for digital Odonata databases to be improved with precisely georeferenced localities worldwide. Though this review is focused on modeling the distribution of Odonata, the inferences and recommendations made apply to all hemimetabolous insects.

## **Introduction**

### ***Species distribution modeling background***

Species distribution models (SDMs) relate known species localities to environmental characteristics to identify other environmentally suitable areas where a given species could occur. SDMs may also be referred to as bioclimatic models, climate envelopes, ecological niche models, habitat models, resource selection functions, range maps, correlative models, and spatial models (Elith and Leathwick 2009). The most basic application of SDMs is to quantify the potential geographic distribution of a species based on scattered records (Finch et al. 2006, Howard 2006). By incorporating environmental predictors and discriminating between each predictor's relative importance, SDMs can improve interpolation of sparse data compared to linear interpolation or convex hull techniques.

Development of an SDM requires species locality data with a geographic precision finer than the desired resolution of predictions and values for relevant environmental predictors for all locations across the extent of interest. The species localities are then compared to the environmental background, a subsample of environmental predictor combinations proportionate to their presence in geographic space. Sampling bias is introduced when sampling the environmental background at species localities is more representative of sampling tendencies than the environmental conditions permitting species occupancy. Several methods of defining the relations between known species presence and the environmental background have been developed.

The environmental envelope method of developing SDMs is the simplest application and also the most similar to the concept of identifying the fundamental niche, or the  $n$ -dimensional hypervolume of all environmental conditions that permit species occupation of a habitat, where  $n$  environmental variables include all conditions necessary for a species (Hutchinson 1958). This concept is necessarily simplified in distribution models, because all required environmental conditions cannot be fully

known or data may not exist quantifying these environmental conditions across geographic space.

The simplification most often used is known as bioclimatic niche modeling, which assumes that the distribution of a species can be modeled as a function of metrics describing the temperature, precipitation, and their seasonality in a region (bioclim metrics). Climatic data reflecting these are other variables are readily and freely available and may be all that is required for broad-scale distribution assessments (Peterson 2006). The earliest applications of species distribution modeling consisted of the environmental envelope method using bioclim metrics (Busby 1991) and is still often used (e.g. Dupin et al. 2011, Hijmans 2012). However, this method often overpredicts distributions, because users may choose not to apply any probability function within the envelope (Finch et al. 2006), and some recorded species localities may be on the limit or even outside of the suitable environmental conditions for that species (i.e. outliers). Localities that may be outside of suitable environmental conditions for a species may belong to vagrants (e.g. Schmidt 1985) or sink populations, but it is difficult to make that determination empirically.

Sophisticated modeling techniques have been developed to overcome the biases and inadequacies in species locality data. Many SDM approaches are known as “presence only,” where species localities are compared against background or pseudo-absence locations. For example, for most invertebrates, distributional data are amassed opportunistically through random and often inefficient sampling (Finch et al. 2006), which form a presence-only dataset. Though species absence data are rarely available, especially at continental scales (Jaeschke et al. 2012), absence data can be misleading because they can indicate either unsuitable habitat, suitable habitat that is unoccupied, or suitable habitat where a species was not detected (Elith and Leathwick 2009).

Typical species distribution modeling approaches produce the apparent species distribution, which is a combination of probability of occurrence and probability of detection (Kery et al. 2010a). For cryptic species, SDMs may at worst predict the

detectability of a species without informing on its probability of occurrence (Kery et al. 2010a). Occupancy models, such as that implemented in the PRESENCE model (<http://www.mbr-pwrc.usgs.gov/software/presence.html>), estimate the percentage of occupied sites by accounting for imperfect detection (MacKenzie 2006). Unlike SDMs, occupancy models explicitly correct for observation and reporting bias, but absence data are generally needed to infer detection probabilities (MacKenzie 2006, van Strien et al. 2013). Additionally, occupancy models require no false positives (Kery et al. 2010a), so the SDM framework is more forgiving.

Mechanistic models can also be developed to analyze species distributions. These models may be better suited for determining the environmental factors limiting species distributions, because only proximal predictors are used (Moenickes et al. 2012). SDMs can be more reliable than mechanistic models at large spatial scales, because small-scale mechanistic studies may fail to capture processes important at large scales (Buckley et al. 2010). This may be why mechanistic models predict larger range shifts in response to climate change than do SDMs (Buckley et al. 2010). Regardless of chosen modeling framework, predictions should be couched with full appreciation of inherent uncertainty (Pearson et al. 2006).

Because species distribution modeling is inherently species-driven, use of a focal group of species can provide comparisons of different SDM techniques and biases. A review of SDMs that have focused on Odonata (Insecta, dragonflies and damselflies) is now provided.

### ***Why Odonata?***

Odonata are one of the best-known orders of freshwater invertebrates, are easily identified to species, are relatively well-collected, occupy a high trophic position, exhibit species-specific habitat requirements, and can be indicators of terrestrial and aquatic environmental health (Watson et al. 1982, Samways 1999, Corbet 2004). Collectively, these traits make them charismatic enough to be considered a “flagship” group of aquatic indicator species (Oertli et al. 2002). Odonata are also effective surrogates for other freshwater taxa (Darwall et al. 2011),

for selecting areas for the conservation of freshwater diversity (Simaika and Samways 2009), and for studying the impacts of climate change on freshwater diversity (Corbet et al. 2006, Hassall and Thompson 2008, Bush et al. 2013).

### **Summary of previous studies**

Of the 26 papers predicting the spatial distribution of Odonata reviewed here, the first was published in 2006 (Finch et al. 2006) and 23 have been published since 2010 (Table 2.1). SDM analysis of Odonata is thus relatively recent considering that ecologists have been developing SDMs since at least 1991 (Busby 1991, Guisan and Zimmermann 2000). These Odonata studies have benefitted from recent species dataset availability sometimes driven by citizen science and from recent advances in model development, calibration, and evaluation, as well as identification of many modeling pitfalls such as overparameterization, poorly selected environmental predictors, effects of resolution and extent, spatially biased species locality data, effect of outliers, and the potential for model performance metric inflation.

Odonata studies have aimed to discover populations of a species on the limit of its known range (Corser 2010), determine the conservation status of data-poor species (De Almeida et al. 2010), and determine regions where additional survey effort is needed to provide decision support for biological action plans (Hassall 2012). Nearly all modeled species were predicted to have larger ranges than recorded in the locality data, but this result is at least partly a symptom of modeling resolution (Hassall 2012).

Several Odonata studies aimed to quantify hotspots for biodiversity and regionally rare species or identify reserve gaps (Finch et al. 2006, Howard 2006, Nóbrega and De Marco 2011, Simaika et al. 2013). Odonata are surrogates for freshwater diversity, so these hotspots may be indicative of overall biodiversity (Darwall et al. 2011). Researchers found that the current reserve network in Africa covers 10.7% of the landscape, but only represents 1.2% of the geographic distributions of Odonata (Simaika et al. 2013), and that areas of greatest Odonata diversity in the Cerrado area of Brazil are not currently protected by existing reserves nor are many range-restricted or threatened species (Nóbrega and De Marco 2011).

Though nearly all species distribution studies empirically quantify the environmental requirements and limitations for a species as a matter of necessity, often the relations are not reported. The relative importance of environmental predictors is a basic output of most SDMs, however, and the hierarchy can be informative. Additionally, the derived environmental predictors' patterns may generate hypotheses about species tolerances which can then be tested (Dormann 2007). For example, determining predictor importance was stated to be an objective of one study which found that cold stenotherm Odonata richness in Alpine ponds was positively related to macrophyte presence but negatively correlated with altitude, though this study was technically not an SDM (Ilg and Oertli 2014).

SDMs have also been used to quantify the dispersal abilities of Odonata with different life histories. Jaeschke et al. (2012) found that obligate biotic interactions are an important consideration in assessments of future climate, because they restrict where a species can disperse. Hof et al. (2012) compared climatic predictions made from models developed with 1988 locality data directly against 2006 survey data and found that models tended to over-predict lotic species compared to lentic species, indicating that lentic species are tracking climate change more rapidly than lotic species.

Numerous studies have assessed the impact of climate change on Odonata with varying conclusions depending on species. Using a mechanistic model, Sondgerath et al. (2012) found that climate change is likely to affect voltinism of Odonata in Europe and could be beneficial. All studies indicate that considerable range shifts should be expected. Some have found that suitable habitat is predicted to decline for the majority of modeled species (Maes et al. 2010, Bush et al. 2014b). Others have found that Odonata may benefit from climate change, but that communities will be more homogenous in future climates (Li et al. 2014). Domisch et al. (2013a) found that climate change may benefit two species of Odonata assuming unlimited dispersal, but may result in range retreat for two others. When dispersal limitations are considered, *Coenagrion ornatum*, *Coenagrion mercuriale*, and *Ophiogomphus cecilia* are

projected to have considerable range retreat, though the predicted ranges expand if dispersal is not considered (Jaeschke et al. 2013). Some species may be able to shift their range altitudinally (Shah et al. 2012), and the largest turnover rates for Odonata will occur at intermediate altitudes (Maes et al. 2010). Range shifts may increase competition with similar species under future climates (Nóbrega and De Marco 2007). But to date only one Odonata study has used SDMs to study niche conservatism among sympatric species. Adaptation to colder and wetter climates has allowed one damselfly in a sympatric pair to expand farther north, though niche differences in the zone of sympatry are negligible (Wellenreuther et al. 2012). Range shifts may also result in species extirpation because of hybridization (Sanchez-Guillen et al. 2013). Though major shifts in species composition are expected under climate change, Bush et al. (2014a) found the most vulnerable species are not taxonomically different from random. SDMs may be used to prepare for range shifts by identifying conservation areas based on the sensitivity-weighted sum of habitat suitability for the most vulnerable species (Bush et al. 2014b).

Several studies have used SDMs to demonstrate the efficacy of different modeling approaches. Kuemmerlen et al. (2014) found that subcatchment-specific models of lotic species incorporating upstream characteristics had significantly greater model performance compared to traditional use of gridded environmental predictors. Similarly, another study that included Odonata found that stream-scale modeling results in less overprediction (Domisch et al. 2013b). Other studies have emphasized replicate observations so that species detection can be considered in distribution modeling (Kery et al. 2010a). SDMs may underestimate species distribution by 60% by ascribing patterns in detectability to species distributions (Kery et al. 2010a), and occupancy models can account for the biases in opportunistically collected citizen-science data (van Strien et al. 2013). Interestingly, comprehensive citizen-science checklist data had the same detection probabilities as monitoring data (van Strien et al. 2013).

## **Modeling considerations and guidance on developing SDMs for Odonata**

### ***Regions and modeling gaps***

Of the 26 Odonata distribution modeling studies in this review, ten were continent-wide (Hassall 2012, Hof et al. 2012, Jaeschke et al. 2012, Sondgerath et al. 2012, Domisch et al. 2013a, Jaeschke et al. 2013, Sanchez-Guillen et al. 2013, Simaika et al. 2013, Bush et al. 2014a, Bush et al. 2014b), though Odonata was not the focus of one of these studies (Domisch et al. 2013a) (Table 2.1). Fewer than 25% of the 5,680 described Odonata species worldwide have been modeled (Kalkman et al. 2008) (Table 2.2).

There have been four SDM studies in Africa (Finch et al. 2006, Domisch et al. 2013a, Sanchez-Guillen et al. 2013, Simaika et al. 2013), including a continental Odonata assessment (Simaika et al. 2013). Two of these studies included northern Africa as part of larger assessments of European fauna (Domisch et al. 2013a, Sanchez-Guillen et al. 2013). Less than half of the 889 Afrotropical Odonata species have been modeled (Kalkman et al. 2008, Simaika et al. 2013).

Even though 14 distribution modeling studies that included Odonata have been performed in Europe (Kery et al. 2010a, Maes et al. 2010, Outomuro et al. 2010, Dorazio and Rodriguez 2012, Hof et al. 2012, Jaeschke et al. 2012, Wellenreuther et al. 2012, Domisch et al. 2013a, Domisch et al. 2013b, Jaeschke et al. 2013, Sanchez-Guillen et al. 2013, van Strien et al. 2013, Kuemmerlen et al. 2014), only three studies have attempted to model 40 or more species (Maes et al. 2010, Hof et al. 2012, van Strien et al. 2013), and two of those covered relatively small parts of the continent: Netherlands and Belgium (Maes et al. 2010, van Strien et al. 2013). Though Odonata was not the focus of several of these European studies, there is still opportunity to learn more about the distributions of the 88 species of European Odonata, especially because most of these have been modeled at a relatively coarse 50 km scale (Hof et al. 2012). Parts of the Middle East were also included in a European fauna assessment (Domisch et al. 2013a).

Two recent studies using the same comprehensive dataset have modeled the distribution of 270 Odonata species in Australia, which is equivalent to 85% of the total fauna of that country, but only 31% of the Australasian fauna (Kalkman et al. 2008, Bush et al. 2014a, Bush et al. 2014b).

Three SDM studies within South America have been published (Nóbrega and De Marco 2007, De Almeida et al. 2010, Nóbrega and De Marco 2011). The distributions of approximately 32% of Neotropical species, 526 of 1,636, have been modeled, but only across limited regions such as central Brazil (Kalkman et al. 2008, Nóbrega and De Marco 2011). No studies of the distribution of Odonata in Central America have been published, though a large-scale Mexican assessment is currently underway (Alex Córdoba, personal communication 2012).

Published studies on the modeled distribution of Odonata in North America have been limited, and only three are known to the author (Howard 2006, Corser 2010, Hassall 2012). The most comprehensive study, which included 176 of the 462 species known from North America (Paulson and Dunkle 2012), had the coarsest resolution of any SDM study in this review, a 2-degree latitude-longitude grid (Hassall 2012).

To the author's knowledge, Asia has had the fewest number of Odonata species modeled across only a small portion of the continent. At least 13 Odonata species were modeled in South Korea as part of a country-wide assessment (Li et al. 2014), and one species, *Epiophlebia laidlawi*, was modeled in the Hindu Kush Himalayan region. An assessment of riverine insects including Odonata in the Pojang region of China is currently in development, though the models are only specific to family because of a lack of a reliable key for Chinese Odonata (Kuemmerlen, personal communication 2014). Given that over 400 species of Odonata occur in the Asian Palaearctic with high endemism in Japan, Korea, and China (Kalkman et al. 2008), the paucity of studies from Asia is alarming and represents a tremendous research opportunity.

Though species distribution modeling may not be well-suited for island biogeography because of limited environmental gradients (Austin 2007), no studies

have been performed on Odonata in any of the world's large island chains such as the Caribbean islands and the Malay archipelago. The lack of studies from the Pacific or Oriental biogeographic regions indicates that the distributions of more than 1,800 species have not been modeled (Kalkman et al. 2008).

There is thus still much more to learn about the distributions of Odonata, even in relatively well-studied regions such as Europe. A considerable factor affecting these studies is the availability of high quality, georeferenced locality data across broad scales. Most studies have used readily available national or regional datasets, and only five studies amassed data from many sources across a broad region for the purpose of modeling (Nóbrega and De Marco 2011, Domisch et al. 2013a, Sanchez-Guillen et al. 2013, Bush et al. 2014a, Bush et al. 2014b), though a thorough collection of records across a broad region had already been assembled in some regions (Simaika et al. 2013).

### ***Species data***

#### *Data availability*

Nine studies have attempted to model between 40 and 526 species in a region, while 16 studies included seven or fewer species (Table 2.1). Most studies used large national databases of dragonflies or benthic macroinvertebrates, though six studies took explicit advantage of citizen-science databases or volunteer-collected data (Kery et al. 2010a, Maes et al. 2010, Dorazio and Rodriguez 2012, Hassall 2012, Wellenreuther et al. 2012, van Strien et al. 2013). It is important to assemble as many records as possible, because incomplete distributional data have been shown to reduce the predictive performance of models (Barbet-Massin et al. 2010, Sánchez-Fernández et al. 2011). Some dragonfly datasets may not be readily available and are thus unknown to researchers who would make good use of them (Berteaux et al. 2010).

#### *Filtering data*

Though methods such as cross-validation reduce the effect of any individual locality records that may be outliers (Fielding and Bell 1997), it is important to review locality data critically to ensure they are accurate and suitable for modeling. Fourteen

studies did not indicate that filtering of species locality data was performed to any degree, which may be because the sources are trusted as expert-reviewed (Simaika et al. 2013). Several studies indicated that species were not modeled if too few records, typically 10 or less, were available (Domisch et al. 2013a, Domisch et al. 2013b, Simaika et al. 2013, Kuemmerlen et al. 2014). Other studies indicated that outlier or taxonomically uncertain records were omitted (Corser 2010, Wellenreuther et al. 2012), and Finch et al. (2006) notes that their study could have been improved by identifying vagrant or migratory records. Li et al. (2014) omitted records from polluted sites or those with large rivers or reservoirs, though it is unclear how these data could have negatively impacted their models based on temperature. If nonclimatic or nonstructural variables are included as environmental predictors, it may be logical to exclude localities within anthropogenically disturbed sites if those effects are not a focus of the study (Buisson et al. 2008b).

#### *Correcting for spatial bias*

Spatially heterogeneous locality data may result in spatially biased predicted distributions (Wolmarans et al. 2010), though some models have been shown to be robust to sampling bias (Loiselle et al. 2008). Models built with biased sampling data may be illustrating the distribution of sampling instead of the distribution of a species, obscuring the relations with environmental predictors that may otherwise be detected (Dennis and Thomas 2000, Kuussaari et al. 2007, Kery et al. 2010b, Szabo et al. 2010). Test datasets may have the same biases as training datasets if both are subsets of the same database, so performance metrics may be artificially inflated (Hijmans 2012). The existence of sampling bias is often unknown, though datasets that combine surveys or include opportunistically collected localities such as citizen-science databases are likely biased. Because there is no field protocol or sampling design to ensure geographical representativeness, these data tend to have an uneven distribution (Dennis et al. 1999, Dennis and Thomas 2000, Kery et al. 2010a, Hassall 2012) and might be biased toward those species that are most interesting to observers and those that are more readily detected (MacKenzie 2006).

Identifying spatial bias is important, yet few studies account for it (Yackulic et al. 2013). Three studies that included Odonata employed occupancy models to account for species detection explicitly (Kery et al. 2010a, Dorazio and Rodriguez 2012, van Strien et al. 2013). Correction factors (Botts et al. 2012) or surrogate measures for observer effort, such as the number of species observed at a location (Szabo et al. 2010), have been used to cope with spatial biases in SDMs. Two Odonata SDM studies attempted to correct for spatial bias. Sanchez-Guillen et al. range (2013) subsampled localities for one damselfly species that had a dense availability of localities in one part of its range. That study only included climatic predictors at a 5-kilometer scale, thus it is unlikely this subsampling resulted in a reduction of information used to inform the model. However, subsampling data based on geographic distance may affect models that use heterogeneous fine-scale predictors by reducing information the model could use to discriminate habitat. Domisch et al. (2013a) simply excluded species from modeling if sampling bias was suspected by determining if all ecoregions where the species is known to occur were not represented in the data.

### ***Data resolution***

The median resolution across all Odonata SDM studies was 2.5 arcminutes (~5 km), though it ranged to as large as 2 degrees. Only 17 species have been modeled at resolutions finer than 1 km<sup>2</sup> (Howard 2006, Corser 2010, Kuemmerlen et al. 2014, Li et al. 2014), though reach-scale modeling arguably uses predictors and makes predictions at a finer resolution (e.g. Bush et al. 2014a, Bush et al. 2014b). Coarse-scale modeling is performed for technical reasons unrelated to species ecology, such as computational convenience, available resolution of predictors, or uncertainty in species locality data (Elith and Leathwick 2009, Domisch et al. 2013b, Jaeschke et al. 2013). However, coarse scales limit the mechanistic inferences that can be made (Wellenreuther et al. 2012) and result in overprediction (Seo et al. 2009, Hassall 2012). Once a resolution is chosen, it is important to only include species locality

records with a resolution equal to or finer than the resolution of the environmental background (Howard 2006, Wellenreuther et al. 2012, Domisch et al. 2013a).

### ***Models***

Thirteen of 26 studies used an ensemble of models, most often implemented using the BIOMOD package in the statistical computing environment, R (Howard 2006, R Development Core Team 2008, Maes et al. 2010, Hassall 2012, Hof et al. 2012, Jaeschke et al. 2012, Shah et al. 2012, Domisch et al. 2013a, Domisch et al. 2013b, Jaeschke et al. 2013, Simaika et al. 2013, Bush et al. 2014a, Bush et al. 2014b, Kuemmerlen et al. 2014). `Maxent` was the most frequent model used individually, likely because several tests have shown that `Maxent` (Phillips et al. 2006) performed as well as or better than other modeling techniques (Elith et al. 2006, Hernandez et al. 2006, Guisan et al. 2007, Wisz et al. 2008, Tognelli et al. 2009). Choice of SDM approach is not trivial and has been shown to influence future projections of species distribution more than choice of general circulation model (GCM) or gas emissions model (GEM) (Buisson et al. 2010, Fordham et al. 2012).

An ensemble removes modeler bias and may produce more robust predictions (Araújo and New 2007, Thuiller et al. 2009). Ensembles can be aggregated by model averaging (Marmion et al. 2009), where the average may be weighted by model performance (Domisch et al. 2013a), or a modeler may choose to only use overlapping areas of predicted suitability across all models (Maes et al. 2010). Using an ensemble via BIOMOD is becoming common among SDM studies (Thuiller et al. 2009). However, the performance benefits and relative ease of using BIOMOD to develop an ensemble of models has encouraged this approach, and 11 of 17 Odonata SDM studies published since 2012 have used an ensemble.

The number of models included in ensembles varied from two to nine models, and the selected models varied considerably. Eleven ensembles included Generalized Linear Models (GLMs), 9 included General Additive Models (GAMs), 8 included Generalized Boosted Models (GBMs), 7 included multivariate adaptive regression splines (MARS), 6 included Artificial Neural Networks (ANNs), 6 included Classified

Tree Analysis (CTA), 5 included Random Forests (RF), 4 included Flexible Discriminant Analysis (FDA), 3 included Boosted Regression Trees (BRTs), 3 included Surface Range Envelopes (SREs), 2 included `Maxent`, and 2 included Mixture Discriminant Analysis (MDA) (Howard 2006, Maes et al. 2010, Hassall 2012, Hof et al. 2012, Jaeschke et al. 2012, Shah et al. 2012, Domisch et al. 2013a, Domisch et al. 2013b, Jaeschke et al. 2013, Simaika et al. 2013, Bush et al. 2014a, Bush et al. 2014b, Kuemmerlen et al. 2014). The details of each model, some of which are regression-based and some are which are machine-learning-based, can be found in the literature (Thuiller et al. 2009).

One of the earliest modeling studies of the spatial distribution of Odonata used a relatively simple model known as `BIOCLIM` that characterizes sites that are located within the environmental  $n$ -dimensional hypervolume occupied by a species (Busby 1991, Finch et al. 2006). Relations between species presence and environmental variables are not derived empirically, instead relying on simple tolerance thresholds for each variable to define the niche space (Busby 1991). Even though this model has apparently fallen out of favor (Elith et al. 2006), `BIOCLIM` was able to produce realistic distributions for 109 of 150 species, though it produced overly broad distributions for 39 species (Finch et al. 2006).

Regression-based models extend environmental envelope approaches by modeling variation within the occupied environmental space and by ranking predictors (Elith and Leathwick 2009). Generalized Additive Models (GAMs), which use non-parametric, data-defined smoothers to describe nonlinear responses (Guisan and Zimmermann 2000, Venables and Dichmont 2004, Elith and Leathwick 2009, Tognelli et al. 2009), were used as the primary models in one Odonata study (Li et al. 2014).

Machine-learning approaches such as Random Forests (RF) and `Maxent` have been used in several Odonata SDMs. `Maxent` estimates species' distributions by finding the distribution of maximum entropy (closest to uniform) such that the expected value of each environmental variable under this estimated distribution

matches its empirical average (Phillips et al. 2004, Phillips et al. 2006). In machine-learning methods, the idea of model selection and tuning is called regularization, which reduces overfitting by making the fitted surface more regular or smooth (Phillips et al. 2006). The regularization procedure adjusts overfitting with respect to the number of training points used to develop the model. Model flexibility can be restricted or maximized by permitting `Maxent` to use quadratic, product, threshold, hinged, and discrete functions in addition to simple linear models (Wilson et al. 2011, Syfert et al. 2013), though `Maxent` will adjust the choice of function with sample size (Fordham et al. 2012).

Occupancy models which intrinsically consider detection probability were used in three studies (Kery et al. 2010a, Dorazio and Rodriguez 2012, van Strien et al. 2013). Occupancy models predict the distribution of species, though they are not always considered SDMs.

Distance-based methods such as `DOMAIN` assess new sites in terms of their environmental similarity to sites of known presence (Carpenter et al. 1993) but have evidently never been used to model Odonata. These methods can be useful for modeling species with very few records that may otherwise be excluded from analysis. Though `Maxent` can model species with very few records (Wisz et al. 2008) and was used for two Neotropical damselflies with only four and five locality records (De Almeida et al. 2010), the results may communicate greater confidence than is warranted. Distance-based methods are understood to be more uncertain than machine-learning-based SDMs.

### ***Number of pseudo-absences***

Presence-only modeling typically requires comparison of species localities to background points known as pseudo-absences. SDMs often select 10,000 background points by default (Thuiller et al. 2009, Merow et al. 2013), and previous work has shown that 8,000 background points is sufficient for robust models (Phillips and Dudik 2008). One recent analysis with fine-scale modeling showed that 30,000 background points resulted in higher model performance (Collins and McIntyre *in*

review), but another study found that 10,000 background points outperformed 40,000 (Sanchez-Guillen et al. 2013). One Odonata study with a small extent used 1,000 background points (Howard 2006).

### ***Environmental variable selection***

#### *Variable relevancy*

Using *a priori* knowledge of individual Odonata species' natural history to select environmental variables could lead to greater model performance and more ecologically relevant models. The concept of species distribution modeling is based on the niche concept (Soberón and Peterson 2005) and niches cannot be defined by the same variables for all species, so it is logical to consider niche definition for individual species. However, species-specific attributes are typically excluded (Finch et al. 2006).

Often the most relevant environmental variables are not readily quantifiable, feasibly measured, or are not available at all locations. Modelers use variables that may be proxies for known mechanisms driving species distributions (Dormann 2007). Models that include environmental variables from multiple spatial scales usually outperform models constructed with variables from only one spatial scale such as climate (Beever et al. 2006), and distributions of freshwater organisms are affected by hierarchical scales of watersheds, reaches, and microhabitats (Poff 1997). Environmental variables representing multiple spatial scales have been used in several studies that included Odonata (Maes et al. 2010, Domisch et al. 2013b, Bush et al. 2014a, Bush et al. 2014b, Kuemmerlen et al. 2014).

#### *Climate*

Some researchers have argued that constructing SDMs solely with climatic predictors is appropriate, because climate is the ultimate driver determining the physiological niche at large spatial scales (Pearson and Dawson 2003). All modeled distribution studies of Odonata in this review that did not employ occupancy models used climatic predictors. There is sound support for these predictors, because the distribution of Odonata is determined by ecophysiological traits, notably

thermoregulatory ability (De Marco and Resende 2002, Corbet 2004, Corbet and May 2008) and heat needed for developmental processes (Pritchard 1982, Pritchard and Leggott 1987). Air temperature may be used as a surrogate for water temperature, because both are strongly correlated (Caissie 2006), but many factors can influence water temperature (Loinaz et al. 2013), and some modelers have used empirical relations to relate the two (Li et al. 2014). Precipitation patterns are also important for Odonata, because they partly determine hydroperiod in lentic waters (Collins et al. 2014) and discharge and the consequent microhabitat structure within rivers (Buisson et al. 2008b). Bioclimatic variables are generally considered to be ecologically relevant, and only seven Odonata studies used additional climatic variables, such as the mean monthly temperature during the activity period of a particular odonate (Jaeschke et al. 2012).

#### *Elevation*

Elevation was included to refine the predicted distribution in seven Odonata SDM studies (Finch et al. 2006, Howard 2006, Nóbrega and De Marco 2007, Corser 2010, De Almeida et al. 2010, Hassall 2012, Wellenreuther et al. 2012). Many climatic or abiotic factors may be correlated with elevation, so empirically derived relations may not be interpretable if elevation is included as an independent variable (Elith and Leathwick 2009). Additionally, the influence of elevation will differ under future or past climates (Peterson 2006). Only one Odonata SDM study included elevation and attempted to project to future climates (Nóbrega and De Marco 2007).

#### *Distance from water courses*

Distance from water courses has been recommended as a useful predictor for several Odonata (Finch et al. 2006, Wellenreuther et al. 2012), though like elevation, this may be a correlated proxy for more proximal predictors and will likely result in poor predictions when extrapolating in space or time (Dormann et al. 2007).

#### *Topography*

Topographic metrics can be used to narrow the definition of suitable habitat, and these metrics are unlikely to change appreciably in future climates. Aspect may

influence photoperiod and solar radiation (Austin 2007) and was included in four Odonata studies, though the contribution of this predictor was not reported in three (Finch et al. 2006, Howard 2006, Corser 2010) and was not important in the fourth (Kuemmerlen et al. 2014). Slope controls water velocity, water oxygen content, weathering, and channel substrate size, and was included in six studies (Finch et al. 2006, Howard 2006, Corser 2010, De Almeida et al. 2010, Domisch et al. 2013b, Kuemmerlen et al. 2014) and was important for several species (De Almeida et al. 2010, Domisch et al. 2013b, Kuemmerlen et al. 2014). The importance of slope is supported by several surveys that found that some lotic Odonata are only found in particular watershed positions (Bahlo 1989, Gibbs et al. 2004). More sophisticated topographic indices describing landscape roughness or wetness were used in five Odonata studies (Howard 2006, Corser 2010, Wellenreuther et al. 2012, Domisch et al. 2013b, Simaika et al. 2013), but the relative importance of these metrics was not reported. Valley confinement is a useful proxy for riverine substrate and the channel response to high flow events and was used in two recent studies, but the relative importance of this variable was not reported (Gallant and Dowling 2003, Bush et al. 2014a, Bush et al. 2014b).

#### *Land cover*

Land cover is important at fine scales (Pearson and Dawson 2003, Pearson et al. 2004), because it can impede a species from occupying part of its otherwise suitable range (Dormann 2007). Though land cover predictors may be largely a function of climate (Thuiller et al. 2004), and the resource gradients that these predictors represent can vary regionally and temporally (Guisan and Zimmermann 2000), the inclusion of land cover data has improved predictive performance for fine-scale models (Luoto et al. 2007, Hopkins 2009). Relatively small catchment percentages of urban land use can produce major biota changes (Wang et al. 2001), and benthic macroinvertebrates including Odonata are known to be sensitive to metals that drain from impervious surfaces (Beasley and Kneale 2003) and to agricultural runoff (Quinn and Hickey 1990, Beketov et al. 2013, Sundermann et al. 2013).

Land cover predictors, such as land cover classes or vegetative indices, were included in seven Odonata SDM studies (Howard 2006, Corser 2010, Maes et al. 2010, Hassall 2012, Wellenreuther et al. 2012, Domisch et al. 2013b, Kuemmerlen et al. 2014), and variables such as upstream developed area and forest were found to be important predictors in some studies (e.g. Maes et al. 2010, Kuemmerlen et al. 2014) but not others (e.g. Wellenreuther et al. 2012, Domisch et al. 2013b). Human population density has been used in one Odonata study (Hassall 2012), and this variable may include information about anthropogenic influences on water bodies not contained in land cover data. Though not represented in Odonata SDM studies, predictors that consider the spatial configuration of land cover classes and riparian areas are known to influence the benthic community, bank erosion, substrate characteristics, and baseflow (Richards et al. 1996, Lammert and Allan 1999, Sponseller et al. 2001, Wang et al. 2001, Wilson et al. 2011).

#### *Discharge*

Hydrologic characteristics are among the most important environmental drivers for freshwater species in rivers (Leathwick et al. 2008, Chinnayakanahalli et al. 2011). Water discharge, river gradient, and other geomorphic factors are critical controls on biological composition, because they determine water velocity and hydraulic depth (Leathwick et al. 2008), which have been shown to be strongly correlated with local-scale distributions of invertebrates (Lamouroux et al. 2004). These factors also control substrate size, sorting, and organic matter deposition (Biggs et al. 1990, Leathwick et al. 2008, Verdonschot and van den Hoorn 2010), and larval dragonflies are known to exhibit a strong preference for substrate type (Suhling 1996, Ward and Mill 2008).

Often strongly correlated with water discharge, drainage area is also an indicator of position within a dendritic network, which has been shown to be directly related to aquatic insect diversity, with well-connected, central communities having greater diversity than more peripheral communities, regardless of local environmental conditions (Altermatt et al. 2013).

Precipitation patterns may be poor proxies for discharge, because evapotranspiration and upstream land cover can cause the relation to vary regionally (Carpenter et al. 1992), though most SDMs only consider precipitation. Hydrologic predictors were only included in four SDM studies that included Odonata (Domisch et al. 2013b, Bush et al. 2014a, Bush et al. 2014b, Kuemmerlen et al. 2014), even though these predictors have a more direct ecological effect than other predictors, possibly because other studies did not consider lotic species separately from lentic ones. Only one study considered hydrological predictors more sophisticated than flow accumulation, such as flow seasonality and seasonal sediment transport (Kuemmerlen et al. 2014). When the relative performance is reported, hydrological predictors are shown to be useful for explaining species distributions (Domisch et al. 2013b, Kuemmerlen et al. 2014).

Flow variability has been found to influence invertebrate communities (Biggs et al. 1990), and extreme peak discharge or low baseflow events have the most explanatory power in European lowland streams (Verdonschot and van den Hoorn 2010). Although more peak flows occur in more dynamic streams, the average water velocity tends to be lower, and low-flow events are more frequent. During low-flow events, silting and low O<sub>2</sub> conditions may make a stream unsuitable for rheophilic species, which are adapted to higher velocities and generally are sensitive to O<sub>2</sub> concentration (Verdonschot and van den Hoorn 2010). Periods of low baseflow may be problematic for lotic Odonata that are only found in fast-flowing rivers (Arnaldo et al. 2010). Not surprisingly, factors that result in altered or impounded flow such as dams influence species distributions (Han et al. 2009), though this type of predictor was not included in any Odonata SDM.

Froude number and substrate roughness have been found to be the major microhabitat and reach-scale variables related to the functional structure of invertebrate communities (Lamouroux et al. 2004), and using more sophisticated hydrologic and hydraulic modeling to produce relevant environmental predictors for SDMs is a frontier of this field.

### *Soils*

Soils may influence the chemistry, hydrology, and substrate of water bodies, and the inclusion of soils data, such as clay content, sand content, and permeability, has been shown to improve SDM predictions (Titeux et al. 2009, Wilson et al. 2011). Soils data were included in four Odonata studies and was relatively important for at least two species (Howard 2006, Corser 2010, Maes et al. 2010, Wellenreuther et al. 2012).

### *Water chemistry*

Water chemistry is very important for invertebrate community composition (Biggs et al. 1990), and the general lack of water quality-related environmental data sets is a notable limitation for distribution modeling of some species (Stockwell and Peters 1999). Unfortunately, monitoring locations are scattered and opportunistic, the data cannot be interpolated between monitoring locations, and the temporal stochasticity of water chemistry severely limits the usefulness of these measurements for SDMs (Wilson et al. 2011). EPA river impairment classifications have been used in an SDM study of freshwater mussels (Weber and Schwartz 2011), but these variables have not been shown to be relevant for Odonata (Collins, unpublished data 2012). Geological variables are typically included as distal proxies for water chemistry (Howard 2006, Corser 2010), though recent empirical analysis may permit more direct variables to be used (Olson and Hawkins 2012).

### *Biotic variables*

Species tend to be bounded by physically stressful conditions in one direction and biologically stressful conditions in the opposite (Brown et al. 1996). Biotic interactions are recognized as being of great importance to SDMs at fine scales, such as 100s of meters (Pearson and Dawson 2003, Guisan and Thuiller 2005, Araújo and Luoto 2007, Soberon 2007, Soberon and Nakamura 2009, Godsoe and Harmon 2012), but inclusion of these data is often considered too difficult (Wilson et al. 2011). Odonata richness has been correlated with the presence of macrophytes (Ilg and Oertli 2014), and Jaeschke et al. (2012) was able to use the distribution of *Aeshna viridis*'s

oviposition host plant to refine climate change projections for that odonate. No other Odonata SDM study included biotic interactions, possibly because species interactions are poorly known. The omission of host dragonfly distributions as predictors was striking in a recent distributional analysis of a parasitic fly dependent on a limited number of odonate species (Guillermo-Ferreira and Vilela 2013).

#### *Overparameterization*

Overparameterization is the effect of training a model with too many predictors or defining the predictor relations too tightly, such that the models are not transferable to new regions or may perform poorly when compared against independent data. To avoid overparameterization, modelers can reduce the number of predictors (Elith et al. 2010a, Anderson and Gonzalez 2011) or use simpler functions to define relations with predictors, such as increasing regularization in Maxent or excluding particular feature types (Anderson and Gonzalez 2011, Warren and Seifert 2011, Cao et al. 2013). If users are interested in which predictors are most important or in interpreting the relations with predictor variables, it is important that predictors not be correlated. If variables are internally correlated, the model may preferentially select one predictor in a correlated pair, such that a modeler could misinterpret the importance or relations with the unselected predictor. Studies typically analyze the Pearson's correlation coefficients between all pairs of environmental predictors and omit variables that are highly correlated, such as those with coefficients greater than 0.8 (Rinnhofer et al. 2012) or 0.7 (Jaeschke et al. 2013). A principal components analysis can also eliminate colinearity between environmental predictors, and this approach has been used in one Odonata study (Wellenreuther et al. 2012). Some studies have reduced the number of predictor variables considerably, such that only three or four predictors are used in model development without sacrificing model performance (Domisch et al. 2013a, Kuemmerlen et al. 2014).

#### *Modeling river species on the scale of individual rivers*

Environmental conditions used for species distribution modeling are most often portrayed in gridded geographic space, where each grid cell is assigned the

average value of an environmental variable within that cell. For riverine species, presence localities, environmental data and predictions are associated with rivers and not necessarily raster cells, so river segments may be the natural choice of background. Compared to representing rivers as raster cells and restricting the background to these rasterized networks, a “landscape-masked” design, treating river segments as the basic unit for background selection and prediction has demonstrated increased model performance (Domisch et al. 2013b). Riverine SDMs permit the consideration of upstream area characteristics on species distribution, an important concept in freshwater systems (Vinson and Hawkins 1998, Malmqvist and Rundle 2002). A recent Australian study adopted a reach-scale approach because most Australian Odonata are lotic (Bush et al. 2014b).

### ***Pond species***

Many regions have numerous, varied, and often well-defined lentic waters that could be compared in with an SDM framework. To date, SDM studies of lentic species have not considered catchment variables. This may be because other approaches to modeling the suitability of specific lentic Odonata habitats are well-suited (Ilg and Oertli 2014).

### ***Dispersal***

Dispersal ability is an important consideration when filtering species locality data or when projecting models to future environmental conditions. Most locality records for Odonata represent adults (Abbott 2006–2014) that could have been collected away from their larval habitat, so modelers need to be cautious that potentially unsuitable areas are not classified as suitable. Fortunately, model performance has not been shown to be affected by species with high dispersal abilities including Odonata (Hallstan et al. 2013).

Most studies assessing climate change impacts to species distributions either assume unlimited dispersal, where predictions can be made across the available geographic space, or no dispersal, where the future distribution is the overlap between the predicted future range and the current range (Pearson et al. 2006, Franklin 2010).

The assumption of unlimited dispersal may overestimate species' ability to track climate change, but dispersal abilities are poorly known for most species (Jaeschke et al. 2013). Measuring dispersal is very difficult, though there is genetic evidence for dispersal across catchments (Hughes et al. 2013). By using natural history information, Jaeschke et al. (2013) determined that six European Odonata can disperse between 0.5 and 14 km per year. Hickling et al. (2005) were able to measure an average northward range shift of 6.8 km per year in 37 non-migratory British Odonata, and Grewe et al. (2013) measured a 6.4 km per year expansion in southern European lentic Odonata but found no consistent expansion in northern or lotic species. Ott (2001) did not provide expansion distances, but indicates that several lentic Odonata spread hundreds of kilometers into Europe and up to 400 m in altitude over two decades. One Odonata study was able to use bioclimatic SDMs to show that lentic species have greater dispersal ability than lotic species (Hof et al. 2012). Lentic species were more likely to fully occupy bioclimatically suitable areas than lotic species. It is thought that lentic species disperse farther and more readily than lotic ones because lentic habitats are less stable spatially and temporally (Hof et al. 2006, Marten et al. 2006). Consequently, lotic species may be under greater risk from climate change than lentic species.

### ***Climate change***

Climate change may benefit certain Odonata with various responses expected. Increased temperatures can lead to more rapid development rates (voltinism) of nymphs (Braune et al. 2008) and thus earlier emergence of adults, which may lead to longer flight seasons (Hassall et al. 2007) and a corresponding extension of northern range limits. Some Odonata that are structurally adapted for dispersal (i.e. wing:abdomen length ratio and wing aspect ratio) have dispersed northward more rapidly than species without these dispersal-related traits (Hassall et al. 2009). Additionally, northern individuals of species known to be shifting north are more plastic in their morphology than individuals from the core range, suggesting these

species have a morphological ability to adapt to new climates, but the extent of this is unknown (Hassall et al. 2008).

Odonata may not be able to adapt to climate change as quickly as it occurs, because populations may be genetically adapted to the climate and photoperiod of their natal region (Johansson et al. 2010). Even different populations from within the same species may have different behavioral responses to temperature, with only some populations seeking out thermal optimums (Leggott and Pritchard 1986). The conservation of localized and otherwise sensitive species must be prioritized, because these species may have difficulties tracking climate change (Shah et al. 2012).

Uncertainty in model predictions to climate change scenarios lies in a limited understanding of species dispersal, biotic interactions, rapid *in situ* adaptation, existing adaptation of populations to local conditions, direct impacts of increased CO<sub>2</sub> concentration, potential inaccuracies in species distribution data sets, and uncertainties in climate change projections (Pearson et al. 2006). When projecting to an ensemble of global climate models or emissions scenarios, it is important to project to each climate data set individually, because an average of different climate models is not meaningful (e.g. Shah et al. 2012).

Future climates may contain novel conditions not included when training SDMs, so some modelers have opted to fade extrapolations in a process known as clamping (Bush et al. 2014b). Other modelers have developed Multivariate Environmental Similarity Surface (MESS) analyses to assess where novel climate may occur (Elith et al. 2010a, Jaeschke et al. 2012). In addition to climate, land cover is also expected to change in the future (Bierwagen et al. 2009), impacting water quality and downstream hydrology. At the time of this review, no known Odonata studies have investigated the impact of future land use.

### ***Limiting extent***

Large modeling extents are often chosen so that the definition of suitable environmental conditions for a species is not limited by training models with a subset of the known range (Collingham et al. 2000), or because a large extent reduces the

likelihood of encountering novel climatic conditions when projecting to future climates (Fitzpatrick and Hargrove 2009). For these reasons, predicted distributions may be truncated when modeling extents are chosen based on political or reserve boundaries (Austin 2007) making model interpretation difficult (e.g. Maes et al. 2010). However, large modeling extents can inflate model performance metrics, and a restricted extent may provide a more ecologically relevant limit the extent of the background sample (VanDerWal et al. 2009, Anderson and Raza 2010, Elith et al. 2010b, Barve et al. 2011). Watershed boundaries are suitable for modeling freshwater species such as Odonata, because that modeling extent “intrinsically considers the environmental conditions responsible [for] shaping and structuring freshwater ecosystems” (Kuemmerlen et al. 2014).

A restricted background may also compensate for potential sampling bias among the presence locations (Phillips et al. 2009, Syfert et al. 2013). For this reason, one Odonata study restricted background selection to areas within 300 km of any Odonata record, assuming that areas beyond that limit were not sampled (Bush et al. 2014b).

### ***Evaluating model performance***

Assessment of model performance has evolved over time. The most straightforward method is visual evaluation and may still have some utility, because patterns, agreement, and local and global similarities can be intuitive (Prasad et al. 2006). Some modelers have used a sensitivity analysis to determine how extreme values in the data affect the resulting distributions, whether the extreme values be errors or outlier populations (Finch et al. 2006). However, repeatable and objective automated methods are more effective, so most studies use test metrics that assess overall model performance.

Sensitivity is the proportion of true positive predictions compared to the number of actual positive sites. Specificity is the proportion of true negative predictions compared to the number of actual negative sites (Fielding and Bell 1997). False-negative predictions may be the more egregious error, because predicting

unsuitable habitat where a species is known to exist is a clear error, where predicting suitability where presence has not been recorded could be attributed to biotic or dispersal-barrier interactions or because of insufficient sampling (Pearson et al. 2006). Sensitivity and specificity can be reported individually, as was done in three studies that included Odonata (Maes et al. 2010, Jaeschke et al. 2012, Kuemmerlen et al. 2014), and are fairly easy to interpret.

The so-called kappa statistic (Cohen 1960) is the proportion of agreement expected after correcting for random chance (Allouche et al. 2006). It can range from -1 to 1, with 1 indicating perfect agreement and negative values indicating discrimination no better than random. It was the most commonly used metric in SDMs until modelers realized it was dependent on species prevalence (Allouche et al. 2006) and has only been used in one Odonata SDM study (Hassall 2012). It also requires that a modeler select a threshold for discriminating between predicted presence and absence.

The area under the receiver operating characteristic curve (AUC) metric is advantageous over the kappa metric, because it is not biased by species prevalence and is threshold-independent (Hanley and McNeil 1982, Fielding and Bell 1997, Guisan and Zimmermann 2000). AUC ranges from 0.5, representing a model that discriminates no better than random, to 1.0, representing perfect discrimination between presences and absences. Subjective guidelines suggest that AUC values above 0.9 describe very good discrimination ability, but the AUC value is dependent on the modeling application (Swets 1988). AUC values between 0.7 and 0.9 may represent accuracies that are useful for some applications (Swets 1988). AUC was the most commonly used test metric among SDM studies that included Odonata. Recent work has shown that AUC can be inflated by modeling large extents (Lobo et al. 2008, Elith et al. 2010b), so modelers must be mindful of this effect. High AUC values in riverine SDMs may be because longitudinal position allows the model to discriminate suitable habitat more closely or because AUC values are artificially inflated by restricting the selection of background data (Buisson et al. 2008b). This possibility

would need to be tested in a separate study, though it is known that TSS, the true skills statistic, is not affected by riverine SDM designs (Domisch et al. 2013b).

TSS is arguably a simpler metric than either kappa or AUC, because it is directly related to sensitivity and specificity. It has been shown to be superior to kappa, but like kappa it requires thresholded presence-absence predictions (Allouche et al., 2006). It has been reported in seven studies that included Odonata (Hassall 2012, Domisch et al. 2013a, Domisch et al. 2013b, Simaika et al. 2013, Bush et al. 2014a, Bush et al. 2014b, Kuemmerlen et al. 2014).

In species distribution studies, model evaluation is often achieved by data resampling, such as split samples, cross-validation, bootstrapping, or through independent data sets (Elith et al. 2006, Elith and Leathwick 2009). Presence-only datasets have geographic and environmental biases, and evaluation through data resampling does not necessarily eliminate those biases. Single split samples, where 30% of the available data are withheld for testing, were used in four studies that included Odonata (Hassall 2012, Jaeschke et al. 2012, Shah et al. 2012, Wellenreuther et al. 2012). Ten-fold cross-validation, one of the best resampling methods (Kohavi 1995), is known to inflate performance metrics (Hijmans 2012). Among studies that included Odonata, ten-fold cross-validation, where each replicate used 70% of data for training and 30% of data for testing, was used in six studies (Finch et al. 2006, Domisch et al. 2013a, Sanchez-Guillen et al. 2013, Simaika et al. 2013, Bush et al. 2014b, Kuemmerlen et al. 2014), and geographically stratified cross-validation was used in one (Jaeschke et al. 2013). Using independent, well-structured, presence-absence datasets for validation is a more reliable, though rarely used, means of model evaluation (Elith et al. 2006, Phillips et al. 2009). Independent survey data were used in three Odonata studies (Hof et al. 2012, Sondgerath et al. 2012, van Strien et al. 2013), and one study included field verification to assess predicted habitat though the target species, *Ophiogomphus anomalus*, was not found at nine predicted locations (Howard 2006).

### ***Threshold selection***

When discriminating between predicted species presence and absence, it has been suggested that permitting equal error rates in omission and commission (i.e. choosing a threshold where sensitivity and specificity are equivalent) is ideal (Fielding and Bell 1997). Maximizing TSS produces a similar effect (Cao et al. 2013, Liu et al. 2013). Though a minimum training presence, or no omission, threshold portrays relatively large predicted areas, it has been shown to be an accurate threshold selection and is suitable when omission is the more egregious error (Cao et al. 2013) and was used in one Odonata study with limited localities (De Almeida et al. 2010). In one Odonata study, a 10<sup>th</sup> percentile training presence threshold was used, because it was assumed that 10% of species localities could have been poorly georeferenced (Sanchez-Guillen et al. 2013).

### **Conclusions and recommendations**

The lack of readily available fine-scale locality data limits the inferences that can be drawn from modeling and has overestimated odonate distributions in some cases, highlighting the need for digital Odonata databases to be improved with precisely georeferenced localities worldwide. Fewer than 25% of all Odonata species have been modeled, and of those that have, the spatial resolution of predictions or modeling approach could be improved.

Species with few presence records are typically excluded to maintain high model performance, so there is an inherent inability for SDMs to model rare species (Simaika et al. 2013), which may limit their utility as a conservation tool for the rarest species which may also be the species of greatest conservation concern. Distance-based methods have shown promise, but these approaches have not been employed for rare Odonata.

The lack of dispersal data for most Odonata is a considerable limitation when assessing how environmental change may affect individual species. Though there is evidence that lentic species are good dispersers, dispersal abilities vary, and some

species, especially lotic species, may not be able to disperse quickly enough to track climate change (Grewe et al. 2013).

It is expected that SDMs conform to the most recent advances in the field, with respect to model development, calibration, and validation, though methods can still be improved. Species-specific predictors are rarely used, either because they are unknown or for logistical convenience. Tailoring predictors to individual species models will likely produce more meaningful and robust predictions. At the time of this review, no SDM studies of Odonata have used the spatial configuration of land use as a predictor. Similarly, no SDM studies of lotic species have included hydrologic modeling to predict how discharge, baseflow, and the frequency and duration of storm events will respond to changes in precipitation and projected land use. These hydrological variables are known to be important, and they will likely change under future conditions. Additionally, no SDM studies have incorporated hydraulic modeling and sediment transport modeling to determine relations between species presence and the magnitude and variability in water velocity and bedload transport, though water velocity and sediment characteristics are known to be proximal predictors of odonate habitat. Hydraulic models could be coupled with hydrologic models to produce sophisticated projections of future species distributions with respect to climate and land-use predictions. Additionally, most studies of Odonata distributions have not considered the watershed characteristics of lentic waterbodies (but see Ilg and Oertli 2014), and these relations could be especially useful in conservation planning of lentic species.

Species distribution modeling is a useful tool in understanding species-environmental relations that has boosted our knowledge about factors limiting the distribution of Odonata. There is also much potential growth for this tool.

Table 2.1. Distribution modeling publications reviewed in this paper, the region of interest, and how many Odonata species were included.

<b>Citation</b>	<b>Region</b>	<b>No. of Odonata species</b>
Finch et al. (2006)	<b>Africa:</b> South Africa	160
Howard (2006)	<b>North America:</b> US: New York: Salmon River watershed	2
Nóbrega and De Marco (2007)	<b>South America</b>	1
Corser (2010)	<b>North America:</b> US: New York	1
De Almeida et al. (2010)	<b>South America:</b> Brazilian Cerrado	2
Kery et al. (2010a)	<b>Europe:</b> Switzerland	1
Maes et al. (2010)	<b>Europe:</b> Belgium	66
Outomuro et al. (2010)	<b>Europe:</b> Spain within the Iberian Peninsula	3
Nóbrega and De Marco (2011)	<b>South America:</b> Brazilian Cerrado	526
Dorazio and Rodriguez (2012)	<b>Europe:</b> Switzerland	1
Hassall (2012)	<b>North America:</b> US & Canada	176
Hof et al. (2012)	<b>Europe</b>	88
Jaeschke et al. (2012)	<b>Europe</b>	1
Shah et al. (2012)	<b>Asia:</b> Hindu Kush Himalayan region	1
Sondgerath et al. (2012)	<b>Europe</b>	1
Wellenreuther et al. (2012)	<b>Europe:</b> Fennoscandia	2
Domisch et al. (2013a)	<b>Europe</b>	4
Domisch et al. (2013b)	<b>Europe:</b> Germany: Westphalia, Hesse, Thuringia, and Baden-Wuerttemberg	5
Jaeschke et al. (2013)	<b>Europe</b>	6
Sanchez-Guillen et al. (2013)	<b>Europe and North Africa</b>	7
Simaika et al. (2013)	<b>Africa</b>	337
van Strien et al. (2013)	<b>Europe:</b> Netherlands	40
Bush et al. (2014a)	<b>Australia</b>	270
Bush et al. (2014b)	<b>Australia</b>	270
Kuemmerlen et al. (2014)	<b>Europe:</b> Germany: Treene catchment	1
Li et al. (2014)	<b>Asia:</b> South Korea	13

Table 2.2. Number of modeled Odonata species relative to Odonata known within biogeographic regions.

<b>Region</b>	<b>No. of Odonata<sup>1</sup></b>	<b>No. of Odonata modeled</b>
Afrotropical	889	337
Oriental	1,665	0
Palearctic	560	102
Neotropical	1,636	529
Australasian	870	270
Pacific	168	0
Nearctic	451	176

1. From Kalkman et al. (2008)

## CHAPTER III

### DANGER OF DISTRIBUTION MODELING WITH COUNTY-SCALE SPECIES DATA

#### Abstract

Citizen-science databases are valuable for developing species distribution models (SDMs), though modelers must be cautious, because as many as 80% of U.S. records of some taxa may be data only georeferenced to county centroids. It is tacitly assumed that SDMs built from county-scale data should be less precise than those built with more accurate localities, but the extent of the bias is currently unknown. Further, the steps to accommodate these data given that the associated true localities may not be readily available. The effect of county-scale data on the spatial extent and accuracy of SDMs relative to true localities is quantified in this chapter. SDMs were developed in MAXENT using Bioclim variables for 283 and 230 species of odonates (dragonflies and damselflies) and butterflies, respectively, using the OdonataCentral and Butterflies and Moths of North America citizen-science databases. Separate SDMs were developed and compared, having filtered the databases to include one species record per county, using: (1) true localities, (2) a corresponding sister dataset of county-centroid coordinates, (3) a dataset where county-averaged environmental conditions were assigned to each record, and datasets including 50/50% mixes of true localities and either (4) county-centroid coordinates, or (5) county-averaged environmental conditions. Models were compared by I, D, and Relative Rank statistics computed with ENMTools and by areal extent of thresholded predictions. County-centroid models overpredicted the areal extent of suitable habitat by 15% on average, although larger sample sizes reduced the disparity. Assigning county-averaged environmental conditions did not offer consistent improvement, though a combination of true localities and county data showed significant improvement. County-scale data are of limited value for developing SDMs unless species are widespread and well-collected or inhabit regions where small, climatically uniform

counties predominate. Three means are suggested in this chapter to encourage accurate georeferencing in citizen-science databases.

## **Introduction**

Many publications and online citizen-science projects within the U.S. have focused on U.S. counties for recording or reporting species records (Appleby 1991, Angelo and Boufford 2000, Donnelly 2004a, b, c, Price and Dorcas 2011, Patterson and Boone 2012). The use of counties as an indication of species presence or absence is often a logistical convenience for display, and it is also a consequence of inaccurate historical data and early distribution cataloguing (Abbott 2006–2014, Opler et al. 2012). For example, sometimes data are recorded only as a specific county because localities are poorly described or imprecise (Graham et al. 2008). Unfortunately, this practice also has been adopted by many scientists and citizen scientists as a convenient resolution for recording data. There is value to county-level data, though including it may provide an overly optimistic view of completeness and extent of data coverage (Table 3.1). Given the value of vouchered data collected by citizen scientists that is now being realized and utilized (Schmeller et al. 2009, Sullivan et al. 2009, Fink et al. 2010, Kery et al. 2010a, Szabo et al. 2010, Wood et al. 2011, Hassall 2012, van Strien et al. 2013), it is important that the impacts of using only county-level species data to examine species distributions be understood.

Citizen-science databases can be used to develop species distribution models (SDMs), which map the geographic distribution of empirically defined suitable environmental space for species. The most common environmental data used with SDMs are climatic variables describing the magnitude and seasonality of temperature and precipitation (Pearson and Dawson 2003). Associating species presence localities with the correct climates is important for SDMs, yet climatic conditions can vary substantially within a U.S. county (Fig. 3.1A and B). Because of the variability of climate within many U.S. county boundaries, species locality data recorded only to the resolution of U.S. county might be of limited use for distribution modeling, but this needs to be tested. Previous studies have shown mixed success in parameterizing

models at coarse scales and then making predictions at fine scales (Lloyd and Palmer 1998, Barbosa et al. 2003, Araújo et al. 2005b, McPherson et al. 2006). Highly uncertain localities such as county-level data could be excluded from modeling, but the reduction in sample size could negatively affect model performance (McPherson et al. 2004, Hernandez et al. 2006), which may be especially true among invertebrates where county-level data predominate (Table 3.1).

Such locality data are typically recorded with coordinates that represent the geographic center (centroid) of the county. In this paper, county-level data refer to records that only include U.S. county location information, and county-centroid data refer to similar records that include the centroid coordinates of a county in place of specific coordinates for the collection location. Imprecise locality information, such as county-level data, are often a consequence of the ability or inclination of a collector to record accurate locations. Our ability to record accurate locations has increased dramatically due to GPS, but accurate locality data does not overcome the limitation of SDMs in terms of microclimates. Microhabitat variables can be critically important in determining localized species presence or absence, but such variables are impractical to model in an SDM framework given the resolution of species locality data, which is typically greater than these microclimates, and the resolution of environmental predictors, which are rarely available at fine scales.

Using the geographic centers of coarse-scale atlas blocks as localities for distribution models (Lloyd and Palmer 1998) assumes either that the centroid is representative of suitable climatic conditions within that block or that the entire block contains suitable conditions (McPherson et al. 2006). In some U.S. counties, the centroid may be representative of typical climatic conditions within the county, and these records may thus be appropriate for use in distribution modeling. However, in some large or mountainous counties, the centroid may not be representative of the typical climate (Fig. 3.2). This is partly because many large and mountainous counties have different climates contained within their borders (Fig. 3.3). Placing a number of points throughout the county to represent the species occurrence could capture the

variability of environmental conditions within the county (Howard 2006), but it is unknown if environmental conditions throughout the county are universally suitable for a species, so this approach is likely to increase uncertainty in modeling attempts (McPherson et al. 2006), especially if the point placement scheme is dependent on county size. A potential solution would be to assign average climatic conditions to county data points, though it is unlikely the average is representative of the conditions at the true locality (Huston 2002). Furthermore, if other environmental variables are used, such as slope or aspect, it may be even less likely that the county centroid or average is representative of the true habitat locality. Another potential solution would be to calculate summary statistics for each variable within each county, such as mean and variance, and use those as predictors. Summary statistics for categorical variables could be achieved by calculating the percentage of each category occurring within each county (e.g. percent north-facing slopes, percent quaternary alluvial deposits) (Anderson and Ferree 2006). Unfortunately, the number of environmental variables escalates quickly with this approach, and it only will be possible to predict at a coarse scale in most instances, so it is unlikely this approach will be adopted by most users.

County-level data may be a considerable problem in invertebrate databases. Invertebrate populations respond quickly to environmental disturbances, and odonates (dragonflies and damselflies) and butterflies have each been used to demonstrate ecological effects of climate change (Kharouba et al. 2009, Breed et al. 2013, Bush et al. 2013, Grewe et al. 2013), a common application of species distribution modeling. Two large, species-presence online datasets, OdonataCentral (<http://odonatacentral.org>) and the Butterflies and Moths of North America (BAMONA; <http://www.butterfliesandmoths.org>), include vouchered records of odonates and lepidopterans (butterflies and moths), respectively, from personal and museum collections and photo records submitted by professional and citizen scientists that are vetted by experts. Species abundance is not recorded in either database. OdonataCentral includes the “dot-map” database compiled by Nick Donnelly (Donnelly 2004a, b, c). Though the “dot-map” database is the most comprehensive

source of U.S. distributional data contained within OdonataCentral, each record corresponds to a U.S. county centroid for a species, and no other metadata are available. Similarly, the BAMONA database was built from the USGS Northern Prairie Wildlife Research Center database, and no metadata are included with the USGS U.S. county records. In the absence of reliable locality data, there is a temptation to use what is available for some species, including county-level data. To make use of the majority of OdonataCentral data which is county level only, Hassall (2012) used a very large grid size. That study concluded that SDMs overpredicted the known ranges of species, but the overprediction may have been due to average environmental conditions within these large grids not representing the environments where the species were collected.

This study predicted that SDMs developed with U.S. county centroids will overpredict the geographic range of suitable conditions as compared to models developed with true localities using odonate and butterfly data as an example. SDMs function on the concept that the ecological niche can be defined reasonably with a limited set of environmental variables (e.g. annual precipitation, maximum summer temperature). The environmental conditions at county centroids may be outside the range of suitable conditions for a species, so using centroid data for SDM development may misrepresent the empirically derived niche, or environmental envelope, and consequently misrepresent the geographic range of suitable conditions for the species. It is predicted that the misrepresentation of the empirically derived niche will result in geographic overprediction, and overprediction will be highest in species that occur in the western U.S. where large counties include a larger range of environmental conditions compared to smaller/eastern U.S. counties (Fig. 3.4). To test these predictions, SDMs were generated using both true localities and corresponding county-level data and combinations of these and of averages. The objective of this study is not to describe the complete bioclimatic niche of these species but rather to describe how modeled niches can differ as an artefact of data

type, and it is assumed that each model developed with true localities is a baseline to which models developed with county-level data can be compared.

## **Methods**

### ***Data sources***

Odonate and butterfly localities were obtained from the OdonataCentral and BAMONA online databases, respectively, in November 2012. These two databases have different biases (Table 3.1), so each is treated separately in this paper. More than 96% of localities from both databases were recorded after 1981, though a few localities were recorded as early as 1930. Species true locality records submitted to OdonataCentral and BAMONA were compared to the founding county-level databases within each database. This was done to assess bias in user-submitted records, for example how often locality records were submitted for U.S. counties without a previous record compared to U.S. counties with a previous record. Table 3.1 shows that U.S. county-level records outnumber true locality records in both databases, and that the majority of U.S. county records do not have a true locality record within the same county. These data suggest that new county records (records where no accurate or inaccurate record for the county was present in the database) are more numerous than would be expected if users ignored county boundaries.

U.S. county records without accurate locality information were excluded from analysis. The OdonataCentral and BAMONA databases were filtered to exclude the following: records outside of the contiguous U.S., inaccurately located data points including county centroids and instances where the plotted coordinates did not fall within the user-entered county, duplicate entries for the same species and locality, records without a photo or specimen voucher, and records that had been invalidated or not yet vetted by expert reviewers. For species that had more than one validated record within a county, only the first record in the database was selected from each county. This one-per-county filter was necessary so the sample size for each species would match the sample size of county centroids for each species. After these filters,

only species that contained ten or more localities were retained for modeling, resulting in a set of 283 species of odonates and 230 species of butterflies within the U.S. Omitting species with fewer than 10 localities is common practice in SDM (Domisch et al. 2013a, Domisch et al. 2013b, Simaika et al. 2013, Kuemmerlen et al. 2014), because the relative importance of individual localities in models developed with fewer than 10 localities is great enough that outliers tend to have considerable influence on distributions. Though these datasets may be spatially biased toward population centers or regions with active collectors, for the purpose of this study, it is assumed that the filtered datasets contain an acceptable representation of the distribution of all species. It is understood that the modeled distributions may not be realistic, but they are useful as a baseline for comparison when comparing models developed with different types of locality data such as county centroids. Sister datasets were created that contained the coordinates for the county centroid of each record contained in the filtered datasets.

To compare if county centroids are more problematic in the western U.S. versus the eastern U.S., species were selected where all filtered records were east or west of the 100<sup>th</sup> meridian. To reduce the effect of sample size on this comparison, a subset of strictly eastern and western species were selected such that the number of records were comparable (Table 3.2 & Appendix). To determine if the effect of using county centroids is influenced by species natural history, the deviation of predicted areas among lentic and lotic Odonata were compared. Lotic Odonata were identified by written habitat descriptions and are identified in the Appendix (Paulson 2009, 2011).

### ***Model development***

Bioclimatic (bioclim) variables were derived from monthly values of maximum and minimum temperature and precipitation from the PRISM 30-arcsecond climatology normals (1971–2000) gridded dataset (<http://www.prism.oregonstate.edu>). These 19 metrics are considered more biologically meaningful than the 36 raw monthly values (Busby 1991). PRISM was chosen because it is more

physiographically sensitive than WorldClim and performs better in mountainous regions (Daly et al. 2008). The better performance of PRISM can be attributed to interpolation method, an increased density of available weather stations, and a peer review procedure that accounts for local knowledge in the development process (Daly et al. 2008). The bioclim grids and the odonate and butterfly datasets were reprojected to NAD\_1983\_Albers to avoid the cell-size bias with latitude present in the native projections of these data.

A principal components analysis (PCA) was performed with the Principal Components tool in ArcGIS 9.3 so that a subset of uncorrelated layers describing climate could be used for model development. The 19 bioclim metrics are often correlated with each other, and using a subset of principal components has been shown to increase model performance by reducing redundant parameters which prevents overfitting (Dupin et al. 2011). SDMs were developed using the first seven principal component grids, which explained 98.5% of the total variance in the original 19 bioclim grids, as environmental background layers.

Modeling was performed in *Maxent* v.3.3.3k (Phillips et al. 2004) using default settings (automatic features, 10,000 background points, regularization multiplier of 1, 500 maximum iterations, convergence threshold of 0.00001, default prevalence of 0.5, non-random seed). The *Maxent* algorithm compares the probability density defined by the environmental space of species localities to the probability density defined by the environmental background and minimizes the relative entropy between them by altering one variable weight at a time (Phillips et al. 2004, Elith et al. 2010b). *Maxent* has been shown to be robust compared to other methods (Elith et al. 2006) and to perform well in the face of spatial errors in training localities (Graham et al. 2008) and reduced sample sizes (Wisz et al. 2008). SDMs were generated for each of the 283 focal odonate species and 230 focal butterfly species using five datasets: (1) the true locality dataset, (2) the corresponding sister dataset of county-centroid coordinates, (3) a dataset where the average environmental conditions within each county were assigned to each record, (4) a dataset including a

50/50% mix of true localities and county-centroid coordinates, (5) a dataset including a 50/50% mix of true localities and records assigned the average environmental conditions within each county. For the two 50/50% mix approaches, the records converted to county-level data were selected randomly, but the same selection of true localities and county-level data were used in both approaches.

The 30-arcsecond native resolution of environmental predictors is sufficient because it is larger than the foraging distance of odonates or butterflies (Baird and May 1997, Corbet 2004, Cant et al. 2005). Some odonates and butterflies are known to disperse, and it is possible that some species localities represent dispersing or migrating adults in environmental conditions unsuitable for reproduction. In those cases, the modeled distribution could be considered the range suitable for detecting the species including dispersing adults. Maxent is known to perform well when some spatial errors are included (Graham et al. 2008), so it is unlikely there will be a substantial effect of including records of potential dispersing or migrating individuals. Most importantly, because the models may not be realistic representations of species distributions but are included as a basis for comparison between different types of species data, identifying these records is not necessary because they will be present in both datasets.

### ***Data analysis***

The model outputs from each dataset were compared in terms of areal extent and niche similarity metrics. For the purposes of this project, models developed with true localities were assumed to represent the true distribution of each species. It is known that locality density will be highest in regions with small counties, but this bias will be consistent between all models being compared. To quantify and compare the areal extent of each modeled range between models developed with each dataset for each species, two thresholds were applied for each species. All grid cells with a predicted value above the threshold are considered suitable, and the number of suitable cells is summed to quantify the areal extent of each distribution. The sensitivity-equals-specificity threshold represents the value where positive and negative

observations have an equal chance of being predicted correctly, and the minimum-training-presence threshold represents the value where a species is predicted to be present at all localities used to train the model (no omission error) (Fielding and Bell 1997, Freeman and Moisen 2008). Overprediction was assessed by the ratio of the areal extent of thresholded model output for each dataset (e.g. county centroid models) compared to the areal extent of the thresholded model output for the true locality models. Comparisons were also made between eastern and western species subsets (Table 3.2).

The niche similarity of models generated with each dataset was compared for each species using ENMTools (Warren et al. 2010). Three statistics were generated: the similarity statistic, *I*, which is a metric used to test if models generated from different populations are identical, Schoener's *D*, which is a metric describing the level of niche overlap, and Relative Rank, *RR*, which is an estimate of the probability that a pair of rasters agree in the relative ranking of any two patches of habitat regardless of the suitability values (Warren et al. 2008, 2010, Warren and Seifert 2011). For both *I* and *D*, a value of 0 represents no niche overlap, and a value of 1 represents identical niches. For *RR*, a value of 0 represents disagreement on the relative quality of every habitat patch (cell) pairing, and a value of 1 represents identical relative ranking of all cell pairs.

AUC (area under the curve) and TSS (true skills statistic) values, each measures of the ability of the model to discriminate between species occurrence and absence, were also compared between models for each species. AUC is threshold-independent, and TSS requires thresholded binary predictions of species presence and absence. Both measures are independent of species prevalence, but TSS is not influenced by modeling extent (Allouche et al. 2006, Lobo et al. 2008). Guidelines suggest that AUC values  $>0.9$  and TSS values  $>0.8$  describe excellent discrimination ability and AUC values  $<0.7$  and TSS values  $<0.4$  describe poor discrimination ability (Landis and Koch 1977, Swets 1988). AUC and TSS was also assessed for county-centroid models using true localities as test data. The minimum-training-presence

threshold minimizes omission rate at the expense of commission (false presence) rate, so lower TSS values using this threshold are expected. The inclusion of AUC and TSS statistics are not intended to justify the hypothesis on the accuracy of SDMs based on true locality data and county-centroid data; that hypothesis is tested using niche similarity statistics and the deviation in the areal extent of predictions compared to models developed with true localities which are assumed to be an accurate baseline for comparison.

## Results

SDMs for 283 species of odonates and 230 species of butterflies in the continental U.S. based on true locality data outperformed corresponding SDMs based on county-centroids, with the county-centroid models producing a median AUC reduction of 0.010 and median TSS reduction of 0.022 and 0.021 using sensitivity-equals-specificity and minimum-training-presence thresholds, respectively, across all species (Wilcoxon signed-rank test p-value < 0.00001 for each comparison). Model performance as assessed by AUC and TSS is further reduced when true localities are used as test data for the county-centroid SDMs. Model performance metrics for true-locality and county-centroid SDMs are summarized in Table 3.3. Though model performance is significantly better using true localities, it varies considerably with species. Values plotted below the 1:1 lines in Figure 3.5 are indicative of greater model performance (AUC or TSS) of the true-locality model. The number of iterations among `Maxent` models varied from 80 to 500 with a median of 500.

Developing niche models with county data led to overprediction, on average, of the geographic representation of the environmental niche (mean: 15%; median: 3.2%; range: -65% to 789%). The mean predicted areas were larger regardless of how the county-level data were treated (Table 3.4). The majority of butterfly and odonate species (n = 288) showed greater than a 1.0% increase in the predicted range when county centroids were substituted for true localities, though 201 species showed a reduction in range by more than 1.0%, and 24 species showed less than 1.0% change (see Appendix). Misrepresentation of the geographic distribution of a species, an

effect of modeling with county centroids, was reduced in more widespread species, which had records in many U.S. counties (some examples in Fig. 3.6A through F). The largest predicted area discrepancies were found in species with few records (Fig. 3.7), though not all species with few records showed large discrepancies. Large sample sizes (>100 locality records) reduced the discrepancies. Geographic overprediction tended to be highest in species that had records in counties with high climatic variance, such as western U.S. counties (Fig. 3.3). The median increases in predicted area using county centroids in the western species subsets as indicated in Table 3.2 and the Appendix were 19.2% and 17.9% for BAMONA and OdonataCentral, respectively. The median increases in predicted area in the eastern species subsets were less: -1.7% and 3.0% for BAMONA and OdonataCentral, respectively ( $p = 0.008$ ). No difference in the degree of overprediction using county centroids was found between lentic and lotic Odonata ( $p = 0.520$ ).

The butterfly and odonate models built from a 50/50% mix of true localities and county-centroids significantly outperformed the models built with county-centroids as assessed by the I, D, and RR metrics compared to the models built with true localities. For the butterfly models, the county average models outperformed the county-centroid models as assessed by the I, D, and RR metrics (Wilcoxon signed-rank test  $p = 0.0179$ ,  $p = 0.0061$ , and  $p = 0.0311$  for I, D, and RR, respectively), and for the odonate models, the county-centroid models outperformed the county average models as assessed by the I, D, and RR metrics (Wilcoxon signed-rank test  $p < 0.00001$  for all three metrics). Considering both butterflies and odonates, the lowest and highest RR metrics for a county-centroid model compared to a true locality model were 0.737 and 0.988. The lowest and highest RR metrics for a county-average model compared to a true locality model were 0.751 and 0.996. The lowest metric values were associated with species with few localities.

## Discussion

The small but significant decreases in model training performance metrics (AUC and TSS) are interesting but do not justify the hypothesis that using county-

level data produce poor predicted distributions. These values show that Maxent is capable of fitting models to localities known to be problematic, and some variation in these scores is expected because Maxent can provide slightly different results with each model run. The greater decrease in model performance when county-level models are assessed with the original true localities is more informative, indicating that species distributions are not well represented by models developed with county-level data.

The comparison of strictly eastern and western species demonstrates that overprediction caused by using county-level data is more problematic in western species than in eastern species, where the modeled distribution may not necessarily be increased. This result may be useful for justifying the use of county-level data in bioclimatic SDMs of eastern U.S. species, though caution is still warranted. No difference was found between lentic and lotic odonate SDMs, so this is not a useful discriminator of when county-centroid data may be less problematic.

The greater performance in the 50/50% mix of true localities and county-level data (either centroids or county-average data) as assessed by the niche similarity metrics is an intuitive result, because half of the points used were identical to the true locality models. There does not seem to be a consistent performance benefit to using county average environmental conditions compared to county centroids or vice versa. The predicted range sizes of models built with county average environmental conditions were closer to models built with true locality data for both butterflies and odonates (Table 3.4), but model comparison using I, D, and RR metrics did not show consistent improvement (Table 3.5).

Though this study modeled butterflies and odonates, the results are likely comparable to any taxa. For widespread species with many county-level data points, the risk of inflating the predicted range of a species is small. This may be especially true for lowland eastern U.S. species. It is already known that model accuracy declines with reduced sample size, with model performance declining by as much as

19% when using 10 samples instead of 100 (Wisiz et al. 2008). Model accuracy may be compromised even further for species with restricted ranges, which could have a corresponding low number of potentially unrepresentative county-centroid records. It may be possible to use county-level data to complement true localities for model development, but the models should be interpreted carefully. Without an independent dataset for comparison, expert opinion on distributions and habitat association may be the best means for determining if models including county-level data are improvements to models developed with only true localities (Burgman 2005, Perera et al. 2012).

Modelers who do not intend to use county-level data in their analyses must be mindful that these data may be present in species locality databases without being labeled as such. Diligent vetting of database records will be required to identify localities that represent county centroids, and the mapped location of centroids may vary with county boundary source and calculation method. A similar problem that modelers face is the intentional blurring of localities in some databases (e.g. IUCN Red List, iNaturalist) when it represents an endangered or sensitive taxon. It is also difficult to determine when users, concerned for the welfare of a taxon, intentionally submit inaccurate localities to citizen science databases.

It is important to understand biases that may be present in citizen-science databases. Citizen-science databases are biased toward the locations of active users, because there are seldom going to be attempts to randomize localities or search beyond what is convenient for these users. The data may suggest some areas to be biodiversity hotspots and others depauperate simply because of differences in effort. For the two databases analyzed in this study, contributors are more likely to submit records with actual coordinates if no record existed in a county previously regardless of the precision of that previous record (Table 3.1).

Database users submit records when they perceive they are contributing new information, and contributing records within a county that already has a record in the database may be perceived as inconsequential. This problem could be addressed in

three ways. First, by developing tools that organize data by geographic units other than county, such as watershed, or by providing flight season charts based on existing data, it would be easier for users to identify knowledge gaps in the database. Second, the perceived value of record-submission would also increase by presenting the data in other formats. By making record submission easier, users would be more likely to submit more records, including those perceived to be more mundane. This can be accomplished by improving the web submission process or by developing record-submission applications for mobile devices. Both of these improvements could have the added effect of improving record accuracy. Finally, incorporating more user-centric tools would motivate many contributors. For example, these databases could keep track of user “life-lists” based on submitted records and list the top contributors by country and state. Though “life-list” tools would be expected to have only limited scientific value, they would increase the record submission rate. Providing such incentives is important (Wood et al. 2011), because the questions that can be answered with citizen-science databases are dependent on the number of quality records they contain, and the results of this chapter indicate that SDMs for species with over 100 county-centroid records are relatively accurate. Citizen-science databases should stress the significance of recording specific locality data, because this chapter shows that species distribution models based on county-level data are inherently flawed.

Table 3.1. U.S. county centroids and true localities in digital invertebrate databases.<sup>1</sup>

<b>Database</b>	<b>Taxa</b>	<b>Unique county-only records</b>	<b>Unique true localities<sup>2</sup></b>	<b>County-only records without a true locality within the county</b>	<b>True localities where a county record is present</b>	<b>True localities that were a new county record</b>
BAMONA	Butterflies <sup>3</sup>	177,545	36,200	168,536	27,225	5,911
OdonataCentral	Dragonflies and Damselflies	94,448	48,130	84,787	20,395	21,551
Moth Photographers Group	Moths	386,138	n.a. (not applicable) <sup>4</sup>	386,138	n.a. <sup>4</sup>	n.a. <sup>4</sup>

Notes:

1. Database statuses as of November 2012.
2. Recorded precision of at least 0.005 decimal degrees (WGS84)  $\approx$  555 m.
3. Moth records from BAMONA were not analyzed.
4. Database does not maintain precise locality data.

Table 3.2. Number of species with all records east or west of the 100<sup>th</sup> meridian.

Database	East of 100 <sup>th</sup> Meridian		West of 100 <sup>th</sup> Meridian	
	No. of species	No. of records	No. of species	No. of records
OdonataCentral	75	Median = 28, SD = 24.85	22	Median = 15, SD = 11.01
BAMONA	63	Median = 37, SD = 49.18	60	Median = 14.5, SD = 5.82
OdonataCentral (subset)	22	Median = 15.5, SD = 10.40	22	Median = 15, SD = 11.01
BAMONA (subset)	30	Median = 20.5, SD = 6.20	30	Median = 19, SD = 5.03

Table 3.3. Median and range of model performance statistics for SDMs developed with true localities and corresponding county centroids.

<b>Model Performance Statistic</b>	<b>True-localities SDMs</b>	<b>County-centroids SDMs</b>
Training AUC	0.925 (0.757 to 0.995)	0.915 (0.733 to 0.996)
Training TSS using sensitivity-equals-specificity threshold	0.689 (0.363 to 0.988)	0.667 (0.325 to 0.987)
Training TSS using minimum-training-presence threshold	0.646 (0.011 to 0.988)	0.625 (0.003 to 0.987)
Test AUC	n.a.	0.908 (0.708 to 0.994)
Test TSS using sensitivity-equals-specificity threshold	n.a.	0.646 (0.271 to 0.981)
Test TSS using minimum-training-presence threshold	n.a.	0.592 (0.001 to 0.981)

Note: County-centroid models were tested using true localities as test data to produce Test AUC and Test TSS

Table 3.4. Mean ratio in predicted area relative to predicted area using true localities.

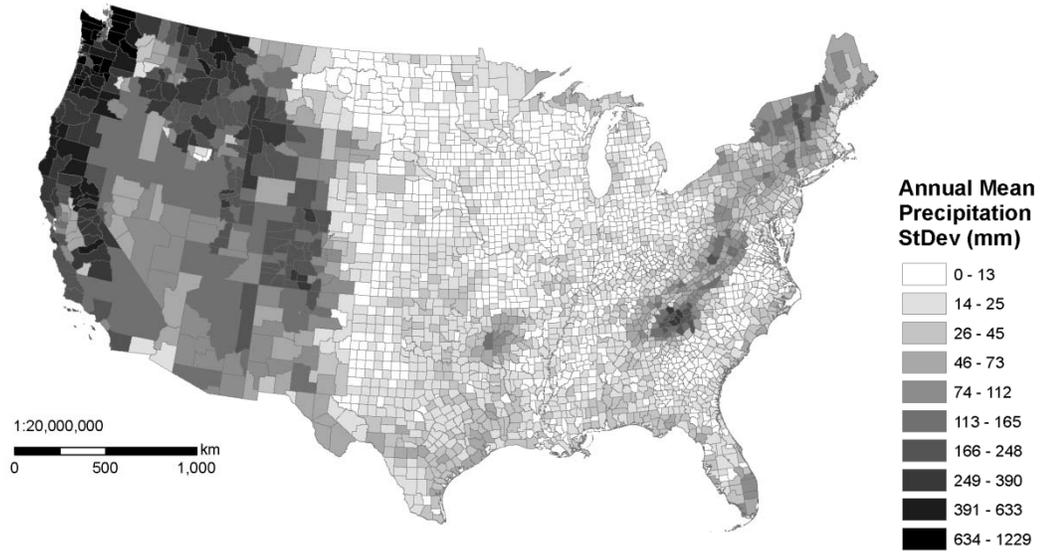
<b>Trial</b>	<b>Equal specificity/ sensitivity threshold (%)</b>	<b>Minimum training presence threshold (%)</b>
BAMONA (n = 230)		
County centroid	106.8	110.5
County average	100.6	101.4
50/50 True locality/ county centroid mix	106.5	109.4
50/50 True locality/ county average mix	102.8	103.3
OdonataCentral (n = 283)		
County centroid	109.4	119.0
County average	100.7	107.9
50/50 True locality/ county centroid mix	105.7	114.2
50/50 True locality/ county average mix	103.3	109.3

Table 3.5. Mean niche similarity metrics compared to true locality models.

<b>Trial</b>	<b>I</b>	<b>D</b>	<b>RR</b>
BAMONA (n = 230)			
County centroid	0.9829	0.8860	0.9188
County average	0.9870	0.8961	0.9247
50/50 true locality/ county centroid mix	0.9915	0.9209	0.9439
50/50 true locality/ county average mix	0.9906	0.9176	0.9349
OdonataCentral (n = 283)			
County centroid	0.9837	0.8917	0.9210
County average	0.9802	0.8810	0.9132
50/50 true locality/ county centroid mix	0.9925	0.9273	0.9475
50/50 true locality/ county average mix	0.9924	0.9264	0.9459

Note: The similarity statistic I, is a metric used to test if models generated from different populations are identical. Schoener's D is a metric describing the level of niche overlap. Relative Rank, RR, is an estimate of the probability that a pair of rasters agree in the relative ranking of any two patches of habitat regardless of the suitability values. See text for interpretation.

A



B

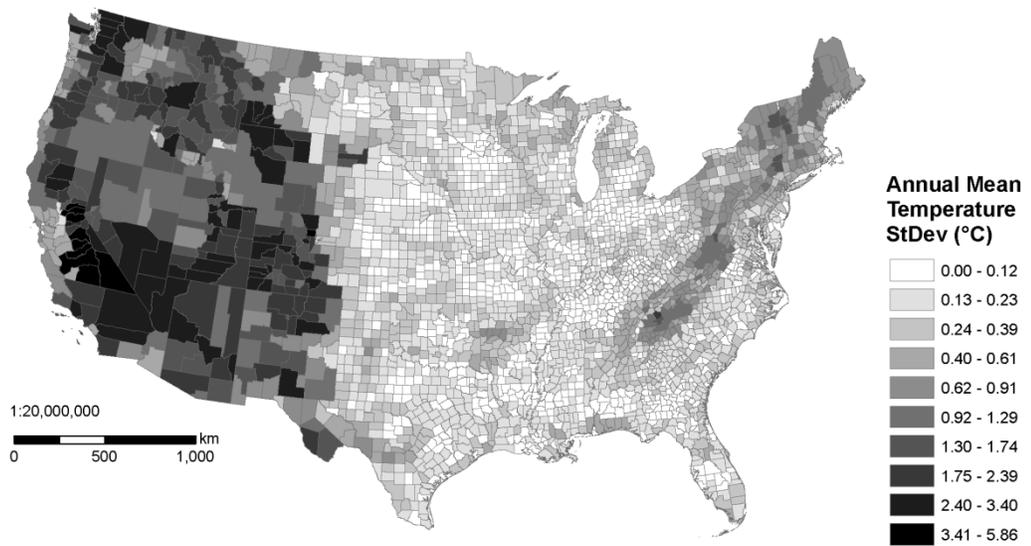
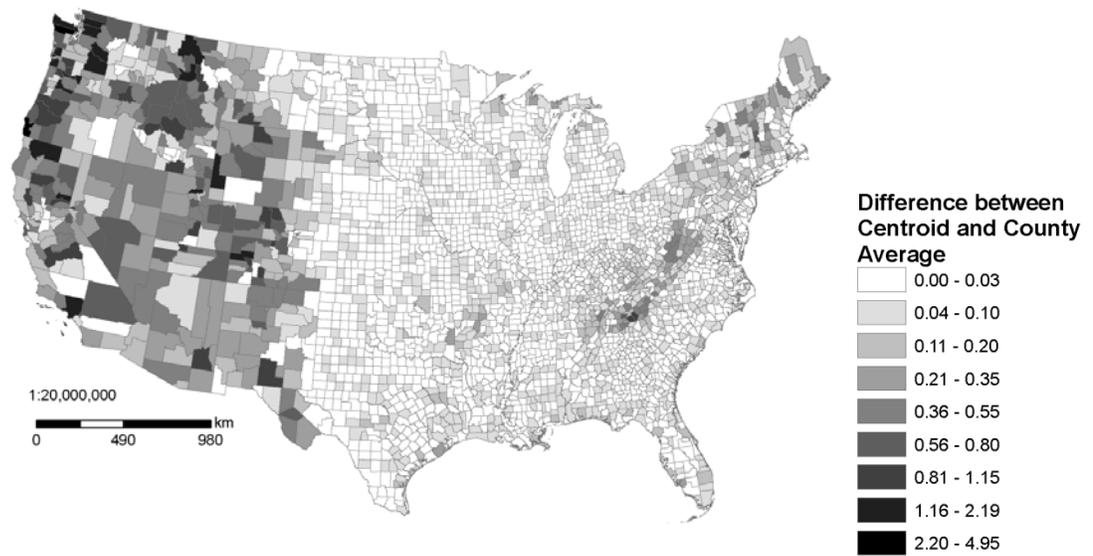
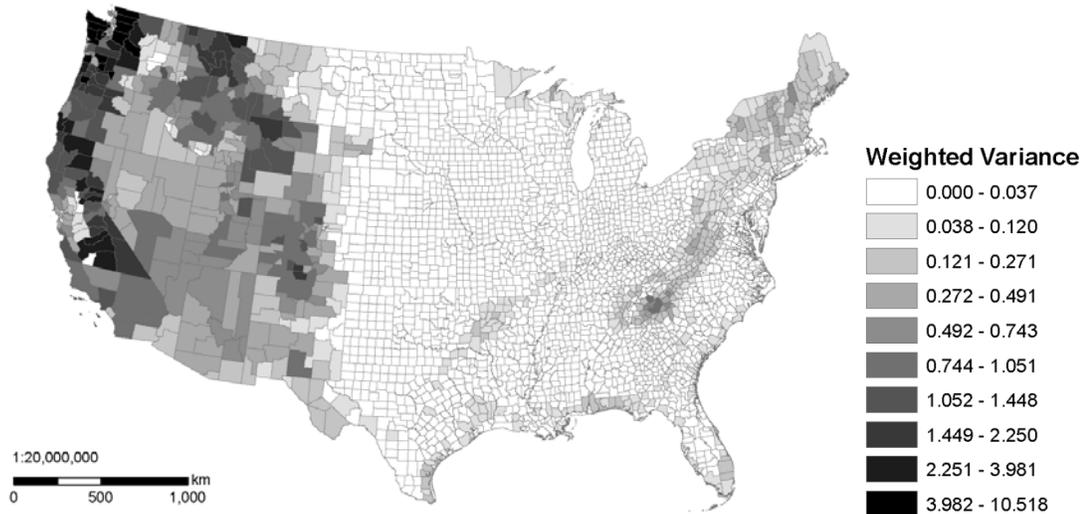


Figure 3.1. Within-county standard deviation of (A) annual precipitation and (B) annual mean temperature in the PRISM dataset within the contiguous U.S.



Note: To develop this figure, a PCA was performed within the contiguous U.S. on 19 normalized bioclimatic variables derived from 30-arcsecond PRISM data. Each component was weighted by the eigenvalue of the PCA to develop an overall climate metric, and the difference between the centroid value and the average value across the county is shown.

Figure 3.2. U.S. county centroids tend to be least representative of average county climate in mountainous and large western counties.



Note: To develop this figure, a PCA was performed within the contiguous U.S. on 19 normalized bioclimatic variables derived from 30-arcsecond PRISM data. The variance of each component across each county was calculated, and the variance values were weighted by the eigenvalue of the PCA to develop an overall climatic variance metric.

Figure 3.3. Climatic variance within U.S. counties is highest in mountainous and large western counties, though not all large counties have varied climate.

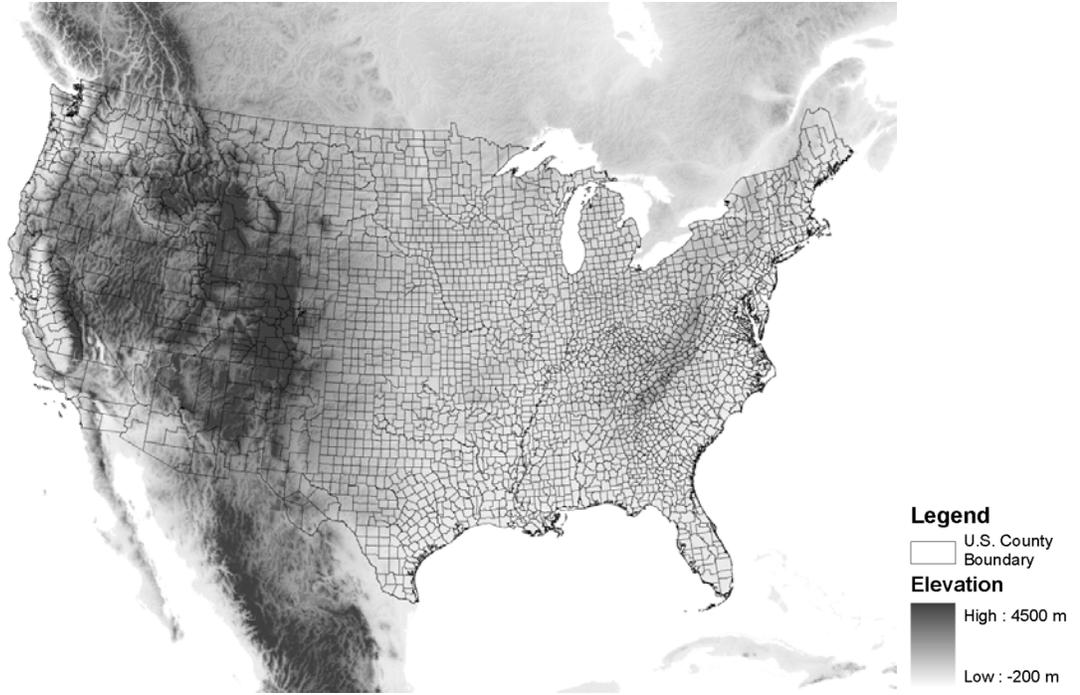


Figure 3.4. The largest U.S. counties containing the largest elevation range tend to be in the western U.S.

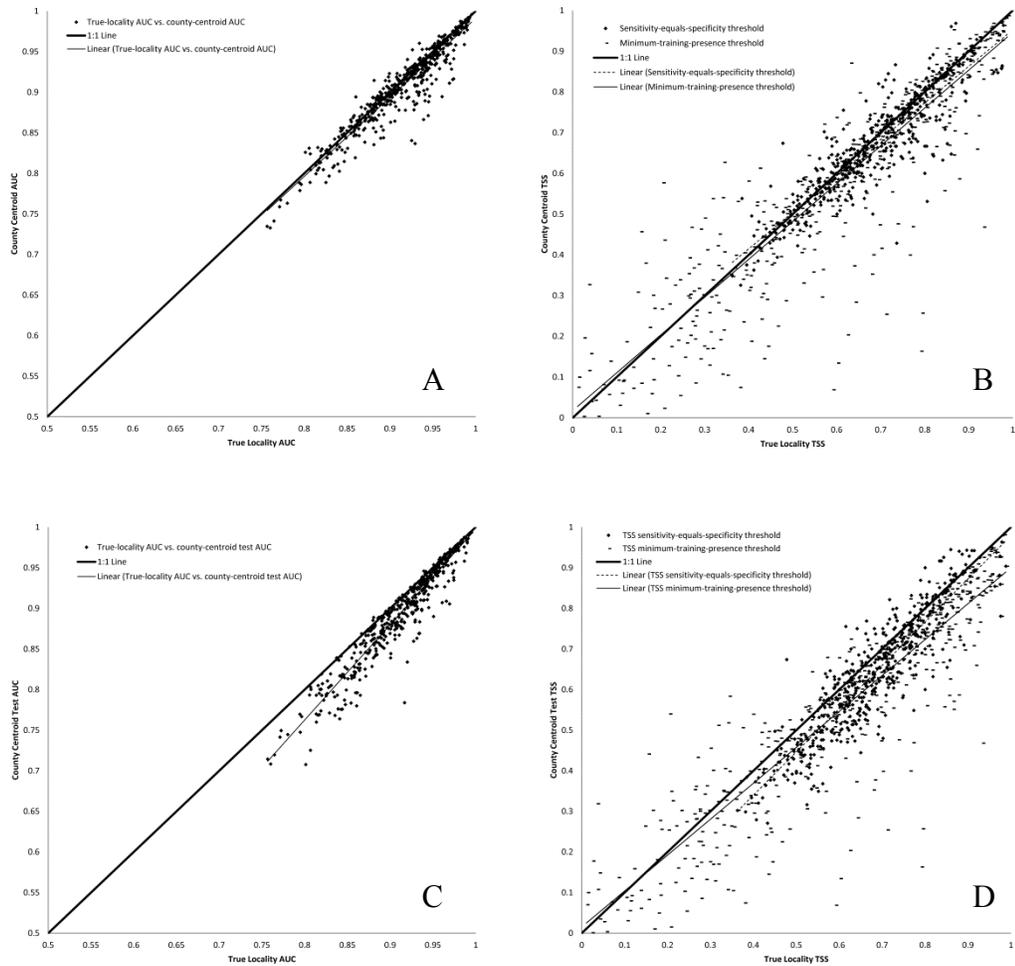
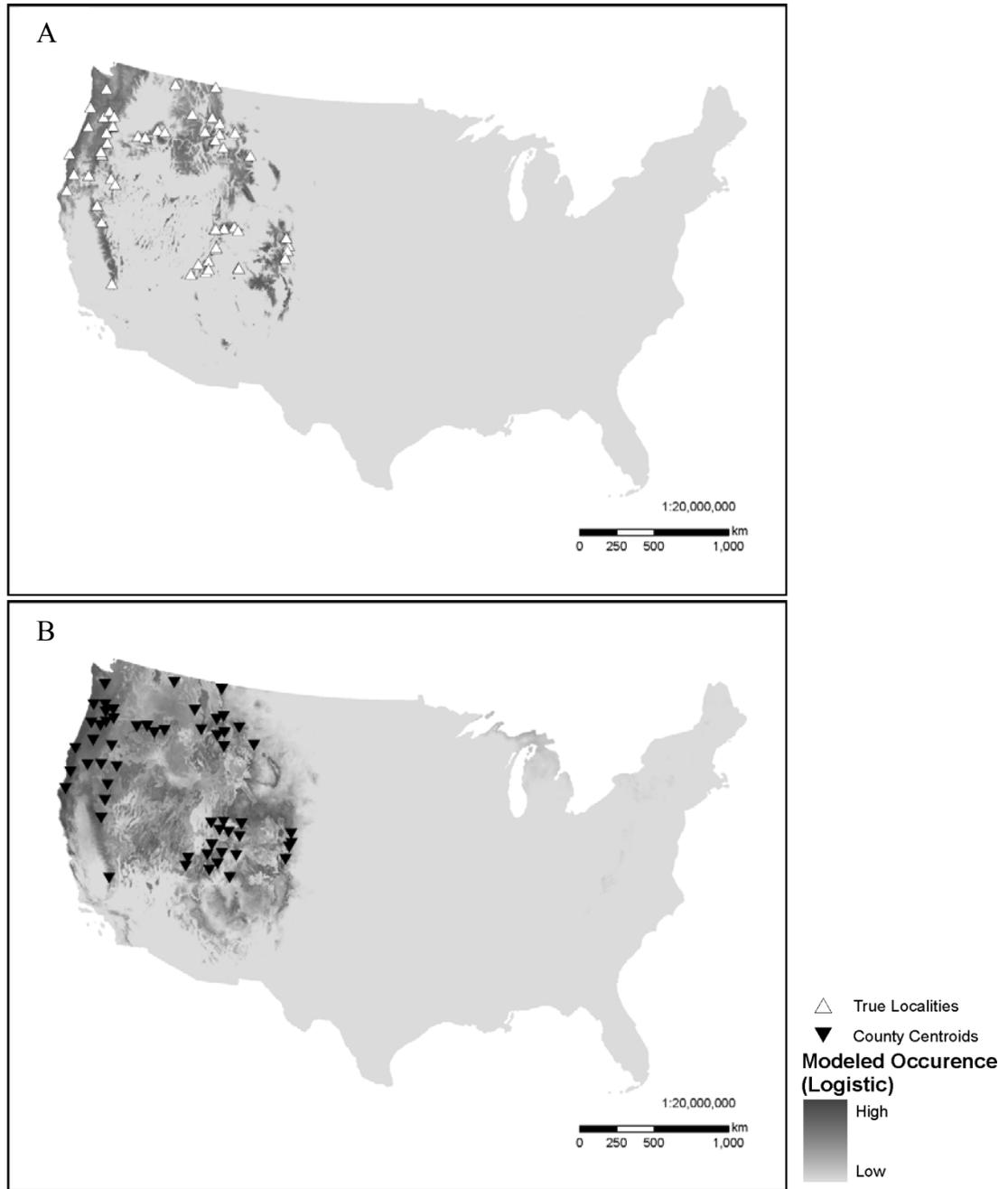
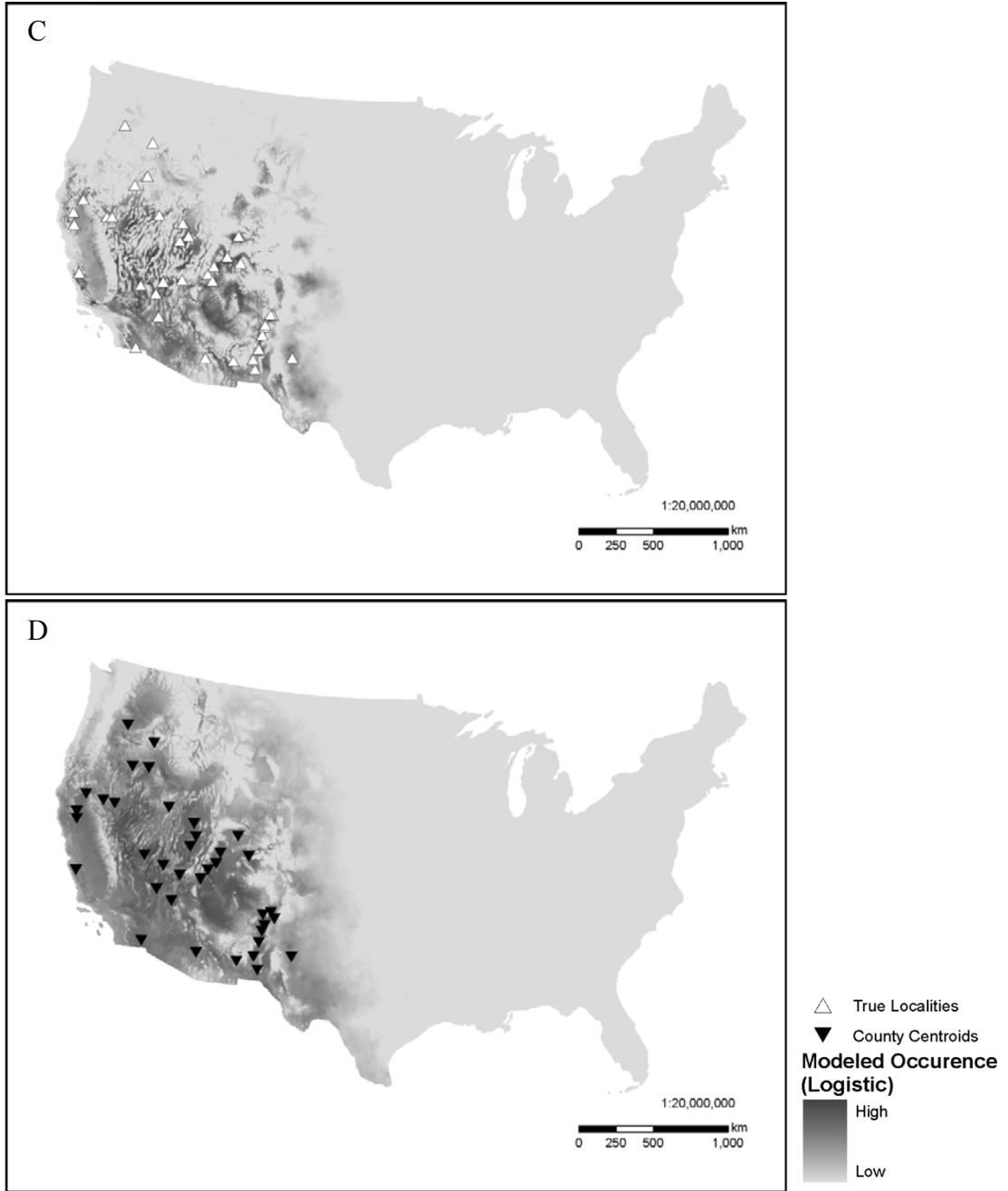


Figure 3.5. Model performance as assessed by (A) AUC or (B) TSS differs between models developed with true localities and models developed with corresponding county centroids. County-centroid models perform more poorly when tested with true localities as assessed by (C) AUC and (D) TSS. Points plotted below the 1:1 lines indicate poorer performance using county centroids. Linear trendlines are included for reference.



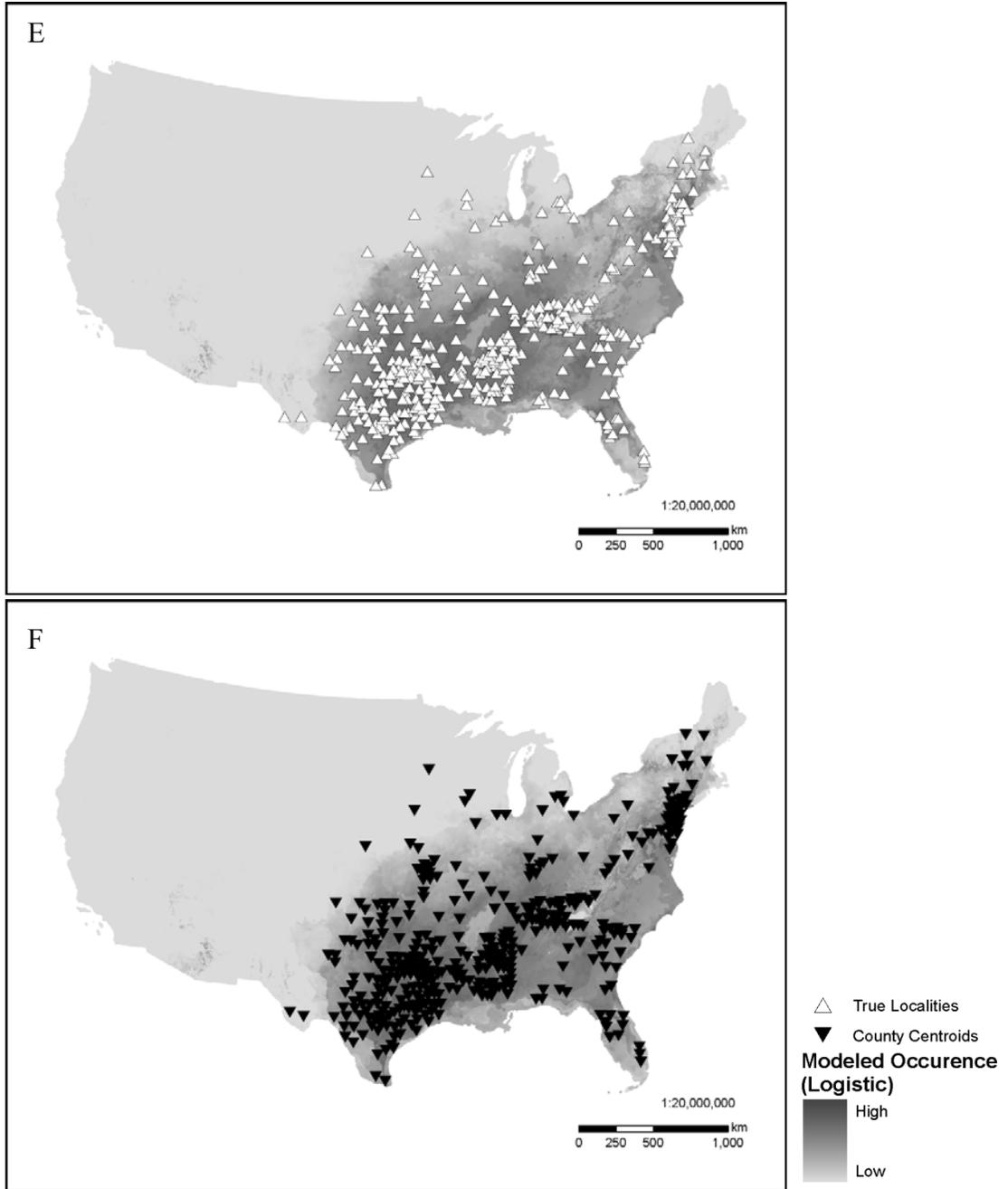
Note: TL = true localities (white triangles), CC = county centroids (black triangles)

Figure 3.6. Predicted ranges using true localities and county centroids for (A) *Somatochlora semicircularis* (n = 55) TL (B) *Somatochlora semicircularis* (n = 55) CC (C) *Erpetogomphus compositus* (n = 37) TL (D) *Erpetogomphus compositus* (n = 37) CC (E) *Ischnura posita* (n = 423) TL (F) *Ischnura posita* (n = 423) CC



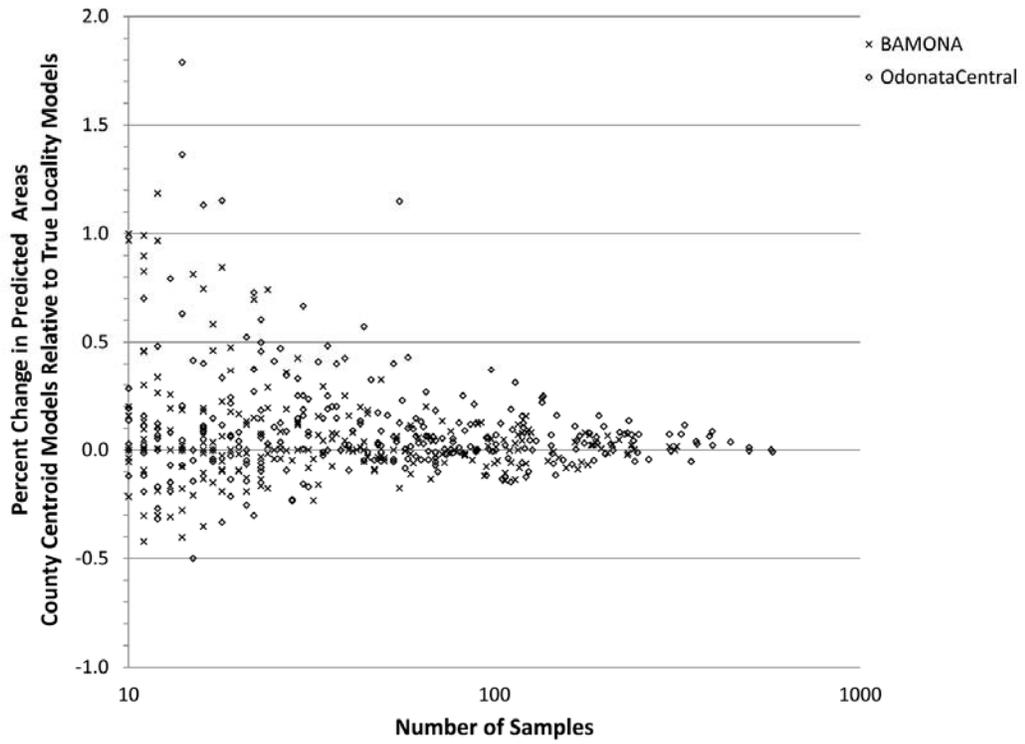
Note: TL = true localities (white triangles), CC = county centroids (black triangles)

Figure 3.6. Continued.



Note: TL = true localities (white triangles), CC = county centroids (black triangles)

Figure 3.6. Continued.



Note: The comparison was made using the sensitivity-equals-specificity threshold for predicted area.

Figure 3.7. The discrepancy in predicted area using U.S. county centroids relative to true localities is greatest for species with few locality records.

## CHAPTER IV

# IMPACT OF SCALE, TEST DATA, AND BACKGROUND SELECTION ON RIVERINE SPECIES DISTRIBUTION MODEL PERFORMANCE

### **Abstract**

Species distribution models (SDMs) often assume that bioclimatic variables are adequate surrogates for environmental data at smaller scales that may otherwise be unavailable. The scale-sensitivity of SDMs was examined by comparing models built with data at each of three scales (bioclimatic, catchment and reach) for stream-obligate Odonata (dragonflies and damselflies) in Maine, USA. This chapter also examined whether using cross-validation (typical for testing the fit of modeled distributions) was comparable to testing SDMs against independent data from beyond the spatial extent of the model (in this case, training with data from Maine and testing with resampled data from Maine versus independent data from New Hampshire). Choice of the standard units for background selection in riverine SDMs was compared, and using river reach segments instead of raster cells improved model performance. Reach- and catchment-scale variables out-performed bioclimatic variables in both training and testing, and this was determined not to be attributable to over-fitting of a greater number of reach- and catchment-scale variables compared to bioclimatic ones. Models tested with cross-validation procedures out-performed models tested with independently collected data, suggesting an inherent bias in cross-validation procedures. Drainage area, water velocity and slope were the most important variables explaining the distribution of lotic Odonata in Maine and New Hampshire, and even when the most influential of these variables (drainage area) was removed, the remaining reach-scale variables still out-performed bioclimatic ones. The results indicate that customary procedures for modeling species distributions for riverine conservation management may be inadequate.

## **Introduction**

Species distribution models (SDMs) operate by analyzing environmental conditions at known locations of a species to determine which environmental variables are the best predictors of the species' distribution and to formulate relations between those environmental variables and species occurrence. These relations can then be projected to unsurveyed regions to generate predictive maps of potentially suitable habitat for a given species. Most SDM studies focus on defining species distributions using climatic metrics derived from historical temperature and precipitation data as environmental predictors (Huntley et al. 2010), a practice known as bioclimatic niche modeling. This practice assumes that climatic variables are adequate surrogates for environmental data from smaller scales that may otherwise be unavailable, in contrast to climate data that are readily available from a variety of sources [Worldclim (<http://worldclim.org>), PRISM (<http://www.prism.oregonstate.edu>), Earth System Grid (<http://www.earthsystemgrid.org>)]. Though some have suggested that physical variables from smaller scales can be explained by climate and have dismissed their use in species distribution modeling (Pearson and Dawson 2003), incorporating fine-scale variables has the clear benefit of increasing the spatial resolution of predicted distributions. The finest resolution of most climatic data, such as PRISM, is 30 arcseconds, which is approximately equivalent to a 1-km cell size, yet other gridded environmental data may be as fine as 30 meters. Moreover, climate data may be too coarse to do an adequate job of explaining species-habitat relations in discretely bounded habitats that occupy a relatively small proportion of the landscape, such as rivers and riparian areas.

Rivers and riparian areas encompass a small proportion of Earth's surface (0.8%), yet they contain a disproportionate number of known species (>6%) (Vorosmarty et al. 2010). Additionally, 65% of global water discharge and the habitats it supports is under a moderate to high threat (Vorosmarty et al. 2010). As many as 10,000 freshwater invertebrates have gone extinct or are highly imperiled because of human activities (Strayer 2006). Quantifying the current distribution of

riverine organisms is a necessary step toward preserving the biodiversity and ecological functions of rivers before they are lost. Bioclimatic niche modeling may not fully capture important processes controlling the distribution of such taxa, which are also dependent on watershed and local conditions (Hopkins and Burr 2009). The environmental variables important to riverine organisms can thus be classified as broad-scale climatic variables, catchment-scale variables describing the watershed upstream of a river segment and local-scale variables describing conditions specific to a single river segment and its riparian area.

To include catchment and local conditions, variables describing the topography, geology, soils, vegetation or hydrology can be used to develop the predicted distribution. Suitable habitat for river organisms may also be defined in terms of variables reflecting anthropogenic influences and nonpoint source pollution, such as indices describing agriculture and development within the watershed of a river reach. These variables may be proxies for known mechanisms driving species distributions, because the causal mechanisms are often not readily quantifiable (Dormann 2007), but they can be useful. Including these environmental attributes that characterize the habitat of a species often serves to restrict the distribution compared to a bioclimatic prediction, and the restricted distribution is considered the realized niche (Brereton et al. 1995). SDMs already can improve the cost-effectiveness of biological surveys by focusing efforts (Busby 1991) and can identify areas for conservation (Rodríguez et al. 2007), but taking a multi-scale approach to species distribution modeling permits management on the much narrower scale of specific river reaches, which can be prioritized for future surveys, conservation and restoration.

Scale also is at issue when testing the fit of modeled distributions. The two standard methodologies—resampling training data (i.e., cross-validation) or using data not used to train the model—may not be equivalent. Ten-fold cross-validation may be one of the best resampling methods (Kohavi 1995), but cross-validation inflates the AUC performance metric because of biases in the training dataset (Hijmans 2012). For this reason, using an independently-collected dataset unlikely to have the same

biases as the training dataset is ideal (Phillips et al. 2009). Ten-fold cross-validation of the Maine training data was compared to an independent test dataset collected in an adjacent U.S. state, New Hampshire, a novel means of validation, to determine if ten-fold cross-validation provides biased results.

Presence-only modeling methods contrast the environmental conditions at presence locations with the environmental conditions at a sample of background locations. The background samples are sometimes called pseudoabsences (Phillips et al. 2009). Previous work has shown that 8,000 background locations is sufficient for robust models (Phillips and Dudik 2008). By default, `Maxent` (one of the most commonly used software packages used to construct SDMs; Elith et al. 2010b) selects a random sample of 10,000 locations from the gridded environmental background, which assumes that that presence data are a random sample of space (Merow et al. 2013). An altered background selection approach can be used to provide an ecologically relevant limit the extent of the background sample (VanDerWal et al. 2009, Anderson and Raza 2010, Elith et al. 2010b, Barve et al. 2011) or to compensate for a known sampling bias among the presence locations (Phillips et al. 2009, Syfert et al. 2013). Riverine SDMs can be constructed by representing rivers as raster cells and restricting the background to these rasterized networks, a “landscape-masked” design (Domisch et al. 2013b), or by treating river segments as the basic unit for background selection and prediction (Fig. 4.1). Presence localities, environmental data and predictions are associated with rivers and not necessarily raster cells in riverine SDMs, so river segments may be the natural choice of background, but the two background selection approaches have not been compared. Furthermore, the effect of increasing the number of background locations has not been tested for riverine SDMs.

To what degree SDMs are scale-sensitive was examined by comparing models built with data at each of three scales (bioclimatic, catchment and river reach) for a model group of riverine organisms. As a relatively well-collected order of insects, Odonata (dragonflies and damselflies) are ideal representatives of riverine biota. These amphibious insects are diverse, occupy high trophic positions and exhibit

species-specific habitat requirements; collectively, these traits make them sensitive and charismatic enough to be considered a “flagship” group of aquatic species indicating environmental and biotic health (Oertli et al. 2002). The habitat requirements of riverine Odonata are an integration of climate, riparian quality and local aquatic conditions, which are a function of the upstream watershed. In this chapter, 22 lotic Odonata species are used to demonstrate the importance of two aspects of developing SDMs on the riverine scale that may otherwise be overlooked: the choice of testing method and the impact of background selection. These species are also used to assess which scale of environmental data is most important for describing the distribution of riverine biota: climate, catchment or local.

## **Methods**

### ***Odonate data sources***

Odonate data used to train the SDMs were obtained from the Maine Damselfly and Dragonfly Survey (MDDS), a six-year survey initiated by the Maine Department of Inland Fisheries and Wildlife and conducted by volunteers (Brunelle and deMaynadier 2005). Only data collected between 1991–2009 were used for this study so as to minimize effects from land-use and climate change that are more likely to accumulate when examining a longer span. Odonate testing data were obtained from the New Hampshire Dragonfly Survey (NHDS), a five-year survey (2007–2011) funded by State Wildlife Grants to the New Hampshire Fish and Game Department and conducted by volunteers. All records in the MDDS and NHDS were confirmed by experts. Both of these databases included localities for Odonata nymphs and adults. Focal species for this study were those restricted to flowing water that have ten or more unique locality records within both the MDDS and NHDS. There were 22 lotic species that fit these criteria (Table 4.1).

Several issues must be considered when modeling at very fine resolutions such as individual river segments. The known species locality data must be carefully vetted to only include localities with a precision less than the chosen resolution. Known

localities used in species distribution modeling are often opportunistic, and their precision is often not recorded, so methods have been developed to estimate precision (Wieczorek et al. 2004). If the number of precise localities is insufficient for modeling, it may be best to resample the environmental data to a resolution that is capable of making the best use of available localities.

The chosen resolution must also have an ecological significance for the species being modeled. The greatest model performance may be achieved at a resolution equivalent to species home range (Graf et al. 2005). Localities that record dispersing organisms from source sites in unsuitable habitat may reduce model performance (Heino 2013), though Maxent and Boosted Regression Trees have been shown to be robust to moderate spatial error in species localities (Graham et al. 2008). A “mass effect” is when this dispersal rate is high enough to cloud effects of environmental control over what appears to be suitable habitat versus what is unsuitable (Heino 2013), and in those cases, the assumptions of species distribution modeling are unsupported. These types of location errors are likely to be more important when using fine-scale environmental data that may contain dramatically different values between adjacent habitats, such as land cover, compared to using climatic data, which are less likely to show such strong heterogeneity.

In this study, the finest spatial resolution used was the river reach. A reach is defined as a stream or river segment between the confluence with a tributary, lake, marsh or swamp and the following confluence. The dendritic network used for this project is the National Hydrography Dataset (NHD), which is a comprehensive set of vector data representing rivers, streams and other waterbodies within the coterminous United States. The NHD was originally produced from USGS hydrologic digital line graph files, which were derived from USGS quadrangle maps, so the definition of river segments is a consequence of those data. The dataset contains 29,983 river segments in Maine, which have an average length of 1.75 km, and 12,118 river segments in New Hampshire, which have an average length of 1.46 km.

To associate species data (typically collected on land) to the appropriate reach, the georeferenced coordinates of all target species localities from the MDDS and NHDS databases were moved in a downslope direction to the closest river reach with TauDEM (<http://hydrology.usu.edu/taudem/taudem5/>). The accurate coordinates for a locality may be the bank of a wide river where the river centerline is farther away from the bank than nearby tributary confluences, so this process better associated each locality with its correct river than a nearest-line analysis would have. All localities moved more than 100 m by TauDEM were checked against the written description of the locality and moved manually to the correct location if required. Localities that could not be resolved with the river network were omitted. Histograms of catchment area for each species' localities were made, and the written descriptions of outlier localities were checked. Locations were only corrected if the written description justified it. The databases were filtered so no species had more than one record per river reach. The earliest species record from each reach was retained.

### ***Environmental data***

All environmental data and species localities were reprojected to NAD\_1983\_Albers to avoid the cell-size bias with latitude present in the native projections of these data. Broad-scale data included bioclimatic (bioclim) variables derived from monthly values of maximum and minimum temperature and precipitation from the PRISM 30-arcsecond climatology normals (1971–2000) gridded dataset (<http://www.prism.oregonstate.edu>). PRISM was chosen because it is more physiographically sensitive than WorldClim (another source of data often used in SDMs; e.g. Fitzpatrick et al. 2013; Seo et al. 2009; Syfert et al. 2013) and performs better in mountainous regions (Daly et al. 2008). Some researchers have argued that using bioclim data is appropriate for SDMs because at large spatial scales, climate is the ultimate driver determining the physiological niche (Pearson and Dawson 2003). With respect to variables important for stream biota, air temperature may be used as a surrogate for water temperature, because both are strongly correlated (Caissie 2006), and precipitation partly determines discharge and consequently the microhabitat

structure available within river reaches (Buisson et al. 2008b). Therefore, bioclim variables should have adequately represented the climate experienced by riverine species.

Catchment-scale data summarize the geology, soils and land use present in the upstream watershed of each river reach. These variables are often surrogates for microhabitat variables that cannot be quantified easily for SDM purposes, though some catchment-scale variables have been shown to be able to predict microhabitat variables important for fish (Mugodo et al. 2006). These predictors are likely to favor the determination of in-stream habitat for Odonata nymphs over adult habitat. Drainage area is the primary catchment-scale variable that reflects habitat capacity and thus population size through extinction dynamics from a classical biogeographic perspective (MacArthur and Wilson 1967). Drainage area is also an indicator of position within a dendritic network, which has been shown to be directly related to aquatic insect diversity (mayfly, stonefly and caddisfly), with well-connected, central communities having greater diversity than more peripheral communities, regardless of local environmental conditions (Altermatt et al. 2013). Underlying geology in watersheds is important to the distribution of benthic macroinvertebrates (Cannan and Armitage 1999), and the inclusion of soil data has been shown to improve model results for insects like butterflies and grasshoppers (Titeux et al. 2009). Predictors, such as geological hardness (percent alluvium in watershed or geological permeability), may also help explain sediment grain size (Snelder et al. 2011), an important microhabitat variable for benthic taxa. Land use is also important at smaller scales (Pearson and Dawson 2003, Pearson et al. 2004) such as the scale of this study. Land use can impede a species from occupying part of its range, suggesting the species is not filling its climatic niche when it actually does (Dormann 2007). Furthermore, benthic macroinvertebrates including Odonata are known to be sensitive to metals that accumulate in streams from surface runoff from impervious surfaces such as roads (Beasley and Kneale 2003) and to pesticides in agricultural runoff (Beketov et al. 2013). Riparian buffers reduce the impact of upstream non-point

source pollution, so agriculture and development inverse buffer widths, indices that consider the pollutant- and nutrient-intercepting properties of forest or wetland riparian buffers when accumulating land use characteristics to river reaches (Baker et al. 2006), were also accumulated for each river reach. Most catchment-scale data were developed with the CA3T NHDPlus Catchment Attribute and Allocation Tool, which allocated and accumulated 30-m raster data describing a variety of environmental variables to individual river reaches, though some catchment-scale data such as 2001 NLCD land use summaries were used as provided by NHDPlus (Table 4.2).

Reach-scale data are local-scale data specific to an individual river reach, where reaches are as defined by the NHD. Water velocity estimates for each river segment were taken from NHDPlus, and those estimates were based on an empirical relation defined by drainage area, mean annual discharge, slope and field discharge measurements (Jobson 1997). Slope for each river segment in NHDPlus was determined from elevation data and a smoothing method that ensured all river segments had a slope  $\geq 0$ . Those river segments intersecting natural or artificial ponds and reservoirs were labeled with a boolean impoundment variable. This variable was included because proximity to dams can influence species distributions by altering hydrologic, sediment, and temperature regimes (Han et al. 2009). Riparian composition was determined with the Zonal Statistics function and 30-m raster data in ArcGIS based off of a 100-m buffer from the river centerline (or the river banks of wide river segments provided as polygons in the NHD) (Table 4.2). These predictors are likely to be useful in determining both in-stream habitat for Odonata nymphs and adult habitat.

### ***Model construction***

Species distribution models were developed in Maxent v.3.3.3k (Phillips et al. 2006) for 22 species of lotic-obligate Odonata within Maine. Maxent is considered one of the most reliable methods for building SDMs, especially when used with limited or biased locality data (Hernandez et al. 2006, Pearson et al. 2007, Wisz

et al. 2008). Default parameters for feature creation, regularization, and prevalence were used.

A Pearson's correlation matrix was calculated within Maine for all environmental layers (Tables 4.2, 4.3). It was found that the strongest correlations were between environmental layers within the climatic and catchment-scale datasets. For all pairs of environmental layers with Pearson's correlation coefficients greater than 0.8, only one layer was retained for modeling (Rinnhofer et al. 2012). To determine which layer to include, models were developed with all 44 environmental variables and for each correlated pair, the variable more often selected by Maxent for the 22 target species was retained for modeling. Using this approach, 17 variables were excluded from modeling (Table 4.3).

### ***Model testing***

There are two ways in which species distribution models are usually tested: via cross-validation (iteratively withholding a portion of the data used to train the model) or less commonly with an independent dataset (data not used to train the model) (Araújo et al. 2005a, Araújo and Guisan 2006, Elith et al. 2006). These techniques were compared, because cross-validation may inflate model performance metrics because of spatial autocorrelation of training and test datasets (Araújo et al. 2005a, Veloz 2009), yet independently collected datasets are not necessarily independent of the biases in the training dataset even though that is generally assumed (Hijmans 2012).

For both techniques, model performance was assessed with the AUC metric, a standard technique for distribution models based on presence-only data (Guisan and Zimmermann 2000). AUC is a threshold-independent measure of model performance (Hanley and McNeil 1982), where performance is assessed as the ability of the model to discriminate between species occurrence and absence. AUC values range from 0.5, representing a model that discriminates no better than random, to 1 (unity), representing perfect discrimination. The AUC metric is advantageous over other

methods (e.g. the kappa metric) because it is not biased by species prevalence (Fielding and Bell 1997).

A ten-fold cross-validation resampling technique (Fielding and Bell 1997, Araújo et al. 2005a) was used to generate ten models for each species, withholding a different 10% of the training localities each time to be used as test data. This method illustrates how sensitive the models are to training locality selection. It is assumed that if a model trained on a portion of dataset predicts the withheld portion of the dataset or if the output variance using a resampling technique is low, then the efficacy of the model has been demonstrated (Smith 1994). However, a subdivided dataset maintains the same biases, if any are present, so the evaluation tends to overestimate the predictive performance of the model to new observations (Edwards et al. 2006).

SDMs also can be tested with an independent dataset, especially when collected in areas not sampled during original model development, to ensure results are sound and are not influenced by potentially biased species location data (Fielding and Bell 1997, Barry and Elith 2006). Testing predictions against an independently collected dataset is rare in species distribution studies (but see Franklin 2002, Elith et al. 2006, Phillips and Dudik 2008, Wisz et al. 2008), and some have suggested this approach is practically impossible when SDMs are developed from museum data (Tognelli et al. 2009). Model performance in this study was assessed with an independent test dataset, the New Hampshire Dragonfly Survey (NHDS), by projecting each modeled species distribution to the adjacent state of New Hampshire. Maine and New Hampshire share similar climates and habitats, so the projection did not include considerably novel environmental conditions. A multivariate similarity surface (MESS) analysis (Elith et al. 2010a) indicated that four New Hampshire river segments containing test localities represented a novel environment where at least one variable was more than 10% outside of its training range. All New Hampshire testing localities that fell within these river segments were excluded from the testing dataset.

### ***Overfitting***

Overfitting occurs when a best-fit model includes the noise in the training data in addition to the core relations with environmental variables and can lead to a misleadingly good fit to the data (Vaughan and Ormerod 2005). Independent test data measures both how well the model generalizes to new environments and the impact of overfitting, whereas resampling techniques only assess overfitting (Harrell et al. 1996, Vaughan and Ormerod 2005). The 27 selected environmental variables may permit the model to overfit, so to measure the impact of overfitting, the number of environmental variables was reduced, and the training AUC and test AUC (using the NHDS) were compared between model runs. Environmental variables with less than 5% contribution to any of the 22 Odonata species models were removed, leaving 18 environmental variables. Another trial was performed where environmental variables with less than a 10% contribution to any of the species models were removed, leaving 11 environmental variables. Ten-fold cross-validation resampling was also performed with all three selections of environmental variables (27, 18 and 11) to assess overfitting.

### ***Background selection***

Presence-only SDM methods, such as *Maxent*, select background points from the modeled extent to represent the range of available environmental conditions (Phillips et al. 2009). When using gridded environmental variables, *Maxent* randomly selects 10,000 background points by default. Catchment-scale and local-scale river reach variables can be represented in a gridded dataset by converting the dendritic network into raster cells so long as all upland, non-river cells are masked out of the analysis. It is important to note that predicted suitability of a river reach does not mean that there is suitable microhabitat throughout that river reach, as macroinvertebrates are unevenly distributed in these environments (Boyero 2003). When using the gridded background approach, care must be taken to select a raster resolution fine enough that no short river segments are excluded from analysis. For the current study, a raster resolution of 30 m was used, which is also the native

resolution of many data sources of environmental variables (Table 4.2). Additionally, species localities must be located on river reach centerlines within that resolution tolerance so that river reach environmental variables are correctly associated with each locality. Background points are selected randomly, so river reaches were sampled proportionately to their prevalence on the landscape, meaning that longer river reaches were sampled more heavily than shorter ones.

Many riverine taxa are constrained by their dendritic network, and it has been argued that modeling these species at the scale of local river reaches is more appropriate than homogenous geographic grids (Buisson et al. 2008b). This suggests that treating each river segment as a discrete unit for both species occurrence, as was done in this study by only including one species locality per river reach, and when selecting background points, may produce more robust models compared to using gridded data. To test which method of background selection produces more robust models, four background selection methods were compared by examining training AUC values (Maine localities) and by test AUC values using the independently collected NHDS as test data. These background selection methods were (1) 9,983 background points randomly selected from 30-m raster grids masked to the NHD river network; (2) 29,983 background points randomly selected from 30-m raster grids masked to the NHD river network; (3) 9,983 randomly selected river segments with one background point per river segment; and (4) all 29,983 river segments in Maine with one background point for each river segment.

### ***Testing for scale effects***

The 27 selected environmental variables are organized into nine bioclim variables, nine catchment-scale variables describing the upstream watersheds of each NHD river segment and nine local-scale variables describing the immediate environment of each river segment (Table 4.2). These scaled sets were used to test which scale was the most important for developing SDMs for riverine biota. Four models were developed for each of the 22 target Odonata species: one using all environmental layers and three using only the environmental layers from each scale

set. Models were evaluated both with training AUC and with test AUC using the independently collected NHDS as test data. The test AUC indicated which models were most robust. It was expected that this analysis would be sensitive to variable selection, where scale sets that include variables allowing for parsimonious discrimination will perform better than other scale sets. To test this sensitivity, scale-specific models were developed excluding the variables that provided the highest model contribution across all species for that scale set. The training and test AUC of these reduced datasets were compared to see if the conclusions about the importance of each scale set held fast.

### ***Statistical tests***

Wilcoxon signed-rank tests were used to compare evaluation metrics among different modeling approaches, pairing by species in all cases. The signed-rank test is widely used for AUC comparison in SDM studies (Araújo and Luoto 2007, Phillips et al. 2009, Reside et al. 2010, Fitzpatrick et al. 2013).

## **Results**

### ***Model testing***

The median ten-fold cross-validated training AUC across the 22 focal Odonata species was the same as the training AUC for a single model run using all training localities, 0.978 (Wilcoxon signed-rank test p-value = 0.054). The median cross-validated test AUC (0.932, max = 0.991, min = 0.847) was higher than the test AUC using the NHDS for the same species (0.849, max = 0.986, min = 0.718). The difference in test AUC between using ten-fold cross-validation and the NHDS data was considerable (max difference = 0.204, min difference = -0.006) (Wilcoxon signed-rank test  $p < 0.00001$ ) (Fig. 4.2).

Removing test localities from four river segments, where the MESS analysis indicated the model was extrapolating more than 10% beyond at least one training variable, impacted 11 of the 22 focal species. For these 11 species, removing the test

localities reduced the test AUC in ten species, and the average difference was 0.002 (Wilcoxon signed-rank test  $p = 0.005$ ).

### ***Background selection***

When selecting background points from regular gridded datasets, increased background points improved the models in terms of training AUC (Wilcoxon signed-rank test  $p = 0.036$ ), but not in terms of test AUC (Wilcoxon signed-rank test  $p = 0.074$ ). When selecting background points using NHD river segments as the standard unit, increased background selection improved both the training AUC (Wilcoxon signed-rank test  $p = 0.008$ ) and test AUC (Wilcoxon signed-rank test  $p = 0.0009$ ) as listed in Table 4.4. There was an improvement in model performance when using river reach segments as the standard unit compared to raster cells for training AUC (Wilcoxon signed-rank test  $p = 0.0003$  for 29,983 background points,  $p = 0.0004$  for 9,983 background points), but not for test AUC (Wilcoxon signed-rank test  $p = 0.75020$  for 29,983 background points,  $p = 0.357$  for 9,983 background points) as listed in Table 4.4.

### ***Scale of environmental data***

Model performance as determined by training AUC for 22 riverine Odonata in Maine was greatest for models using all 27 independent environmental variables (median AUC = 0.978) as shown in Fig. 4.3. When comparing models developed with only climate data, catchment-scale data, or local reach-scale data, the reach-data models performed better than the catchment-data models in terms of test AUC (Wilcoxon signed-rank test  $p = 0.002$ ), but not in terms of training AUC (Wilcoxon signed-rank test  $p = 0.388$ ). The catchment-data models performed better than the climate-data models both in terms of training AUC (Wilcoxon signed-rank test  $p < 0.00001$ ) and test AUC (Wilcoxon signed-rank test  $p = 0.0005$ ). Though the training AUC for models built with all environmental variables was greater than the training AUC for reach-data models (Wilcoxon signed-rank test  $p < 0.00001$ ), the test AUC for reach-data models was greater than the test AUC for models built with all environmental variables (Wilcoxon signed-rank test  $p = 0.014$ ).

For most focal species, drainage area, water velocity and reach slope were the three greatest-contributing variables for models built with all variables. When the greatest-contributing variable to the catchment-scale models across all target species, drainage area, was omitted, median training AUC fell from 0.945 to 0.924, and median test AUC fell from 0.836 to 0.799, though both were still greater than the training and test AUCs for climate-data models. When the greatest-contributing variable across all species for the reach-scale models, water velocity, was omitted, median training AUC fell from 0.952 to 0.884 and median test AUC fell from 0.906 to 0.856. The reduced test AUC for the reach-data models without water velocity was not significantly different from the test AUC using all 27 environmental variables (Wilcoxon signed-rank test  $p = 0.503$ ) or from the test AUC for catchment-data models (Wilcoxon signed-rank test  $p = 0.262$ ). When both water velocity and reach slope were omitted from the reach-data models, the training and test AUCs dropped to 0.828 and 0.821, respectively. The reach-data model without water velocity or reach slope is not significantly better than the climate-data model in terms of training AUC, but it is in terms of test AUC (Wilcoxon signed-rank test  $p = 0.0002$ ).

### ***Overfitting***

The median cross-validated test AUC was 0.932 (max = 0.991, min = 0.847) when using all 27 independent environmental variables. A reduction in cross-validated test AUC of 0.044 compared to the training AUC (max reduction = 0.086, min reduction = 0.006) indicates the model may be modestly overfit for some species (Fig. 4.2). The median cross-validated test AUCs for the 9-variable bioclim, catchment- and reach-scale SDMs, 0.750, 0.910 and 0.927, respectively, are lower than the corresponding median cross-validated training AUCs, 0.853, 0.943 and 0.952, which indicates different degrees of overfitting for some species. Of the three scales (bioclim, catchment and reach), the bioclim models were the most overfit. The median test AUC using the NHDS as test data was 0.849 for a 27-variable model, 0.836 for an 18-variable model and 0.868 for an 11-variable model. However, a

possible improvement in test AUC with reduced number of variables was not significant as determined by a Wilcoxon signed-rank test.

Though the test AUC is smaller than the training AUC for most models regardless of scale, suggesting potentially overfit models, the disparities between the two are greatest for models developed with climate data (Fig. 4.3). The disparities between training AUC and test AUC are smallest for reach-scale models as determined by Wilcoxon signed-rank tests (Fig. 4.3).

### ***Model performance by species***

Some species such as *Gomphus vastus*, *Neurocordulia yamaskanensis* and *Ophiogomphus howei* performed well regardless of testing dataset (Fig. 4.2). Other species such as *Didymops transversa*, *Gomphus descriptus*, *Hetaerina americana* and *Lanthus parvulus* performed well in training but suffered in testing (Fig. 4.2). The difference between ten-fold cross validation training and test AUCs indicates these latter species' models are not any more overfit than other focal species.

### **Discussion**

The significant reduction of test AUC using the independently collected NHDS dataset compared to the average test AUC using ten-fold cross validation shows that resampling methods have an inherent bias and may artificially inflate model performance metrics. The test AUC using the NHDS dataset is still fairly high, suggesting the models are robust and generalizable (Swets 1988). When modeling riverine biota on the scale of individual river reaches, the restriction of background data may artificially inflate AUC values compared to similar SDM studies of terrestrial taxa, which is another reason why independent test data are important. Omitting New Hampshire test localities in river reaches, which required model extrapolation, had the surprising consequence of reducing model performance. This indicates that the models performed well even under moderate extrapolation from the training background.

When SDMs are developed using NHD river segments as the standard unit of discrimination instead of gridded data, a small but significant improvement in model performance was found. This is contrary to an earlier study which found no difference between these approaches (Domisch et al. 2013b). It should be noted that this choice of background is also less computationally intensive than 30 m gridded data. The difference between the two background selection approaches should be that longer river segments will be sampled more often when using gridded data. By treating river segments as equal units regardless of length, more habitat combinations are sampled with the same number of background points, and this may explain the improved performance. Similarly, model performance is improved when all river segments are used for the background (29,983 background points compared to 9,983). Phillips and Dudik (2008) states that the increase in predictive performance with increased background points plateaus after 8,000 background points, but this may not be true for riverine SDMs. This chapter indicates that some applications would benefit from modelers using a greater number of background points.

SDMs developed for riverine biota with local reach-scale variables outperformed models developed with catchment-scale variables or climate-scale variables, depending on comparison metric. Both the models built with reach-scale variables and models built with catchment-scale variables outperformed bioclim models. It may be that test model performance is low for bioclim models because the chosen extent is limited. If climatic conditions beyond the tolerance of the focal species were not included in the background sample, roughly monotonic response curves should be obtained. However, the extent contains elevations varying from sea level to 1,606 m and corresponding varied climates, and the response curves to bioclim variables are not monotonic (not shown), so the chosen extent is unlikely to be the primary cause for low model test performance. Other studies have used smaller extents to model species distributions (Maes et al. 2010). There may be conditions in the background sample that are more unsuitable for the focal species in terms of reach-scale or catchment-scale variables than in terms of climate, allowing the reach-scale

and catchment-scale models to discriminate favorable and unfavorable habitat more effectively. The default regularization value was used for all models. An increased Maxent regularization parameter for bioclim models could reduce overfitting and the disparity in training versus test AUC, though other studies have found the default value to be optimum or nearly so (Anderson and Gonzalez 2011, Cao et al. 2013).

The most important variables across nearly all target species were found to be drainage area, water velocity and reach slope. Even when these important variables were excluded from catchment-data and local reach-data models, these models still performed better than did bioclim models. Drainage area is a proxy for flow permanence, peak storm discharges, corresponding mean substrate sizes, water temperature, nutrient and organic matter accumulation and river structure and community composition as per the river continuum concept (Vannote et al. 1980), so it is not surprising that this variable contributed heavily to all species' models. In a similar study modeling fish species in a dendritic network, relatively high AUC values were attributed to longitudinal position, a metric highly correlated with drainage area, because it helped the model discriminate suitable habitat more closely than did bioclim variables (Buisson et al. 2008a, 2008b). For example, if a riverine species does not occupy headwater streams, a model can eliminate over two-thirds of the available habitat with this metric, such is true because headwater streams account for over two-thirds of the total stream length in typical river systems (Freeman et al. 2007).

Models for some medium-to-large river species such as *G. vastus*, *N. yamaskanensis* and *O. howei* performed very highly in both training and testing. Models for other species such as *G. descriptus* and *L. parvulus* performed well in training but suffered in testing. Ten-fold cross validation did not show these species' models to be any more overfit than other target species, so it is likely that the environmental variables that most consistently define their environmental niche were not included. For example, if biotic layers were not included, such as those representing the aquatic plant used for oviposition (Jaeschke et al. 2012), the models

may perform poorly. *Calopteryx* requires aquatic vegetation for oviposition, though it is unknown how the microhabitat of *G. descriptus* and *L. parvulus* could be better represented. The differences in test AUC between species indicate that the same environmental variables may not explain the distribution of all species equivalently.

Though bioclimatic variables may produce adequate species distribution models for some purposes, finer scale environmental data, such as those that can be summarized at the reach- and catchment-scales, permit fine-resolution predictions and increased model performance. Ten-fold cross-validation is an important tool for determining if a model is overfit, but it may not be the best means of assessing model performance. An independently collected species locality dataset from an adjacent area can be an effective means of judging model performance provided that the environmental conditions in the test dataset are a subset of those for training. Background selection is an important consideration for all SDM applications, though choosing between a gridded background and one using river segments as a basic unit of discrimination is a unique consideration for riverine SDMs. More effort may be required to produce riverine SDMs if relevant hydrological, geological, land use, and physical variables potentially important to a riverine species are not readily available or if species locality data cannot be easily associated with rivers. However, predictive tools such as SDMs at river and riparian scales are sorely needed, as these habitats are some of the most strongly and immediately affected by regional and local anthropogenic change. Furthermore, this fine-scale approach incorporating predictors from multiple spatial scales allows for a new array of ecological and conservation questions to be answered.

Table 4.1. Number of unique localities for the 22 modeled species in the Maine Damselfly and Dragonfly Survey (MDDS) and New Hampshire Dragonfly Survey (NHDS).

<b>Species</b>	<b>Number of Unique Localities in the MDDS (1991–2009)<sup>1</sup></b>	<b>Number of Unique Localities in the NHDS (2007–2011)</b>
<i>Boyeria grafiana</i>	81	21
<i>Boyeria vinosa</i>	161	144
<i>Calopteryx amata</i>	90	47
<i>Calopteryx maculata</i>	192	213
<i>Didymops transversa</i>	94	81
<i>Gomphus abbreviatus</i>	30	45
<i>Gomphus adelphus</i>	142	47
<i>Gomphus descriptus</i>	33	41
<i>Gomphus vastus</i>	13	23
<i>Hetaerina americana</i>	12	16
<i>Lanthus parvulus</i>	30	21
<i>Macromia illinoiensis</i>	166	64
<i>Neurocordulia obsoleta</i>	60	38
<i>Neurocordulia yamaskanensis</i>	27	16
<i>Ophiogomphus aspersus</i>	73	39
<i>Ophiogomphus carolus</i>	124	17
<i>Ophiogomphus howei</i>	33	14
<i>Ophiogomphus mainensis</i>	127	22
<i>Ophiogomphus rupinsulensis</i>	92	34
<i>Progomphus obscurus</i>	10	17
<i>Stylogomphus albistylus</i>	144	50
<i>Stylurus scudderi</i>	12	38

<sup>1</sup> Most MDDS records were collected during the volunteer survey from 1999 to 2004

Table 4.2. The 27 environmental variables used for modeling, listed by scale (climatic, catchment or reach).

Climate	Mean Diurnal Temperature Range (BIO2) <sup>1</sup>
	Maximum Temperature of Warmest Month (BIO5) <sup>1</sup>
	Temperature Annual Range (BIO7) <sup>1</sup>
	Mean Temperature of Wettest Quarter (BIO8) <sup>1</sup>
	Mean Temperature of Driest Quarter (BIO9) <sup>1</sup>
	Precipitation of Wettest Month (BIO13) <sup>1</sup>
	Precipitation Coefficient of Variation (BIO15) <sup>1</sup>
	Precipitation of Driest Quarter (BIO17) <sup>1</sup>
Precipitation of Warmest Quarter (BIO18) <sup>1</sup>	
Catchment	Upstream Drainage Area <sup>2</sup>
	Area-weighted Percent Agriculture (2001 NLCD) <sup>2</sup>
	Area-weighted Percent Forest & Wetland (2001 NLCD) <sup>2</sup>
	Area-weighted Percent Open Water (2001 NLCD) <sup>2</sup>
	Inverse Buffer Width from Agriculture Averaged Across Ag. Cells <sup>3</sup>
	Inverse Buffer Width from Developed Land Averaged Across Dev. Cells <sup>3</sup>
	Mean Human Population Density <sup>3</sup>
	Area-weighted Percent Surficial Alluvium <sup>3</sup>
Mean Permeability (Soil L1 Horizon) <sup>3</sup>	
Reach	Mean Annual Water Velocity <sup>2</sup>
	Mean Reach Slope <sup>2</sup>
	Sinuosity of River Segment
	Impounded (Boolean)
	Majority Surficial Geology Unit within 100 m of River <sup>4</sup>
	Area-weighted Percent Karst Geology within 100 m of River <sup>4</sup>
	Mean Permeability (Soil L1 Horizon) within 100 m of River <sup>4</sup>
	Mean pH (Soil L1 Horizon) within 100 m of River <sup>4</sup>
Weighted Average Sand Percentage (Soil L1 Horizon) within 100 m of River <sup>4</sup>	

<sup>1</sup> Derived from PRISM 1970–2000, 30-arcsecond resolution climate data (<http://www.prism.oregonstate.edu>)

<sup>2</sup> Used variable as provided with NHDPlus ([http://www.horizon-systems.com/NHDPlus/NHDPlusV1\\_home.php](http://www.horizon-systems.com/NHDPlus/NHDPlusV1_home.php))

<sup>3</sup> Accumulated with the CA3T NHDPlus Catchment Attribute Allocation and Accumulation Tool

<sup>4</sup> Summarized with Zonal Statistics function in ArcGIS

Table 4.3. Environmental variables excluded from modeling because of high correlation (&gt;0.8) with variables from Table 4.2.

Climate	Annual Mean Temperature (BIO1) <sup>1</sup>
	Isothermality (BIO3) <sup>1</sup>
	Temperature Seasonality (BIO4) <sup>1</sup>
	Min Temperature of Coldest Month (BIO6) <sup>1</sup>
	Mean Temperature of Warmest Quarter (BIO10) <sup>1</sup>
	Mean Temperature of Coldest Quarter (BIO11) <sup>1</sup>
	Annual Precipitation (BIO12) <sup>1</sup>
	Precipitation of Driest Month (BIO14) <sup>1</sup>
	Precipitation of Wettest Quarter (BIO16) <sup>1</sup>
Precipitation of Coldest Quarter (BIO19) <sup>1</sup>	
Catchment	Area-weighted Percent Development (2001 NLCD) <sup>2</sup>
	Area-weighted Percent Native Vegetation (2001 NLCD) <sup>2</sup>
	Weighted Average Percent Imperviousness (2001 NLCD) <sup>3</sup>
	Area-weighted Percent Karst Geology <sup>3</sup>
	Mean pH (Soil L1 Horizon) <sup>3</sup>
	Mean Sand Area-weighted Percentage (Soil L1 Horizon) <sup>3</sup>
Reach	Mean Annual Flow <sup>2</sup>

<sup>1</sup> Derived from PRISM 1970–2000, 30-arcsecond Resolution Climate Data (<http://www.prism.oregonstate.edu>)

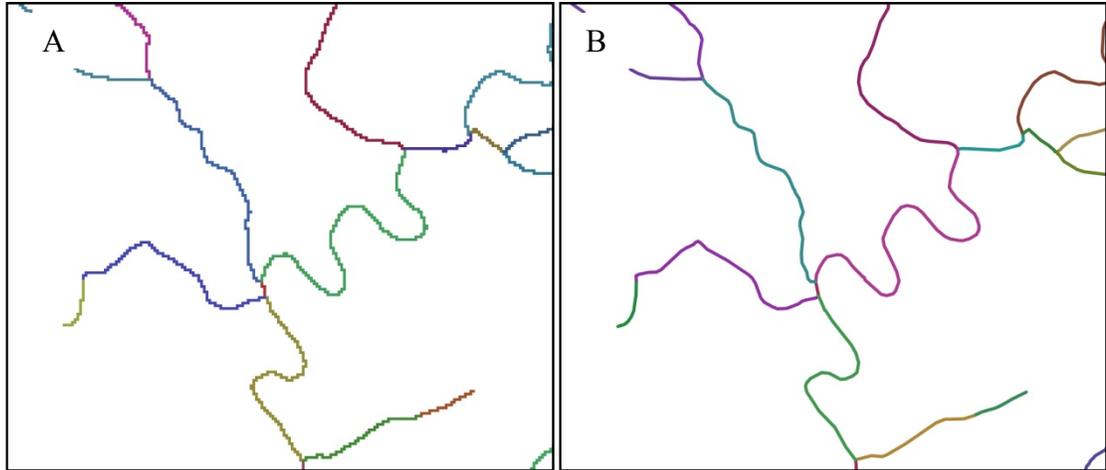
<sup>2</sup> Used variable as provided with NHDPlus ([http://www.horizon-systems.com/NHDPlus/NHDPlusV1\\_home.php](http://www.horizon-systems.com/NHDPlus/NHDPlusV1_home.php))

<sup>3</sup> Accumulated with the CA3T NHDPlus Catchment Attribute Allocation and Accumulation Tool

Table 4.4. The background selection method used in species distribution modeling of riverine biota (raster predictors versus NHD river reach tabular data) can make small differences in model performance.

<b>Background selection method</b>	<b>Median Training AUC</b>	<b>Median Test AUC using the NHD</b>
29,983 background points from raster	0.974	0.839
9,983 background points from raster	0.972	0.824
29,983 background points from NHD river reaches (all Maine reaches)	0.978	0.849
9,983 background points from NHD river reaches	0.977	0.841

Note: Using NHD river reaches over raster backgrounds significantly improved training AUC but not test AUC, and using more background points significantly improved training AUC for either background selection method, but only significantly improved test AUC when NHD river reaches were the standard unit.



Note: (A) A 30-m resolution raster representation of a river network includes many cells within a river reach with identical environmental conditions, but (B) individual reach units includes no repetition. Colors are intended for visual discrimination between river reaches.

Figure 4.1. For species distribution models, segments of a river network can be represented either by a gridded dataset or as individual reach units.

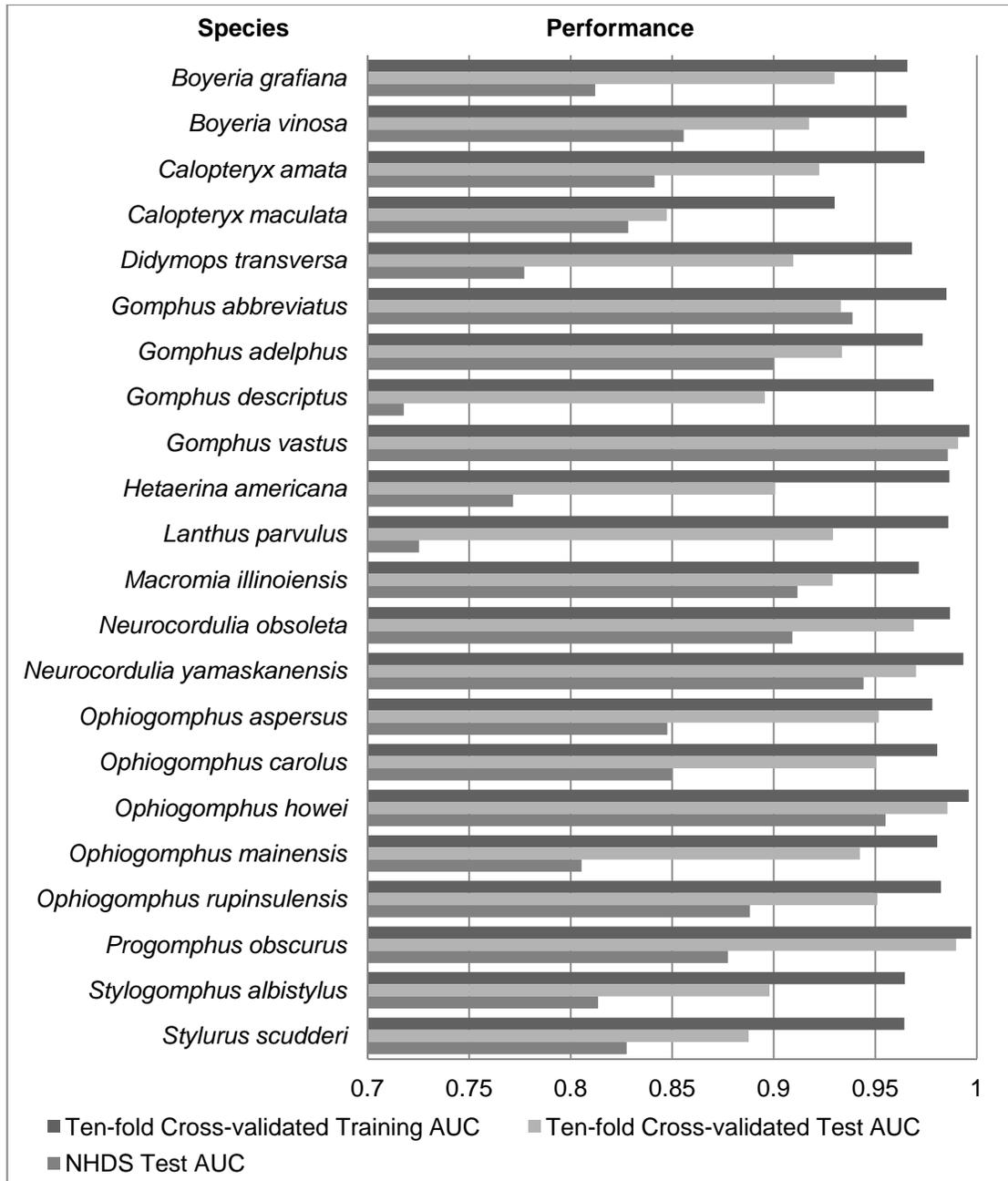
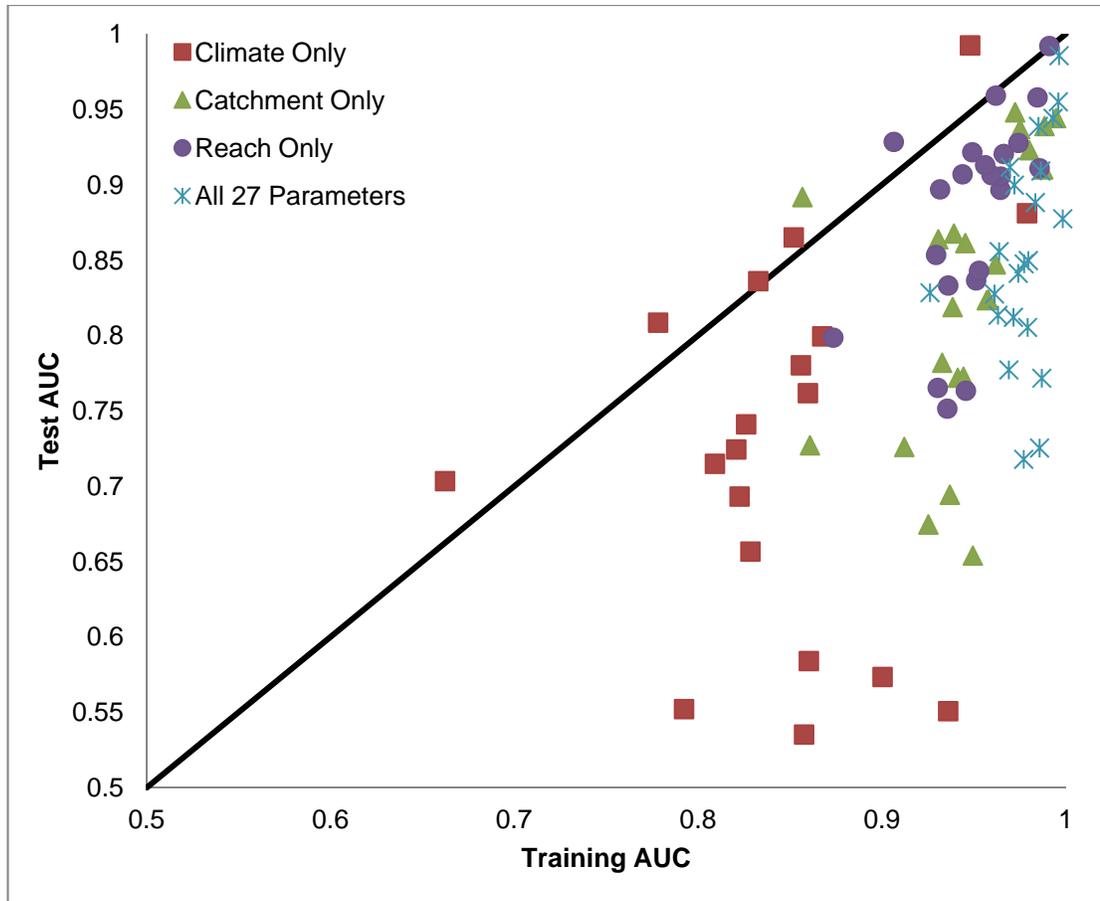


Figure 4.2. Model performance as assessed by AUC was high for most focal species, though cross-validated AUC metrics are often higher than test AUC from an independent dataset.



Note: Points that fall below the diagonal (equal value) black line have smaller test AUCs, determined with the independently collected NHDS, than training AUC. Model performance between sets of scale variables follow a similar pattern as training AUC for test AUC, except that models built with reach-scale variables outperform models built with all environmental variables.

Figure 4.3. Model performance for 22 riverine Odonata in Maine judged by training AUC is greatest for models built with all environmental variables, followed by models built with only reach-scale variables and models built with only catchment-scale variables, and trailed by models built with only climate variables.

## CHAPTER V

### CORRECTING SAMPLING BIAS IN SPECIES DISTRIBUTION MODELS

#### Abstract

Availability of species locality data can vary dramatically between regions. Traditionally, single representatives from clustered localities are selected for use in species distribution models (SDMs). Although this may not reduce the efficacy of bioclimatic-scaled models, information may be lost when developing finer-scaled SDMs with highly heterogeneous environmental data. Geographic thinning was compared to several alternative bias correction techniques. SDMs were developed in `Maxent` for 48 species of dragonflies and damselflies in a multi-state region using eight strategies: no correction, geographic thinning of training localities, target group survey (TGS) background sampling restriction, and biased background sampling using TGS record count across NHD river reaches, 8-digit, and 12-digit USGS subwatersheds, and reclassified watershed counts. Each approach was performed twice, each time excluding a different test region: New Hampshire or West Virginia. SDMs were also developed by training only with Maine localities. Differences between sampling from raster grids and sampling from NHD river reaches was compared. TGS background restriction and count bias reduced model performance for most species. Geographic thinning of training localities improved performance for nearly all species using one test dataset but not the other, and the 8-digit TGS count bias improved model performance for all but one species, offering a greater improvement in model performance than locality thinning for one test dataset but not the other. The multi-state model was more effective than the model of an adjacent state. Using NHD river reaches for background selection improved model performance. Some attempts at reducing sampling bias may instead reduce model performance. Geographic thinning of training localities or bias correction using TGS counts across watersheds may only improve models for some regions and some

species. Using larger SDM training regions with variable data density are more effective than smaller regions with more uniform data.

## **Introduction**

Biased sampling may yield biased species distribution models (SDMs) that illustrate the distribution of sampling instead of the distribution of a species. In such cases, factors that are determined to be important may be indicative of where sampling is likely to occur more than where a species is likely to occur. In extreme cases, incorrect conclusions can be drawn from poorly constructed models that do not consider bias. Caution is needed when making conservation planning decisions because of potential bias (Costa et al. 2010). Sound management decisions are difficult unless all of the decisions of the modeling process are documented and evaluated (Rodriguez-Castaneda et al. 2012). However, SDM developers rarely account for sampling bias (Yackulic et al. 2013).

Sampling bias may not be considered because model performance may not be adversely affected, even though sampling bias can lead to misleading results (Wolmarans et al. 2010). This is especially true when using cross-validation or other resampling techniques to divide a locality dataset into training and testing groups (Fielding and Bell 1997). If the training and test datasets are not independent, the same sampling biases may be present in both datasets, and model performance metrics will be inflated (Hijmans 2012). Not only will the apparent model accuracy built from biased data be higher than true model accuracy, the threshold values used to assess which model values represent species presences and species absences will also be higher than optimal thresholds (Bean et al. 2012).

For the relatively few studies that have considered sampling bias, three primary approaches have been used to compensate for it. One involves thinning the species locality dataset, and two involve altering the background selection (i.e. the environmental layer(s)). Thinning locality points based on geographic distance is often used, because geographic sampling bias usually leads to environmental bias

(Anderson and Gonzalez 2011) attributable to autocorrelation between nearby localities or clusters of localities (Dormann et al. 2007, Elith and Leathwick 2009). When using bioclimatic environmental variables, clustered localities may all represent very similar climates such that the model may be misled into considering that environment more suitable than other localities with fewer samples. By omitting localities such that remaining localities are not autocorrelated, are not within known dispersal distances, or are not clustered geographically, the effect of sampling bias may be reduced. The drawback to thinning localities geographically is that novel environments and information that could be useful for model development are omitted. This is especially true when fine-scale models are built using environmental variables at multiple scales: modeling the distribution of a species at fine scales while also consistently modeling the large-scale distribution can produce robust and reliable conservation maps (McPherson et al. 2006, Vallecillo et al. 2009, Niamir et al. 2011, Marcer et al. 2012). The omission of localities based on geographic distance may not impact bioclimatic models, but information may be lost for fine-scaled predictors. Therefore, thinning localities by geographic distance may compromise fine-scaled distributions, but this evidently has not been quantified before.

Another approach to compensating for biased sampling is to develop a bias (background sampling) grid based on known biases in sampling. A bias grid has the same extent and resolution as the environmental predictors and is either indicative of the likelihood sampling occurred at a given location or the level of sampling effort at that location. The rationale in the use of a bias grid is that if background point selection has the same sampling bias as the species locality data, the bias effect will cancel out (Phillips et al. 2009, Merow et al. 2013). This will result in localities that have fewer neighbors being given greater weight in the model (Clements et al. 2012).

If a modeler has information on the distribution of survey effort across the landscape, this survey effort map can be used as a bias grid. The importance of sampling bias is difficult to evaluate when using presence-only localities, because sampling effort is typically unknown (Merow et al. 2013, Yackulic et al. 2013).

Surrogate measures that are known to influence sampling distribution can be used, such as distance from roads or towns, in place of survey effort maps (Dudik et al. 2005). Alternatively, a bias grid can be developed by constructing a model relating presence points to estimates of sampling effort such as distance to urban centers and roads, elevation, and topographic roughness (Phillips et al. 2009). For example, Elith et al. (2010a) recommend using a bias grid that maps relative sampling intensity with a Gaussian kernel. The bias value for each cell is determined by summing the weighted distances from each cell to each locality, where each distance is weighted by the dispersal capability of the target species with a Gaussian function (Elith et al. 2010a, Clements et al. 2012). The development of this type of bias grid is nontrivial, however, and may take many days of computation (Clements et al. 2012).

The most common method of accounting for sampling bias involves “target group survey” (TGS) localities, which are the presence localities of other species with a similar life-history strategies (Merow et al. 2013, Syfert et al. 2013, Yackulic et al. 2013). TGS bias grids restrict background selection to only those locations where a TGS species was recorded. Sampling bias is not treated explicitly and may not be known, but it is assumed that both the training localities and TGS localities have the same bias if any (Phillips et al. 2009). Using a TGS background may be a more reasonable approach to choosing pseudo-absences than random selection, because it is logical to assume that the target species was not observed at locations where similar species were documented. TGS localities may also be geographically and environmentally closer to training localities, because collectors tend to revisit previously surveyed areas (Mateo et al. 2010).

Sampling bias may also be an artifact of aggregating data from multiple sources. Though opportunistic sampling data are less ideal than is systematic, well-designed sampling (Schreuder et al. 2001), and opportunistic data may be geographically clustered or of varying quality (Snall et al. 2011), standardized sampling of broad regions over time is rarely performed (Danielsen et al. 2005, Brotons et al. 2007), especially for taxa of marginal public interest such as many

invertebrates. Not all museum and vouchered citizen-science data are opportunistic, but survey protocols are rarely available or may vary from one region (i.e. state) to another. For instance, state agency natural history databases are curated in different manners and with different objectives. In some instances, species localities are only stored if those species are considered rare in the state, and if the species status is revised, no additional records of those species are recorded (personal communication, Steve Roble 11 Apr. 2013). Few studies have investigated the consequences of aggregating species data from multiple sources for SDMs, though this approach makes optimal use of existing data (Boakes et al. 2010, Sarda-Palomera et al. 2012).

Correcting for geographical sampling bias has been shown to improve model predictions developed with a biased dataset (Bystriakova et al. 2012, Syfert et al. 2013). Syfert et al. (2013) corrected for bias by developing bias grids that counted the number of TGS localities within a grid cell but did not test the effect of different bias grids. Riverine systems accumulate the effects of upstream factors and thus allow for different bias grids to be used (from climatic region to watershed down to individual reach) and thus form a good test system to examine the efficacy of different bias-reduction schemes. Because of the distribution of lotic species along dendritic networks and potential differences in sampling efforts when surveying lotic species, different approaches for developing bias grids are available for riverine SDMs. Using watersheds as units for discriminating sampling effort is logical because some surveys such as those performed by the Maryland Biological Stream Survey are known to have focused on particular watersheds.

To address these deficiencies, the following objectives were pursued: (1) to compare the efficacy of geographic thinning of training localities versus eight TGS sampling bias correction techniques on SDMs for a flagship indicator group of lotic invertebrates over an extensive geographic region and (2) to compare models developed for a multi-state region against those developed for a single state.

## **Methods**

### ***Focal extent***

In this study, the finest spatial resolution used was the river reach (a stream or river segment between the confluence with a tributary, lake, marsh, or swamp and the subsequent confluence). The dendritic network used for this project was the National Hydrography Dataset (NHD), which is a comprehensive set of vector data representing rivers, streams, and other waterbodies within the coterminous United States. The NHD is divided into 21 water resource regions within the U.S. Those regions selected for this project included the Northeast, the Mid-Atlantic, the Great Lakes, and the Ohio drainages. The extent was clipped to exclude states where little or no lotic data were obtained on the focal taxa of interest (Insecta: Odonata, dragonflies and damselflies), such as Rhode Island, Connecticut, Massachusetts, Kentucky, and North Carolina. The focal extent thus included Maine, New Hampshire, Vermont, New York, New Jersey, Pennsylvania, Ohio, southeastern Michigan, northeastern Indiana, Delaware, Maryland, West Virginia, and Virginia within the Mid-Atlantic water resource region. The dataset contained 360,791 stream segments within the focal extent and is shown in Fig. 5.1.

### ***Species data***

Vouchered localities for stream and river-obligate Odonata were obtained from multiple sources throughout the focal extent (Table 5.1). All records in these databases were confirmed by experts. Several issues must be considered when modeling at fine resolutions such as individual river segments. The known species locality data must be carefully vetted to only include localities with a precision less than the chosen resolution. Localities that record dispersing organisms from source sites in unsuitable habitat may reduce model performance (Heino 2013), though Maxent (the modeling package used; Phillips et al., 2006) has been shown to be robust to moderate error in localities (Graham et al. 2008). A “mass effect” is when this dispersal rate is high enough to cloud effects of environmental control over what appears to be suitable habitat versus what is unsuitable (Heino 2013), and in those

cases, the assumptions of species distribution modeling are unsupported. These types of location errors are likely to be more important when using fine-scale environmental data that may contain dramatically different values between adjacent habitats, such as land cover, compared to using climatic data, which are less likely to show such strong heterogeneity.

To associate species data (typically collected on land) with the appropriate reach, the georeferenced coordinates of all target species localities were moved in a downslope direction to the closest river reach with TauDEM (<http://hydrology.usu.edu/taudem/taudem5/>). This process better associated each locality with its correct river than a nearest-line analysis would have, because the accurate coordinates for a locality may be the bank of a wide river where the river centerline is farther away from the bank than nearby tributary confluences. All localities moved more than 100 m by TauDEM were checked against the written description of the locality and moved manually to the correct location if required. Localities that could not be resolved with the river network were omitted. Histograms of catchment area for each species' localities were made, and outlier locations were corrected if the written description justified it. The databases were filtered so no species had more than one record per river reach. The earliest species record from each reach was retained. After this filtering process, 5,524 records of 48 focal lotic odonates remained and are listed in Table 5.2.

### ***Environmental data***

All environmental data and species localities were reprojected to NAD\_1983\_Albers to avoid the cell-size bias with latitude present in the native projections of these data which was typically WGS 84. Broad-scale data included bioclimatic (bioclim) variables derived from monthly values of maximum and minimum temperature and precipitation from the Worldclim 30-arcsecond dataset (<http://www.worldclim.org>). Some researchers have argued that using bioclim data is sufficient for SDMs because at large spatial scales, climate is the ultimate driver determining the physiological niche being modelled (Pearson and Dawson 2003).

With respect to variables important for stream biota, air temperature may be used as a surrogate for water temperature because of substantial cross-correlation (Caissie 2006). Precipitation partly determines discharge and consequently the microhabitat structure available within river reaches (Buisson et al. 2008b). Bioclim variables, therefore, should have adequately represented the climate experienced by riverine species.

Catchment-scale data summarize the geology, soils, and land use present in the upstream watershed of each river reach. These variables are often surrogates for microhabitat variables that cannot be quantified easily for SDM purposes, though some catchment-scale variables have been shown to be able to predict microhabitat variables important for fish (Mugodo et al. 2006). Drainage area is the primary catchment-scale variable that reflects habitat capacity and thus population size through extinction dynamics from a classical biogeographic perspective (MacArthur and Wilson 1967). Drainage area is also an indicator of position within a dendritic network, which has been shown to be directly related to aquatic insect diversity, with well-connected, central communities having greater diversity than more peripheral communities, regardless of local environmental conditions (Altermatt et al. 2013). Underlying geology in watersheds is also important to the distribution of benthic macroinvertebrates (Cannan and Armitage 1999), and the inclusion of soil data has been shown to improve model results for insects like butterflies and grasshoppers (Titeux et al. 2009). Land use is also important at smaller scales (Pearson and Dawson 2003, Pearson et al. 2004), such as the scale of this study, because land use can impede a species from occupying part of its range, suggesting the species is not filling its climatic niche when it actually does (Dormann 2007). Furthermore, benthic macroinvertebrates, such as Odonata, are known to be sensitive to metals that accumulate in streams from surface runoff from impervious surfaces such as roads (Beasley and Kneale 2003) and to pesticides in agricultural runoff (Beketov et al. 2013). Riparian buffers may reduce the impact of upstream non-point source pollution, so agriculture and development inverse buffer widths, indices that consider

the pollutant- and nutrient-intercepting properties of forest or wetland riparian buffers when accumulating land-use characteristics to river reaches (Baker et al. 2006), were also accumulated for each river reach. Most catchment-scale data were developed with the CA3T NHDPlus Catchment Attribute and Allocation Tool, which allocated and accumulated 30-m raster data describing a variety of environmental variables to individual river reaches, though some catchment-scale data such as 2001 National Land Cover Database (NLCD; <http://www.mrlc.gov>) land use summaries were used as provided by NHDPlus as listed in Table 5.3.

Reach-scale data are local-scale data specific to an individual river reach, where reaches are as defined by the NHD. Water velocity estimates for each river segment were taken from NHDPlus, and those estimates were based on an empirical relation defined by drainage area, mean annual discharge, slope, and field discharge measurements (Jobson 1997). Slope for each river segment in NHDPlus was determined from elevation data and a smoothing method that ensured all river segments had a slope  $\geq 0$ . Those river segments intersecting natural or artificial ponds and reservoirs were labeled with a boolean impoundment variable. This variable was included because proximity to dams can influence species distributions by altering hydrologic, sediment, and temperature regimes (Han et al. 2009). Riparian composition was determined with the Zonal Statistics function and 30-m raster data in ArcGIS based off of a 100-m buffer from the river centerline (or the river banks of wide river segments provided as polygons in the NHD) (Table 5.3). Summarizing a raster layer around streams in the NHD is no small task. For each NHD water resource region (i.e. Mid-Atlantic), a field called "FIDCopy" was added to the `nhdflowline.shp` attribute table and assigned the same value as the "FID" field. When handling the NHD, it is logical to use the unique COMID field to identify stream segments, but the Zonal Statistics tool in ArcGIS will not function with the long integers in the COMID field, so an intermediate step was required. The first 99,999 features in `nhdflowline.shp` were exported to a new file called `nhdflowline1.shp`. The remaining features were exported to a new file called

`nhdflowline2.shp`. A 100-m buffer was performed around all river centerlines. This centerline buffer is not meaningful to characterize the riparian area for wide rivers, so a buffer from river bank polygons was used, which is available in the NHD for wide rivers. These rivers were removed from `nhdflowline1.shp` and `nhdflowline2.shp` and were treated separately. Zonal Statistics of the raster data (e.g. NLCD forest cover) were performed for each buffer. The results were joined to the original `nhdflowline.shp` using the `FIDCopy` field. Once completed, the `nhdflowline.shp` from each NHD water resource region were merged into a single shapefile that was subsequently converted to a 30-m raster for use in `Maxent`.

### ***Model development***

Species distribution models were developed in `Maxent` v.3.3.3k (Phillips et al. 2006). `Maxent` is considered one of the most reliable methods for building SDMs, especially when used with limited or biased locality data (Hernandez et al. 2006, Pearson et al. 2007, Wisz et al. 2008), and is considered a reasonable alternative to an ensemble of multiple models (Araújo and New 2007). Default parameters for feature creation, regularization, and prevalence were used. A Pearson's correlation matrix was calculated within the focal extent for all environmental layers (Tables 5.3 and 5.4). For all pairs of environmental layers with Pearson's correlation coefficients greater than 0.8, only one layer was retained for modeling (Rinnhofer et al. 2012). Seventeen variables were thus excluded from modeling (Table 5.4).

Models were developed using gridded background data, where a 30-m grid cell was the sampling unit, and using species with data (SWD) format (see `Maxent` tutorial, <http://www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc>), where a river reach was the sampling unit. Models were developed with no bias correction scheme as a baseline. Models also were developed using training localities and background from Maine and then tested with data from New Hampshire, neighboring regions with relatively high data density (Table 5.2).

Seven bias correction schemes were tested. Models were developed using thinned species locality data, where the maximum number of localities farther than 25 km from any other locality for a given species was retained. A distance of 25 km was chosen because that is approximately equivalent to the greatest dispersal distance of any target species (Stettmer 1996, Corbet et al. 2006, Grewe et al. 2013, Jaeschke et al. 2013). The second scheme was essentially a target group survey (TGS) mask, where background points (i.e. pseudo-absences) are only selected from stream reaches where any other lotic odonate had been collected. The third scheme summed all TGS species records for each stream reach, and used that count as a bias value. This is comparable to the sampling bias correction used in Syfert et al. (2013). The fourth and fifth bias correction schemes summed all TGS species records within 8-digit and 12-digit USGS watersheds. USGS 8-digit watersheds are approximately 181,000 hectares in size, whereas 12-digit subwatersheds are typically between 4,000 to 16,000 hectares, with some as small as 1,200 hectares. The sixth and seventh bias correction schemes reclassified the positive 8-digit and 12-digit watershed counts using Jenks natural break values such that they varied from 1 to 10.

Maxent has the ability to use bias grids to preferentially select background points (Phillips et al. 2009). Maxent accepts bias grids as described above and will sample the background proportionately to the bias count (Phillips et al. 2009). If the bias in the background sample is equivalent to the bias in the species locality points, the model results will not be affected by the bias (Phillips et al. 2009, Merow et al. 2013). To determine which bias correction scheme was most appropriate, two independent test datasets were used. Models were developed with all data from the focal extent excluding New Hampshire and then tested with New Hampshire Dragonfly Survey (NHDS) data, and similarly, models were developed by excluding West Virginia and then tested with West Virginia Dragonfly and Damselfly Atlas (WVDDA) data (Table 5.2). Model performance with either test dataset was assessed by the test AUC metric, which is threshold-independent and not influenced by species

prevalence (Hanley and McNeil 1982, Fielding and Bell 1997, Guisan and Zimmermann 2000).

To apply the bias correction schemes with SWD format, 30,000 background stream segments were selected in proportion to their bias value from the 360,791 total stream segments. The bias value of each stream segment was divided by the sum of all bias values. The results were then summed cumulatively, such that each stream reach was assigned a value between 0 and 1. Random numbers were used to sample from this cumulative weight list, such that the background was sampled in a similar manner as `Maxent` would with a bias grid. The difference is that background selection in `Maxent` would also be weighted by stream segment length.

## **Results**

For all cases tested, developing `Maxent` models with the SWD format where the standard unit for background selection was the stream reach outperformed sister models where background points were selected by `Maxent` from rasters (Table 5.5). For 19 of 22 species with more than 10 training localities in Maine and 10 testing localities in New Hampshire, the multi-state model projected and tested in New Hampshire performed better than the Maine-trained model (Table 5.5).

For the WVDDA test dataset, thinning the training dataset considerably improved predictions for most species (Table 5.6). For the NHDS test dataset, thinning the dataset decreased model performance for 16 of 24 species with more than 10 training and testing localities (Table 5.7). Thinning the training dataset resulted in larger predicted areas for many species (Fig. 5.2)

Restricting background selection to TGS stream reaches produced worse modeling performance using the WVDDA test dataset for 11 out of 15 species (Table 5.6). Restricting background selection in the same manner but incorporating a bias count produced worse modeling performance for 8 out of 15 species (Table 5.6). The same background selection schemes using the NHDS test dataset both produced worse modeling performance for 23 out of 24 species (Table 5.7).

The 8-digit watershed and 12-digit subwatershed bias correction schemes improved model performance for 14 out of 15 species using the WVDDA test dataset. Model performance was better using the 8-digit watershed bias correction scheme compared to the 12-digit subwatershed bias correction scheme. The watershed bias correction schemes reclassified to scale of 1 to 10 performed worse for nearly all species (Table 5.6). The 8-digit watershed and 12-digit subwatershed bias correction schemes improved model performance for 7 and 2 species, respectively, out of 24 species using the NHDS test dataset. Similar to the WVDDA test dataset, the watershed bias correction schemes reclassified to a scale of 1 to 10 performed worse for nearly all species (Table 5.7). Similar to reducing the number of training localities, applying a bias correction scheme for background selection resulted in larger predicted areas for many species (Fig. 5.2).

To summarize, the result of spatial bias correction techniques varied with species, and no single technique improved model performance for all species. Training models with data from a multi-state region, even when potentially biased, resulted in greater predictive performance than models trained only with relatively dense data from a single state. Restricting the environmental background to locations where other lotic Odonata had been recorded resulted in poor predictive performance for most species. However, both reducing the number of training localities through geographic thinning and using a biased environmental sampling approach based on the sum of lotic Odonata records within watersheds improved predictive performance in many cases. It is important to note that all spatial bias correction techniques degraded model performance for some species. It was also found that developing models that treated stream reaches as individual units resulted in improved model performance compared to representing streams as rasters.

## Discussion

Model performance was high for most species. The worst model performance was for widespread species (e.g. *Calopteryx maculata* and *Stylogomphus albistylus*), although some widespread species performed relatively poorly in one test dataset but not the other (e.g. *Boyeria vinosa*, *Didymops transversa*, *Hetaerina americana*). This is consistent with previous SDM studies that have shown that models for widespread species and those with broad ecological tolerances perform more poorly than for specialized species with restricted ranges (McPherson et al. 2004, Elith et al. 2006, Hernandez et al. 2006, Mateo et al. 2010, Sarda-Palomera et al. 2012). Alternatively most *Ophiogomphus* species are specialized (Dunkle 2004, Gibbs et al. 2004), and the predictive performances of these species were high.

Predicted distributions may include rivers where the target species are not known to occur (Fig. 5.2). This is either because the rivers are undersampled, a factor that was not included in the list of environmental predictors precludes occupation of those rivers, or it is an artifact of the modeling approach, because presence-only SDMs like from `Maxent` tend to overpredict compared to presence-absence models (Brotons et al. 2004, Sarda-Palomera et al. 2012). The predicted distribution of many species was greater when bias correction was applied, which is consistent with a previous study that corrected for sampling bias with a TGS bias correction scheme (Bystriakova et al. 2012). The bias correction scheme may be restricting the full range of environments from being sampled, and the tail ends of the empirically defined suitability relations are poorly defined. This would be the opposite effect of using overly broad background extents, which are effectively masked out with TGS background selection methods, where predicted ranges are artificially constrained and model performance metrics inflated (VanDerWal et al. 2009, Elith et al. 2010b).

The varying model performances for species that were common to both test datasets (Tables 5.6 and 5.7) may be because the predictive power of a model varies geographically, which is something that is rarely examined. The biases in the NHDS may be comparable to the biases in the Maine Damselfly and Dragonfly Survey

(MDDS), which was the largest source of training data for many species (Fig. 5.1, Table 5.1). Most attempts to correct for bias decreased model performance as assessed by the NHDS (Table 5.7), which may be expected if the models were biased toward that part of the focal extent. Models trained only on Maine data performed worse than the multi-state models, demonstrating that the other localities are adding value to the model, possibly because a larger portion of the environmental niche is being characterized. This also discounts the notion that the multi-state model may have a performance advantage by being biased toward the northern part of the focal extent, because the Maine-trained model would be expected to have a greater advantage in this respect. Conversely, the WVDDA is the largest data source in the southern portion of the focal extent (Fig. 5.1, Table 5.1), so when those data are withheld, correcting for a biased sampling distribution may be more important, resulting in increased model performance when either training localities are thinned or a biased background selection method is used (Table 5.6). An alternative explanation is that environmental bias in the aggregated species locality data does not affect the predicted distributions, which has been argued by other authors (Kadmon et al. 2004, Loiselle et al. 2008), so any attempts to compensate for it may be misdirecting the models.

This study showed that traditional TGS bias correction schemes, TGS masking or TGS count bias (Mateo et al. 2010, Syfert et al. 2013), almost universally reduced model performance compared to random background selection (no bias correction), which is consistent with previous studies (Elith and Leathwick 2007, Chefaoui and Lobo 2008). These methods may restrict how much of the focal extent can be sampled, limiting the potential combinations of environmental predictors used to construct the model. For example, for this study, the number of TGS locations was approximately 1,900, which is much less than the 30,000 unique background samples used for the other models. Mateo et al. (2010) suggest that selecting random pseudo-absences may be preferable to TGS background selection when the number of available background localities from all similar species is small.

Modifying the regularization parameter has been shown to reduce the effect of sampling bias (Anderson and Gonzalez 2011) and may be easier to implement than other bias correction schemes, though relaxed regularization may also overpredict if the SDM is not overfit. Compensating for sampling bias for a dataset that appears to be spatially biased or for one where the bias is completely unknown does not guarantee that the model will be improved. Sampling bias should not be outright ignored, but it may not be manifested in model results. The use of multiple bias correction schemes is recommended to determine which one(s) is/are most effective for a particular dataset. Geographically structured cross-validation (Brown 2014) may be a useful tool for evaluating bias correction when data are not structured into geographic subsets as they were for this study.

Table 5.1. Lotic Odonata records were obtained from multiple sources, many of which are not publicly available because of data sensitivity concerns.

<b>Database</b>	<b>Years of survey data used in this study</b>	<b>Number of species records used</b>
Maine Damselfly and Dragonfly Survey (MDDS)	1991–2009	2200
Maryland Department of Natural Resources & Maryland Biological Stream Survey	2001–2011	309
Maryland Natural Heritage Program	1995–2008	48
New Hampshire Dragonfly Survey (NHDS)	2007–2011	1184
New York Dragonfly and Damselfly Survey (NYDDS)	2005–2009	233
OdonataCentral	1996–2010	409
Ohio Odonata Survey	1995–2009	348
Pennsylvania Natural Heritage Program	1995–2003	38
West Virginia Dragonfly and Damselfly Atlas	1995–2010	633
Virginia Natural Heritage Program (Virginia Department of Conservation and Recreation)	1995–2011	29
Vouchered observations that were not available in other databases (mostly PA records from Ben Coulter with additional MD and VA records from Steve Collins, Bill Hubick)	2003–2011	93

Table 5.2. The number of unique localities available varied among the 48 focal odonates.

Species	Number of unique localities	Number of NH Localities	Number of WV Localities
<i>Archilestes grandis</i>	28	0	11
<i>Argia sedula</i>	46	0	22
<i>Argia tibialis</i>	87	0	25
<i>Argia translata</i>	127	0	75
<i>Boyeria grafiana</i>	162	21	12
<i>Boyeria vinosa</i>	502	144	38
<i>Calopteryx amata</i>	176	47	17
* <i>Calopteryx angustipennis</i>	12	0	6
<i>Calopteryx dimidiata</i>	24	10	0
<i>Calopteryx maculata</i>	802	213	162
* <i>Cordulegaster bilineata</i>	8	0	1
* <i>Cordulegaster diastatops</i>	72	1	0
<i>Didymops transversa</i>	214	81	15
<i>Gomphus abbreviatus</i>	84	45	0
<i>Gomphus adelphus</i>	207	47	4
<i>Gomphus descriptus</i>	97	41	6
* <i>Gomphus fraternus</i>	35	0	2
* <i>Gomphus lineatifrons</i>	11	0	4
<i>Gomphus lividus</i>	136	17	48
* <i>Gomphus quadricolor</i>	40	7	6
* <i>Gomphus rogersi</i>	42	0	2
* <i>Gomphus spicatus</i>	51	0	0
<i>Gomphus vastus</i>	67	23	11
<i>Gomphus viridifrons</i>	27	0	13
* <i>Helocordulia selysii</i>	20	0	0
* <i>Helocordulia uhleri</i>	153	1	0
<i>Hetaerina americana</i>	147	16	46
* <i>Hetaerina titia</i>	7	0	1
<i>Lanthus parvulus</i>	77	21	6
<i>Lanthus vernalis</i>	49	10	1
<i>Macromia illinoiensis</i>	302	64	23
* <i>Macromia taeniolata</i>	21	0	5
* <i>Neurocordulia michaeli</i>	75	0	0
<i>Neurocordulia obsoleta</i>	101	38	0

Table 5.2. Continued.

<b>Species</b>	<b>Number of unique localities</b>	<b>Number of NH Localities</b>	<b>Number of WV Localities</b>
<i>Neurocordulia</i> <i>yamaskanensis</i>	67	16	4
* <i>Ophiogomphus anomalus</i>	112	0	0
<i>Ophiogomphus aspersus</i>	124	39	0
<i>Ophiogomphus carolus</i>	166	17	1
<i>Ophiogomphus howei</i>	51	14	1
<i>Ophiogomphus mainensis</i>	171	22	4
<i>Ophiogomphus</i> <i>rupinsulensis</i>	163	34	6
<i>Progomphus obscurus</i>	51	17	0
* <i>Somatochlora linearis</i>	41	1	8
<i>Stylogomphus albistylus</i>	387	50	41
<i>Stylurus amnicola</i>	19	16	0
* <i>Stylurus plagiatus</i>	30	0	0
<i>Stylurus scudderi</i>	59	38	0
<i>Stylurus spiniceps</i>	74	35	2

Note: Not all species contained a sufficient number of records in the New Hampshire (NH) and West Virginia (WV) test datasets, and those that contained fewer than 10 training and fewer than 10 testing localities in either NH or WV were omitted from analysis (\*).

Table 5.3. The environmental variables used for modeling listed by scale (climatic, catchment, or reach).

Climate	Annual Mean Temperature (BIO1) <sup>1</sup>
	Mean Diurnal Temperature Range (BIO2) <sup>1</sup>
	Temperature Seasonality (BIO4) <sup>1</sup>
	Maximum Temperature of Warmest Month (BIO5) <sup>1</sup>
	Minimum Temperature of Coldest Month (BIO6) <sup>1</sup>
	Mean Temperature of Wettest Quarter (BIO8) <sup>1</sup>
	Mean Temperature of Driest Quarter (BIO9) <sup>1</sup>
	Annual Precipitation (BIO12) <sup>1</sup>
	Precipitation Coefficient of Variation (BIO15) <sup>1</sup>
Catchment	Upstream Drainage Area <sup>2</sup>
	Area-weighted Percent Agriculture (2001 NLCD) <sup>2</sup>
	Area-weighted Percent Forest & Wetland (2001 NLCD) <sup>2</sup>
	Area-weighted Percent Open Water (2001 NLCD) <sup>2</sup>
	Inverse Buffer Width from Agriculture Averaged Across Agriculture Cells <sup>3</sup>
	Inverse Buffer Width from Developed Land Averaged Across Developed Cells <sup>3</sup>
	Mean Human Population Density <sup>3</sup>
	Area-weighted Percent Surficial Alluvium <sup>3</sup>
Mean Permeability (Soil L1 Horizon) <sup>3</sup>	
Reach	Mean Annual Water Velocity <sup>2</sup>
	Mean Reach Slope <sup>2</sup>
	Sinuosity of River Segment
	Impounded (Boolean)
	Majority Surficial Geology Unit within 100 m of River <sup>4</sup>
	Area-weighted Percent Forest within 100 m of River <sup>4</sup>
	Area-weighted Percent Karst Geology within 100 m of River <sup>4</sup>
	Mean Permeability (Soil L1 Horizon) within 100 m of River <sup>4</sup>
	Mean pH (Soil L1 Horizon) within 100 m of River <sup>4</sup>
Weighted Average Sand Percentage (Soil L1 Horizon) within 100 m of River <sup>4</sup>	

<sup>1</sup> Worldclim 30-arcsecond resolution climate data (<http://www.worldclim.org>)<sup>2</sup> Used variable as provided with NHDPlus ([http://www.horizon-systems.com/NHDPlus/NHDPlusV1\\_home.php](http://www.horizon-systems.com/NHDPlus/NHDPlusV1_home.php))<sup>3</sup> Accumulated with the CA3T NHDPlus Catchment Attribute Allocation and Accumulation Tool<sup>4</sup> Summarized with Zonal Statistics function in ArcGIS

Table 5.4. Environmental variables excluded from modeling because of high correlation (>0.8) with variables from Table 5.3.

Climate	Isothermality (BIO3) <sup>1</sup>
	Temperature Annual Range (BIO7) <sup>1</sup>
	Mean Temperature of Warmest Quarter (BIO10) <sup>1</sup>
	Mean Temperature of Coldest Quarter (BIO11) <sup>1</sup>
	Precipitation of Wettest Month (BIO13) <sup>1</sup>
	Precipitation of Driest Month (BIO14) <sup>1</sup>
	Precipitation of Wettest Quarter (BIO16) <sup>1</sup>
	Precipitation of Driest Quarter (BIO17) <sup>1</sup>
	Precipitation of Warmest Quarter (BIO18) <sup>1</sup>
	Precipitation of Coldest Quarter (BIO19) <sup>1</sup>
Catchment	Area-weighted Percent Development (2001 NLCD) <sup>2</sup>
	Area-weighted Percent Native Vegetation (2001 NLCD) <sup>2</sup>
	Weighted Average Percent Imperviousness (2001 NLCD) <sup>3</sup>
	Area-weighted Percent Karst Geology <sup>3</sup>
	Mean pH (Soil L1 Horizon) <sup>3</sup>
Mean Sand Area-weighted Percentage (Soil L1 Horizon) <sup>3</sup>	
Reach	Mean Annual Flow <sup>2</sup>

<sup>1</sup> Worldclim 30-arcsecond resolution climate data (<http://www.worldclim.org>)

<sup>2</sup> Used variable as provided with NHDPlus ([http://www.horizon-systems.com/NHDPlus/NHDPlusV1\\_home.php](http://www.horizon-systems.com/NHDPlus/NHDPlusV1_home.php))

<sup>3</sup> Accumulated with the CA3T NHDPlus Catchment Attribute Allocation and Accumulation Tool

Table 5.5. Using stream reaches as the standard unit for background selection instead of a raster background improved model performance for 20 of 22 species (indicated with \*). Using a larger training extent (northeastern U.S. versus Maine) further improved model performance in New Hampshire for 19 of 22 species (indicated with +).

Species	No. of Training samples		No. of Test samples	Training AUC	Test AUC	Training AUC	Test AUC	Training AUC	Test AUC
	Northeast U.S.	Maine	NHDS	Raster background		Stream reach as background		Maine training	
<i>Boyeria graefiana</i> * <sup>+</sup>	141	80	21	0.973	0.909	0.985	0.949	0.981	0.739
<i>Boyeria vinosa</i> * <sup>+</sup>	358	160	144	0.932	0.887	0.962	0.902	0.971	0.788
<i>Calopteryx amata</i> * <sup>+</sup>	129	90	47	0.985	0.898	0.994	0.961	0.971	0.706
<i>Calopteryx maculata</i> * <sup>+</sup>	589	187	213	0.873	0.733	0.919	0.837	0.941	0.758
<i>Didymops transversa</i> * <sup>+</sup>	133	92	81	0.974	0.910	0.984	0.944	0.984	0.787
<i>Gomphus abbreviatus</i> * <sup>+</sup>	39	30	45	0.992	0.982	0.998	0.989	0.995	0.965
<i>Gomphus adelphus</i> * <sup>+</sup>	160	138	47	0.985	0.958	0.995	0.977	0.975	0.847
<i>Gomphus descriptus</i> * <sup>+</sup>	56	33	41	0.982	0.793	0.993	0.922	0.988	0.706
<i>Gomphus vastus</i> * <sup>+</sup>	44	13	23	0.996	0.990	0.999	0.993	0.999	0.787
<i>Hetaerina americana</i>	131	12	16	0.974	0.883	0.987	0.876	0.988	0.934
<i>Lanthus parvulus</i> * <sup>+</sup>	56	30	21	0.959	0.822	0.977	0.950	0.983	0.698
<i>Macromia illinoiensis</i> * <sup>+</sup>	238	162	64	0.971	0.933	0.987	0.961	0.978	0.811
<i>Neurocordulia obsoleta</i> * <sup>+</sup>	63	60	38	0.994	0.969	0.998	0.983	0.995	0.964
<i>Neurocordulia yamaskanensis</i> <sup>+</sup>	51	27	16	0.994	0.971	0.998	0.967	0.998	0.911
<i>Ophiogomphus aspersus</i> * <sup>+</sup>	85	71	39	0.986	0.967	0.994	0.984	0.989	0.810
<i>Ophiogomphus carolus</i> * <sup>+</sup>	149	123	17	0.987	0.948	0.996	0.974	0.983	0.876
<i>Ophiogomphus howei</i> * <sup>+</sup>	37	33	14	0.996	0.982	0.999	0.991	0.998	0.962

Table 5.5. Continued.

Species	No. of Training samples		No. of Test samples	Training AUC	Test AUC	Training AUC	Test AUC	Training AUC	Test AUC
	<i>Northeast U.S.</i>	<i>Maine</i>	<i>NHDS</i>	<i>Raster background</i>		<i>Stream reach as background</i>		<i>Maine training</i>	
<i>Ophiogomphus mainensis</i> * <sup>+</sup>	149	125	22	0.986	0.952	0.995	0.978	0.981	0.785
<i>Ophiogomphus rupinsulensis</i> *	129	91	34	0.986	0.965	0.996	0.986	0.990	0.902
<i>Progomphus obscurus</i> *	34	10	17	0.991	0.972	0.980	0.978	0.998	0.979
<i>Stylogomphus albistylus</i> * <sup>+</sup>	337	142	50	0.942	0.811	0.971	0.823	0.971	0.754
<i>Stylurus scudderi</i> * <sup>+</sup>	21	12	38	0.996	0.932	0.998	0.975	0.976	0.785
<b>Median</b>	129	75.5	38	0.985	0.940	0.994	0.971	0.983	0.799

Note: Model performance was assessed using the New Hampshire Dragonfly Survey (NHDS) as test data. Only species with more than 10 training and 10 test samples were included.

Table 5.6. Performance of bias correction schemes relative to no bias correction using West Virginia Dragonfly and Damselfly Atlas (WVDDA) as test data.

Species	No. of Training samples	No. of Test samples	Training AUC	Test AUC	Difference in Test AUC relative to no bias correction						
			<i>No Bias</i>	<i>Localities thinned by 25 km</i>	<i>TGS Background</i>	<i>TGS Count Bias</i>	<i>TGS 8-digit watershed count bias</i>	<i>TGS 12-digit sub-watershed count bias</i>	<i>TGS 8-digit watershed count bias re-classified</i>	<i>TGS 12-digit sub-watershed count bias re-classified</i>	
<i>Archilestes grandis</i>	17	11	0.985	0.481	0.047	0.354	0.489	0.349	0.294	0.153	0.208
<i>Argia sedula</i>	24	22	0.989	0.911	0.003	-0.011	0.038	0.056	0.043	0.023	0.032
<i>Argia tibialis</i>	62	25	0.983	0.878	0.023	0.024	0.068	0.056	0.077	0.012	0.058
<i>Argia translata</i>	52	75	0.977	0.913	-0.026	0.014	0.057	0.059	0.056	0.024	0.042
<i>Boyeria grafiana</i>	150	12	0.986	0.894	-0.024	-0.132	-0.016	0.026	0.034	-0.035	0.021
<i>Boyeria vinosa</i>	464	38	0.966	0.676	0.082	-0.446	-0.062	0.090	0.045	-0.020	0.021
<i>Calopteryx amata</i>	159	17	0.991	0.914	0.001	-0.222	-0.074	0.024	0.004	0.013	0.006
<i>Calopteryx maculata</i>	640	162	0.938	0.570	0.081	-0.164	0.195	0.139	0.109	-0.005	0.054
<i>Didymops transversa</i>	199	15	0.984	0.752	0.050	-0.356	-0.068	0.106	0.043	0.016	0.006
<i>Gomphus lividus</i>	88	48	0.978	0.815	-0.004	-0.041	0.092	0.113	0.082	0.041	0.058
<i>Gomphus vastus</i>	56	11	0.999	0.996	0.003	-0.147	-0.168	-0.001	-0.001	0.001	0
<i>Gomphus viridifrons</i>	14	13	0.963	0.934	0.004	0.032	0.045	0.045	0.052	0.019	0.041
<i>Hetaerina americana</i>	101	46	0.989	0.919	0.029	-0.249	-0.106	0.042	0.038	0.012	0.023
<i>Macromia illinoensis</i>	279	23	0.985	0.917	0.034	-0.328	-0.136	0.045	0.047	0.015	0.043
<i>Stylogomphus albistylus</i>	346	41	0.971	0.746	0.113	-0.443	-0.044	0.082	0.080	-0.049	0.035
Median	101	23	0.984	0.894	0.023	-0.147	-0.016	0.056	0.047	0.013	0.035
Median of species common to NHDS and WVDDA test datasets	199	23	0.985	0.894	0.034	-0.249	-0.068	0.045	0.043	0.001	0.021

Note: Test AUC improvements are indicated in bold. Only species with more than 10 training and 10 test samples were included. Shaded species are common to both NHDS and WVDDA test datasets.

Table 5.7. Performance of bias correction schemes relative to no bias correction using New Hampshire Dragonfly Survey (NHDS) as test data.

Species	No. of Training samples	No. of Test samples	Training AUC	Test AUC	Difference in Test AUC relative to no bias correction						
			No Bias	Localities thinned by 25 km	TGS Background	TGS Count Bias	TGS 8-digit watershed count bias	TGS 12-digit sub-watershed count bias	TGS 8-digit watershed count bias re-classified	TGS 12-digit sub-watershed count bias re-classified	
<i>Boyeria grafiana</i>	141	21	0.985	0.949	0.001	-0.186	-0.211	-0.035	-0.050	-0.031	-0.042
<i>Boyeria vinosa</i>	358	144	0.962	0.902	-0.047	-0.336	-0.234	0.007	-0.033	0.007	-0.019
<i>Calopteryx amata</i>	129	47	0.994	0.961	-0.007	-0.187	-0.149	-0.035	-0.030	-0.022	-0.030
<i>Calopteryx maculata</i>	589	213	0.919	0.837	-0.030	-0.081	-0.013	0.004	-0.012	0.015	-0.012
<i>Didymops transversa</i>	133	81	0.984	0.944	-0.020	-0.153	-0.147	-0.038	-0.049	-0.022	-0.049
<i>Gomphus abbreviatus</i>	39	45	0.998	0.989	0.002	-0.148	-0.186	-0.007	-0.026	-0.003	-0.015
<i>Gomphus adelphus</i>	160	47	0.995	0.977	0	-0.403	-0.517	-0.023	-0.047	-0.014	-0.034
<i>Gomphus descriptus</i>	56	41	0.993	0.922	0.004	-0.315	-0.304	-0.059	-0.060	-0.027	-0.063
<i>Gomphus vastus</i>	44	23	0.999	0.993	0.003	-0.078	-0.066	0.001	-0.008	0	-0.004
<i>Hetaerina americana</i>	131	16	0.987	0.876	-0.009	-0.207	-0.096	0.068	0.038	0.024	0.018
<i>Lanthus parvulus</i>	56	21	0.977	0.950	-0.030	-0.179	-0.189	-0.058	-0.079	-0.037	-0.054
<i>Lanthus vernalis</i>	39	10	0.967	0.728	-0.042	0.076	0.147	-0.052	-0.073	-0.039	-0.035
<i>Macromia illinoiensis</i>	238	64	0.987	0.961	0.002	-0.253	-0.226	-0.029	-0.073	-0.019	-0.046
<i>Neurocordulia obsoleta</i>	63	38	0.998	0.983	-0.003	-0.119	-0.123	-0.016	-0.025	-0.008	-0.019
<i>Neurocordulia yamaskanensis</i>	51	16	0.998	0.967	-0.029	-0.079	-0.089	-0.013	-0.034	-0.010	-0.032
<i>Ophiogomphus aspersus</i>	85	39	0.994	0.984	-0.005	-0.303	-0.309	-0.023	-0.046	-0.013	-0.033
<i>Ophiogomphus carolus</i>	149	17	0.996	0.974	-0.008	-0.388	-0.528	-0.038	-0.066	-0.020	-0.045
<i>Ophiogomphus howei</i>	37	14	0.999	0.991	0.001	-0.283	-0.403	-0.010	-0.043	-0.005	-0.023
<i>Ophiogomphus mainensis</i>	149	22	0.995	0.978	0.003	-0.318	-0.394	-0.028	-0.034	-0.016	-0.032
<i>Ophiogomphus rupinsulensis</i>	129	34	0.996	0.986	-0.011	-0.234	-0.217	-0.017	-0.044	-0.008	-0.029
<i>Progomphus obscurus</i>	34	17	0.980	0.978	-0.047	-0.038	-0.060	0.005	-0.008	0.005	0.001
<i>Stylogomphus albistylus</i>	337	50	0.971	0.823	0.038	-0.365	-0.239	0.003	-0.052	-0.012	-0.043
<i>Stylurus scudderi</i>	21	38	0.998	0.975	-0.006	-0.274	-0.327	-0.020	-0.032	-0.008	-0.028
<i>Stylurus spiniceps</i>	39	35	0.999	0.988	-0.003	-0.049	-0.051	0.006	0.002	0.003	0.002

Table 5.7. Continued.

Species	No. of Training samples	No. of Test samples	Training AUC	Test AUC	Difference in Test AUC relative to no bias correction						
			<i>No Bias</i>	<i>Localities thinned by 25 km</i>	<i>TGS Background</i>	<i>TGS Count Bias</i>	<i>TGS 8-digit watershed count bias</i>	<i>TGS 12-digit sub-watershed count bias</i>	<i>TGS 8-digit watershed count bias reclassified</i>	<i>TGS 12-digit sub-watershed count bias reclassified</i>	
Median	107	36.5	0.994	0.971	-0.006	-0.197	-0.200	-0.018	-0.039	-0.011	-0.031
Median of species common to NHDS and WVDDA test datasets	141	50	0.985	0.944	-0.007	-0.187	-0.149	0.001	-0.033	-0.012	-0.030

Note: Test AUC improvements are indicated in bold. Only species with more than 10 training and 10 test samples were included. Shaded species are common to both NHDS and WVDDA test datasets.

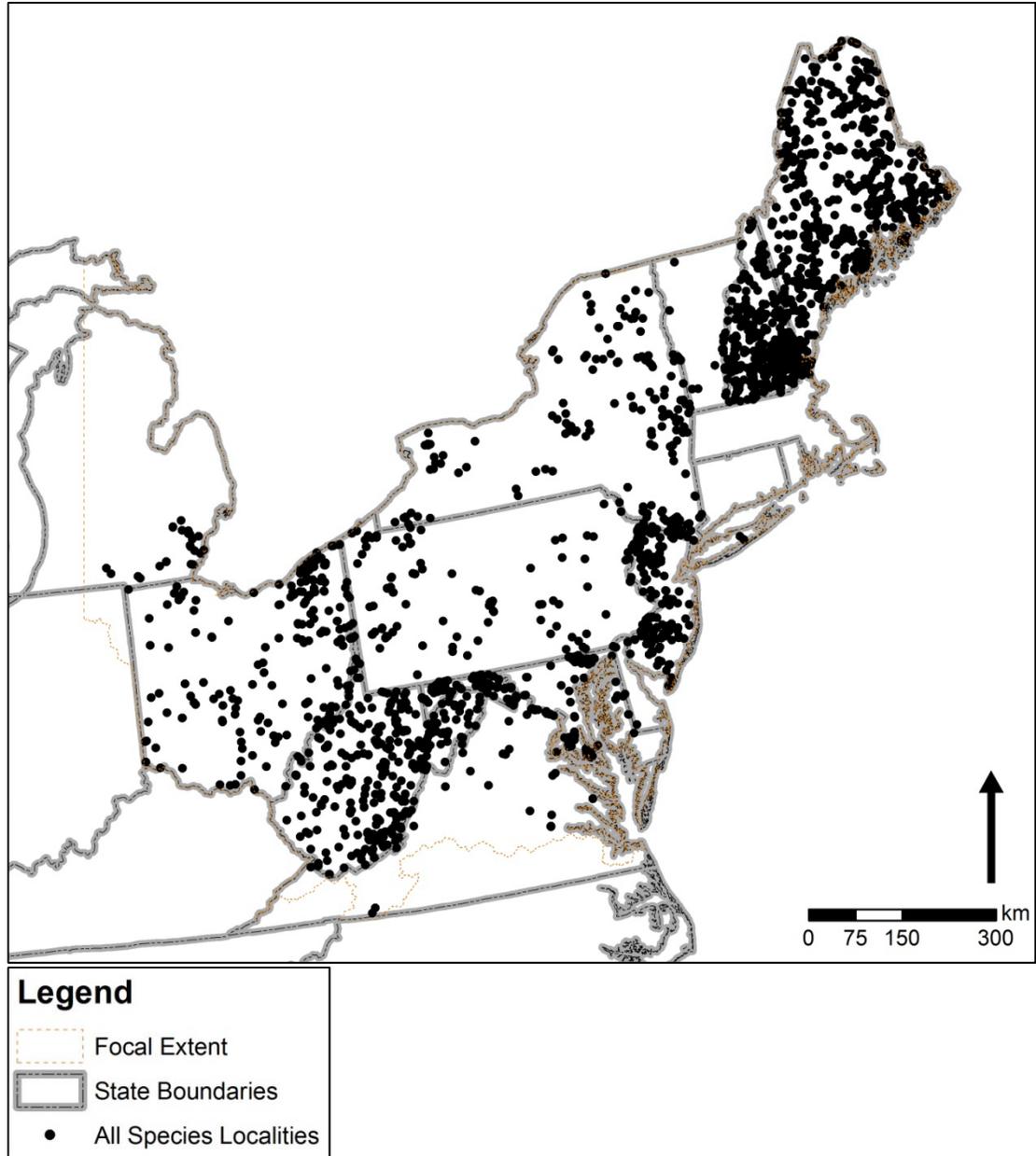
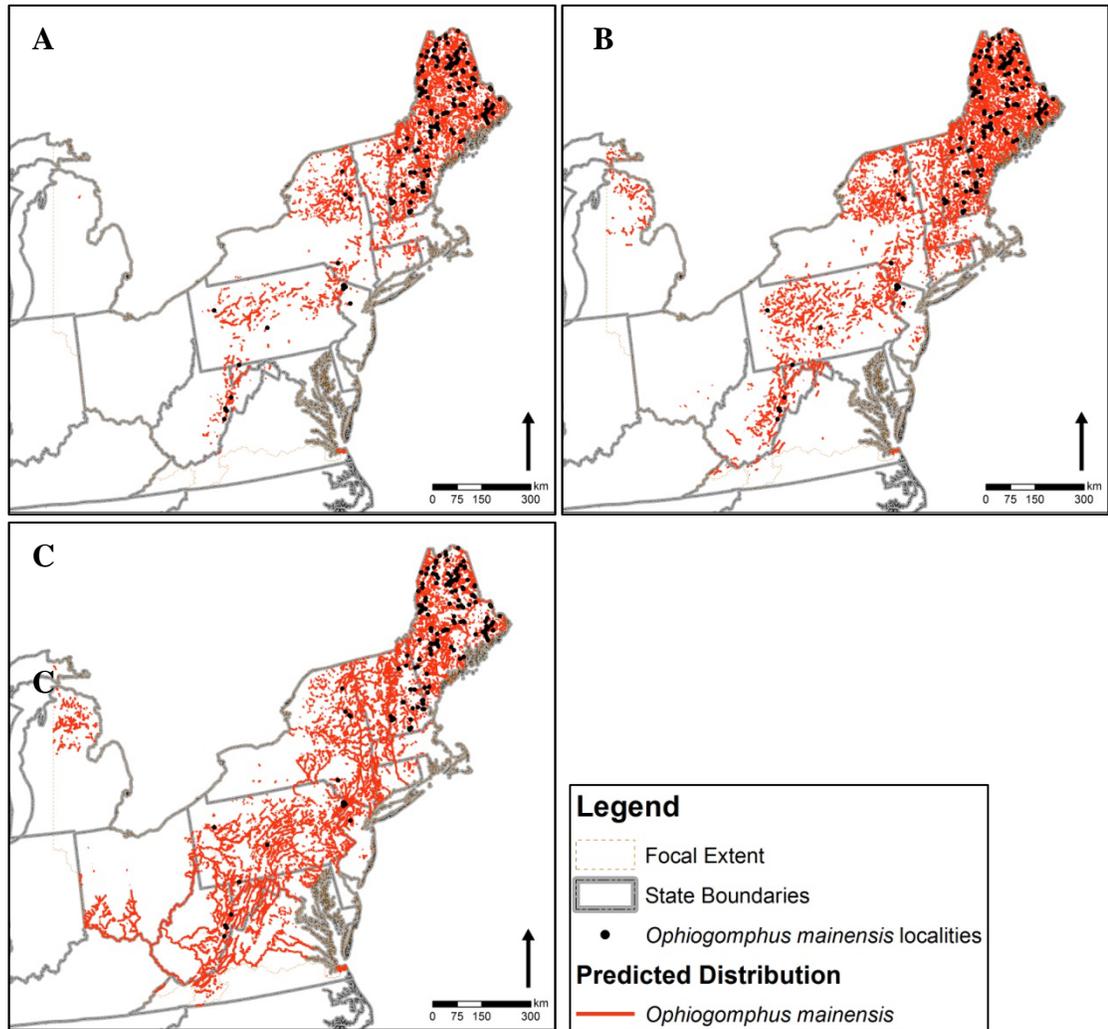


Figure 5.1. Lotic odonate data were obtained from several sources and densities varied across the northeastern U.S. focal extent.



Note: The trend of increased overprediction with a thinned training dataset or bias correction also is evident in other species tested (not shown) and may occur when sampling bias correction is not required.

Figure 5.2. Predicted distribution of *Ophiogomphus mainensis* using (A) no bias correction, (B) thinned training localities, and (C) an 8-digit USGS watershed (HUC8) TGS count bias correction.

## CHAPTER VI

# IDENTIFYING REFUGIA IN THE FACE OF CLIMATE CHANGE: PROJECTING FINE-RESOLUTION DISTRIBUTION MODELS OF RIVERINE DRAGONFLIES TO FUTURE CLIMATES

### Abstract

Lotic odonates (dragonflies and damselflies), amphibious indicators of river and riparian health, are excellent representatives of riverine niche diversity. These species are relatively well-surveyed, so riverine species distribution models (SDMs) can quantify the distribution of these niches throughout dendritic networks and predict how future climates may impact habitat availability. Locality data from state surveys were combined to generate river-specific SDMs for 15 species of lotic odonates throughout a 784,982 km<sup>2</sup> portion of the northeastern U.S. using climatic, catchment, and local predictors. Projections to 2080 (CCSM4 and HadCM3-ES global climate models and RCP 4.5 and 8.5 gas-emissions scenarios) indicate the number of suitable river reaches will drop by 45% to 99% depending on species, with 935 km of river (434 river segments) identified as climatic refugia for 20% or more of these indicator species. Contractions of suitable future niche space were evident, meaning that even lotic species that are not considered imperiled under current conditions may become so in future climates.

### Introduction

River biodiversity faces many threats including flow alteration, water extraction, and increased temperatures or changes in the quantity and seasonality of precipitation because of climate change (Simaika et al. 2013). The future trend of several of these threats depends on political and social actions, which are difficult to predict, though future climate can be predicted with greater certainty than other anthropogenic stressors (Intergovernmental Panel on Climate Change 2013). These predictions can be used to develop conservation management strategies to retain river biodiversity and function.

Though climate change studies of invertebrates have mostly looked at the advantage some species will have in a warmer climate, coldwater species may be negatively affected, resulting in range retreat (Jaeschke et al. 2013, Suhling and Suhling 2013). Odonata (dragonflies and damselflies, collectively often called dragonflies) are one of the best-known orders of freshwater invertebrates, are relatively well-collected, occupy a high trophic position, and exhibit species-specific habitat requirements (Corbet 2004). For these reasons, dragonflies are effective surrogates for other freshwater taxa (Darwall et al. 2011) and for selecting areas for the conservation of freshwater diversity (Simaika and Samways 2009). Furthermore, Odonata are useful for studying the impacts of climate change on freshwater diversity because much their development is closely tied to temperature, and temperature optima are thought to be primary factors limiting species distributions (Corbet et al. 2006, Hassall and Thompson 2008, Bush et al. 2013). In addition, lotic Odonata are susceptible to increased rainfall frequency, because rain after emergence significantly decreases survival (Thompson 1990). Rainfall intensity and river flooding in the northeastern U.S. is projected to increase (National Research Council 2014), so lotic Odonata populations may be negatively affected during emergence, and existing locales may no longer be suitable. Finally, adults are vagile enough to potentially respond to climate-induced range shifts.

The habitat requirements of riverine Odonata are an integration of climate, riparian quality, and local aquatic conditions, which are a function of the upstream watershed. Non-climatic factors including topography, hydrology, and land use restrict the distribution of lotic species (Collins and McIntyre *in review*), so projecting species distributions to future climates while not considering these factors may grossly overestimate available habitat. If habitats are not available in newly climatically suitable locations, lotic species will not be able to colonize these otherwise climatically suitable locations (Jaeschke et al. 2013).

Species can respond to climate change in three ways: dispersal to suitable climatic conditions resulting in a range shift or range expansion, adaptation without

dispersal, or extinction (Coope 1995, Hickling et al. 2005, Hof et al. 2011). Dispersal is only possible for most Odonata during a relatively short window when adults emerge, and highly specialized species or species with low dispersal rates may lag behind climate changes, such that some invertebrate species may fail to colonize northwards (Hickling et al. 2005). The limited dispersal abilities of lotic Odonata also means that habitat fragmentation attributable to non-climatic factors may affect these species more than lentic species (Grewe et al. 2013). The presence of climatic refugia assuming no dispersal may be especially important for species with low population sizes that may not be able to track climate change. These refugia for Odonata may also be likely spots for high freshwater diversity overall (Simaika et al. 2013).

Unfortunately, dispersal abilities and colonization rates of Odonata are poorly known for many species (Jaeschke et al. 2013). Whereas lentic Odonata have been documented to be dispersing northward with a warming climate an average of 115 km per decade, lotic Odonata have not expanded their range (Hickling et al. 2005, Grewe et al. 2013). Well-known species that perform long-distance dispersal or migration are lentic (May 2013), and it is thought that lentic species disperse farther and more readily than lotic ones because lentic habitats are less stable spatially and temporally (Hof et al. 2006, Marten et al. 2006). Dispersal estimates are available for only a few lotic species (Stettmer 1996, Hickling et al. 2005, Corbet et al. 2006, Jaeschke et al. 2013), and these studies had varied methods and sample sizes. Of those lotic species where dispersal is known, it may vary from 1 to 13 km per generation (Stettmer 1996, Hickling et al. 2005), and larval development times vary from 1 to 3 or more years (Corbet et al. 2006). Range shifts in lotic Odonata have been recorded to be 41 to 73 km in two species of *Calopteryx* damselflies and 104 km in the dragonfly *Gomphus vulgatissimus* over an approximately 25-year period (Hickling et al. 2005). These data roughly translate to a possible dispersal distance of 30 km for damselflies and 200 km for dragonflies by 2050, or 50 km for damselflies and 350 km for dragonflies by 2080 (Table 6.1). A high dispersal ability does not necessarily translate to high success in colonizing new habitats effectively. For example, Jaeschke et al. (2013) found that

incorporating species-specific dispersal abilities into species distribution model (SDM) projections significantly limited the projected distribution. By comparing SDM projections that ignore dispersal abilities to projections assuming no dispersal, upper and lower boundaries of projected future range size can be determined, even if the upper boundaries may be unrealistic (Franklin 2010, Jaeschke et al. 2013).

Some recent studies have investigated the potential affect of climate change on Odonata (Ott 2010, Jaeschke et al. 2013), but no investigation has shown how U.S. species will be affected. Although lotic species do not dominate U.S. diversity, 18 of the 37 most imperiled odonates in the U.S. require flowing streams, (Bick 2003, Dunkle 2004). Climate change may put an additional stressor on these organisms, including species that are not currently imperiled. This study intended to determine how both natural and anthropogenic factors restrict the present-day and future projected ranges of lotic Odonata and how dispersal limitations may further restrict their projected ranges. Assessing fine-scale climate change impacts across a broad region for freshwater taxa, and establishing a baseline for where conservation efforts are best focused is urgent, and this study aims to assist that effort.

## **Materials and methods**

### ***Focal extent***

In this study, the finest spatial resolution used was the river reach (a stream or river segment between the confluence with a tributary, lake, marsh, or swamp and the following confluence). The dendritic network used for this project is the National Hydrography Dataset (NHD; <http://nhd.usgs.gov/>), which is a comprehensive set of vector data representing rivers, streams and other waterbodies within the coterminous United States. The NHD was originally produced from USGS hydrologic digital line graph files, which were derived from USGS quadrangle maps. The NHD is divided into 21 water resource regions within the U.S. Those regions selected for this project include the Northeast, the Mid-Atlantic, the Great Lakes, and the Ohio drainages. The

extent was clipped to exclude states where little or no lotic georeferenced dragonfly data are available, such as Rhode Island, Connecticut, Massachusetts, Kentucky, and North Carolina. The focal extent included Maine, New Hampshire, Vermont, New York, New Jersey, Pennsylvania, Ohio, southeastern Michigan, northeastern Indiana, Delaware, Maryland, West Virginia, and the portion of Virginia within the Mid-Atlantic water resource region. The dataset contained 360,791 stream segments within the focal extent of 784,982 km<sup>2</sup> (Fig. 6.1).

### ***Species data***

Future projections tend to be more consistent for widespread species and highly restricted species with narrow niches (Buisson et al. 2010). The study species consisted of both widespread species (e.g. *Stylurus spiniceps*) and restricted species (e.g. *Ophiogomphus* sp.) (Tennessee 1993, Dunkle 2000, 2004, Gibbs et al. 2004) (Table 6.1). Vouchered localities for stream and river-obligate Odonata were obtained from multiple expert-confirmed sources (Table 6.2) and were carefully vetted.

To associate species data (typically collected on land) with the appropriate river reach, the georeferenced coordinates of all study species localities were moved in a downslope direction to the closest reach with TauDEM (<http://hydrology.usu.edu/taudem/taudem5/>). Because the accurate coordinates for a locality may be the bank of a wide river where the river centerline is farther away from the bank than nearby tributary confluences, this process better associated each locality with its correct river than a nearest-line analysis would have. All localities moved more than 100 m by TauDEM were checked against the written description of the locality and moved manually to the correct location if required. Localities that could not be resolved with the river network were omitted. Histograms of catchment area for each species' localities were made, and outlier locations were corrected if the written description justified it. The databases were filtered so no species had more than one record per river reach. The first species record from each reach was retained. After this filtering process, 5,524 records of 48 lotic odonates remained (Fig. 6.1). To ensure climatic tolerances were conservatively represented, only species that have a

majority of their known range within the focal extent were retained for modeling. Additionally, only species with sufficient records for testing and high model performance were retained (see Species distribution modeling below). This additional filtering resulted in 1,680 records of 15 lotic odonates (Tables 6.1 and 6.2).

### ***Environmental data***

Environmental variables that described the climate, land use, soils, geology, and topography within each stream's watershed and its riparian area were used for SDM development (Table 6.3). The dendritic network of 360,791 stream reaches within the focal extent was taken from the National Hydrography Dataset (NHD). Climate values for each stream reach were taken from the 30-arcsecond Worldclim bioclimatic dataset (Hijmans et al. 2005). Values of other environmental variables for each stream reach were extracted from 30-m raster grids, some of which were developed with the CA3T NHDPlus Catchment Attribute and Allocation Tool. Pearson's correlation coefficients for all environmental variables were calculated, and one variable was omitted for all pairs with a coefficient greater than 0.8 (Rinnhofer et al. 2012). In each correlated pair, the variable with the higher predictive capacity was retained.

### ***Future climate ensemble***

The large number of permutations possible between all Global Climate Models (GCMs) and Gas Emission Scenarios (GEMs) cover a wide range of potential future climates. This uncertainty necessitates ensemble forecasting in SDM studies (Buisson et al. 2010). Many ecological studies have projected species distributions to future climates, though investigating the range of potential climate scenarios is a relatively new and infrequent phenomenon (Buisson et al. 2010). Use of a single GCM in SDM studies seems to be a matter of convenience that is not statistically justified (Fordham et al. 2011); fortunately new tools have made ensembles easier to implement (Thuiller et al. 2009).

Producing SDMs with individual GCMs and then displaying the agreement and disagreement between those predictions is known as producing an SDM ensemble, which may be applied as the average or median of SDM predicted probabilities or as frequency histograms of predictions (Araújo and New 2007). If a threshold is used to discriminate between predicted presence and absence, the primary difference in these two ensembles is when the threshold is applied. If the predicted probabilities from each SDM are averaged and then a threshold is applied, model uncertainty is combined with uncertainty attributable to the GCM. Therefore, it is best to apply a threshold to each SDM, and then aggregate those results.

Global climate model (GCM) predictions statistically downscaled to Worldclim (Hijmans et al. 2005, Ramirez and Jarvis 2010) are used regularly for SDM projections to future climates (Domisch et al. 2011). Two commonly used GCMs were used for future climate projections: the National Center for Atmospheric Research's CCSM4 and the Met Office Hadley Centre's HadGEM2-ES. Both of these GCMs are well-established, though HadGEM2-ES, which incorporates dynamic vegetation, ocean biology, and atmospheric chemistry, has a relatively high climate sensitivity compared to other models (Andrews et al. 2012). Climate sensitivity is the temperature change resulting from doubling the atmospheric CO<sub>2</sub> concentration. These models do not represent a comprehensive range of model-projected future climates, but two plausible outcomes.

Two GEMs were selected, representative concentration pathways (RCP) 4.5 and 8.5, which represent the mid-range and 90<sup>th</sup> percentile of the projected emissions range (Moss et al. 2010). RCP 8.5 illustrates increasing greenhouse gas emissions over time and increased use of cropland and grasslands driven by increased global population and represents a global temperature anomaly of 4.9°C by 2100, which is roughly equivalent to the commonly used (but now outdated) SRES A1F1 scenario (Riahi et al. 2007, Van Vuuren et al. 2011, Rogelj et al. 2012). RCP 4.5 illustrates a stabilized total radiative forcing by 2100 and decreased use of cropland and grassland because of yield increases, dietary changes, and reforestation. RCP 4.5 represents a

global temperature anomaly of 2.4°C, which is roughly equivalent to the outdated SRES B1 scenario (Moss et al. 2010, Rogelj et al. 2012). Though choice of GEM makes little difference on SDM projections in the short term, it may be important for projections made to 2080 (2070–2099) (Buisson et al. 2010). Use of multiple GCMs and GEMs generates an ensemble output that brackets a range of possible outcomes.

### ***Species distribution modeling***

Fine-scale models for the study species of lotic dragonflies in the northeastern U.S. focal extent were developed in Maxent v.3.3.3k using default parameters for regularization, prevalence, and feature creation. No manipulation of locality data or background selection was performed to compensate for sampling bias, because previous analysis indicated that these measures did not improve predictive ability for this dataset (Chapter V). Foregoing gridded raster datasets, models were developed with SWD (species with data) format, where each stream reach was the basic unit for prediction and background selection. Not only does this greatly speed processing, using stream reaches as background units was found to improve predictive ability (Collins and McIntyre *in review*). Precisely 30,000 stream reaches were randomly selected for the background.

To assess model performance, two independent test datasets were used. Models were trained with all data from the focal extent excluding New Hampshire and then tested with New Hampshire Dragonfly Survey (NHDS) data, and similarly, models were trained by excluding West Virginia and then tested with West Virginia Dragonfly and Damselfly Atlas (WVDDA) data. Model performance with either test dataset was assessed by the test AUC metric, which is threshold-independent and not influenced by species prevalence (Hanley and McNeil 1982, Fielding and Bell 1997, Guisan and Zimmermann 2000). Only those species with 10 or more records in either of these databases and those with a relatively high test AUC value (greater than 0.89) (see Swets, 1988) were retained for modeling, resulting in the 15 study species projected to future climates (Table 6.1).

The 15 study species are found in wooded landscapes, with trees required by adults for daytime roosting (e.g. the crepuscular *Neurocordulia yamaskanensis*), for shade (e.g. *Boyeria grafiana*), or perching (e.g. *Gomphus adelphus*). Some inhabit small streams (e.g. *Calopteryx amata*, *Lanthus parvulus*) while others inhabit large rivers (e.g. *Neurocordulia yamaskanensis*, *Ophiogomphus rupinsulensis*). Most are tied to a preferred substrate type, such as mud (e.g. *Gomphus abbreviatus*), silt (e.g. *Ophiogomphus rupinsulensis*), sand (e.g. *Ophiogomphus aspersus*), or rocks (e.g. *Ophiogomphus mainensis*). Some species (e.g. *Ophiogomphus* sp.), have very short adult flight periods, whereas others (e.g. *Boyeria grafiana*) are much longer. Most require pristine rivers, but some are known to be more tolerant of anthropogenic effects (e.g. *Ophiogomphus rupinsulensis*) (Gibbs et al. 2004, Paulson 2011).

Though land use will almost certainly change in response to climate change and human population increases, future land use and human population scenarios are not readily available (but see Bierwagen et al., 2009) and will be highly uncertain because land use change also depends on political developments. Therefore projected species distributions were made that incorporated differences in future climates (9 variables) but kept the other 19 environmental variables constant. Models were projected to 2080 (2070–2099).

A second set of models was developed with bioclimatic data only and then masked by the models that considered bioclimatic and non-climatic environmental variables (Fordham et al. 2012). This approach was used to identify habitat that may have otherwise been considered suitable if fine-scale modeling was not considered.

Each projection was thresholded using the equal sensitivity-specificity threshold for the current model, such that correctly predicted presences and correctly predicted absences have the same probability of occurring (Fielding and Bell 1997). The projections were evaluated individually (as in Buisson et al., 2010). Future localities were identified that were common to each GCM and those where one GCM indicated future suitability and one GCM indicated future unsuitability.

Species richness was determined for each stream reach for present-day conditions and for the four projections to 2080 assuming no dispersal and unlimited dispersal. Species-rich streams assuming no dispersal were identified as refugia for freshwater diversity.

## Results

Model performance determined by test AUC was high for all species, with a median value of 0.974 (Table 6.4). Models built with fine-scale non-climatic factors such as watershed and riparian characteristics restricted available habitat by a median of 77% (minimum 46%, maximum 88%) compared to bioclimatic models, as assessed by length of suitable streams (Table 6.4).

Assuming unlimited dispersal, future climates are expected to be detrimental (decreased habitat availability) for all 15 study species. The ranges will retreat to a median of 7% to 51% of their former size, varying with GCM/GEM selection. Retained habitat is river that theoretically does not require dispersal to occupy because it is considered suitable under both current and future climates. Assuming no dispersal, the median range retreat varies from 7% to 50% of the former range size depending on GCM/GEM selection (Table 6.4). Newly available habitat, river that was not predicted to be suitable under current climate but will be suitable under future climates, is minimal. The median amount of newly available river varies from 0% to 1.6% of the former range size depending on GCM/GEM selection (Table 6.4). The most vulnerable species to climate change were *Lanthus parvulus*, *Stylurus scudderi*, and *Stylurus spiniceps*, and the least affected were *Gomphus abbreviatus* and *Neurocordulia yamaskanensis*. Choice of GCM had a considerable impact, with the HadCM3-ES GCM showing less future habitat availability compared to the CCSM4 GCM for both GEMs (RCP 4.5 and 8.5) for all but one species, *Ophiogomphus rupinsulensis* (Table 6.4). Choice of GEM also had a considerable impact, with a median habitat reduction of 71 and 50% under RCP 8.5 compared to RCP 4.5 for the HadCM3-ES and CCSM4 GCMs, respectively (Table 6.4).

Lotic Odonata diversity will decline throughout the region, especially in southern locales (Figs. 6.2 and 6.3). Refugia for lotic Odonata diversity were identified by considering rivers with predicted suitable habitat in both current and future climates under both GCMs and GEMs, a conservative ensemble assuming no dispersal (Fig. 6.4). Four-hundred thirty-four river segments representing 935 km of river were identified as climatic refugia for 3 or more species assuming no dispersal and a consensus of climate projections (Table 6.5).

## **Discussion**

Based on experiments with three lentic species, the optimum air temperatures for larval growth in Odonata is between 21 and 29°C (Krishnaraj and Pritchard 1995, Flenner et al. 2010, Suhling and Suhling 2013). When the temperature is either warmer or cooler than the optimum temperature for a particular hemimetabolous insect such as a lotic Odonata species, the larval growth rate and ultimate size is reduced, which can affect adult mortality and reproduction (Sweeney and Vannote 1978). Within the focal extent the average temperature of the hottest month currently varies from 18.6 to 32.2°C, which falls within 3°C of the optimum temperature range for odonate growth. This range is projected to vary from 22.1 to 40.5°C by 2080 depending on GCM and GEM (comparing two GCMs, CCSM4 and HadGEM2-ES, and two GEMs, RCP 4.5 and RCP 8.5). Regardless of GCM or GEM, some parts of the focal extent are projected to extend beyond the optimum temperature range in summer.

Odonata are a relatively ancient order (Corbet 2004), and their current cosmopolitan distribution and high diversity are indications that they are robust to change. However, it is thought that the current high Odonata species diversity in the northeastern U.S. may be a result of recent glaciation (Dunkle 2000), so many of the species of interest have evolved in a relatively stable and recent climate. Therefore, these species may not be capable of surviving projected climate shifts or dispersing quickly to track climate change. For example, Grewe et al. (2013) found that European lotic Odonata species have not expanded their range northward in response

to climate change, suggesting that lotic species are less capable of colonizing new habitats than lentic species. Though voltinism is not known for many of the study species, the majority of them are assumed to be semivoltine or partivoltine (Table 6.1), indicating that they require relative habitat stability over two or more years for development (Corbet et al. 2006), and explaining why they may have a lower propensity for dispersal.

Unlike other riverine species such as fish, where movement is restricted to dendritic networks, lotic Odonata have the ability to disperse between river catchments as adults (Chaput-Bardy et al. 2008, Smith et al. 2009), allowing for potential climate adaptation. This study shows that relatively few of the focal lotic Odonata in the northeastern U.S. will benefit from projected climate change by expanding their current range, and the range of most species will contract.

Lotic Odonata may suffer from changes in temperature and the seasonality of precipitation. Increased temperature has also been shown to impact mortality of some Odonata when sharing an environment with colonizing species but not when living alone (Suhling and Suhling 2013).

Increased temperature may retard diapauses in lotic species, resulting in reduced survivorship, because diapauses help to avoid periods of low resource availability (Harrington et al. 2001, Hassall and Thompson 2008, Grewe et al. 2013, Jaeschke et al. 2013). Voltinism may also be reduced at the southern range limits of lotic Odonata under future climates (Braune et al. 2008), which could lead to local extirpations. If perennial streams become intermittent during summer droughts, these taxa could suffer (Braune et al. 2008), though the ability of most lotic species to tolerate periods in non-flowing pools is unknown.

It is important to note that microclimates and springs may reduce the magnitude of change predicted for the study species. The climate projections used in this study were downscaled to 30-arcsecond grids, but climates can vary at a much smaller scale (Suggitt et al. 2011). Sheltered canyons or shaded streams may be

buffered from the effects of increased air temperature (Braune et al. 2008), and small-scale climatic refugia were not considered in these models (Franklin et al. 2012). Furthermore, streams and rivers that are spring-fed or receive a large portion of discharge from groundwater are cooler and so will also be buffered from increased air temperature.

Species may not be impacted uniformly by a changing climate, and local populations currently on the low threshold of suitable climate may benefit by increased reproduction, which in turn should favor migration and dispersal (Corbet, 2004). The reduction in lotic Odonate diversity at southern rivers observed in this study may be partly because southern species were not selected because their range extended beyond the focal extent. The reduction also may be offset by southern species expanding their range northward. For example, *Gomphus dilatatus*, which is a southern species not modeled in this study, was first discovered on the James River in central Virginia in 2011, though it is not known if this represented a previously undocumented population or a northward range extension (Abbott 2006–2014).

The influence of landuse conduits, such as river systems, or barriers, such as mountains or urban areas, were not considered in this study, because lotic odonates have been documented dispersing overland (Chaput-Bardy et al. 2008). These conduits and barriers may mean that the landscape is highly heterogeneous with respect to the dispersal ability of lotic Odonata, though the relative influence of these factors requires further study. Additionally, the thermal tolerance of Odonata nymphs and adults is poorly known for most lotic species such as those in this study. Though studying the physiological response to increased temperature may provide a clearer projection of future distributions, the current study based on empirical distribution data provides an important overview of projected distribution changes. Not only may climate may be changing more rapidly than these species can adapt, its detrimental effects may occur before studies on the physiology and dispersal ability of individual species are performed. If dispersal distance is itself a function of climate (Hill et al. 1999), then dispersal data could be of little consequence. Using current knowledge to

identify which species will be most affected by climate change and where climatic refugia may persist is important for conservation management. The refugia identified in this study may also be important for other benthic invertebrates with overland dispersal abilities such as mayflies, stoneflies, and caddisflies.

The 434 river segments (935 km) identified as climatic refugia share several traits compared to rivers with currently high lotic odonate richness and other rivers within the focal extent (Table 6.6). These rivers are heavily forested, both within the catchment and riparian areas, and have correspondingly little agriculture and low human population density within their catchments. They have larger drainage areas and shallower slopes than current rivers with high richness. Unsurprisingly, rivers identified as climatic refugia also have lower annual, summer, and winter temperatures. They also currently experience greater temperature and precipitation seasonality and lower annual rainfall than other rivers.

Not only does this study provide detailed distributions that will enable close monitoring of lotic Odonata species, the predicted response of individual species can be used to track climate change effects on rivers. An adaptive management plan could be initiated where conservation and restoration are triggered once populations of species identified to be sensitive to climate change are observed changing. As an extreme measure, assisted migration could be considered if species do not track climate change and may be otherwise lost (Kreyling et al. 2011), though transporting entire communities may not be feasible or advisable. Additionally, many streams in the region will experience considerable species extirpations, therefore the communities and ecological functions of these systems are likely to change. Developing strategies to maintain communities and ecological functions of these systems will be necessary.

Relatively few streams are identified in this study as substantial refugia for lotic Odonata in the face of climate change, so it is critical that these systems and catchments are managed to preserve freshwater diversity. Creation or extension of protected areas should be considered which retain populations but also increase

landscape permeability. Most of the study species are not currently considered to be imperiled (Bick 2003, Dunkle 2004), so the substantial predicted range reductions of otherwise widespread species provide a sobering reminder of how climate will influence lotic freshwater diversity in the northeastern U.S.

Table 6.1. Estimated dispersal distances for the study lotic Odonata species. When voltinism or dispersal capability was unknown for a species, values based on other species within the same genus or family were assumed. Gen = generation.

Species	Known species voltinism (years/gen)	Assumed voltinism based on genera and family data (years/gen) <sup>1</sup>	Known dispersal of genus (km/gen)	Assumed dispersal (km/gen)	Dispersal distance by 2050	Dispersal distance by 2080
<i>Boyeria grafiana</i>		2.0		10	200	350
<i>Calopteryx amata</i>		1.5	1	1	27	47
<i>Gomphus abbreviatus</i>		2.5	13	13	208	364
<i>Gomphus adelphus</i>		2.5	13	13	208	364
<i>Gomphus descriptus</i>		2.5	13	13	208	364
<i>Gomphus viridifrons</i>		2.5	13	13	208	364
<i>Lanthus parvulus</i>		2.5		10	160	280
<i>Neurocordulia yamaskanensis</i>		2.0		10	200	350
<i>Ophiogomphus aspersus</i>		2.5	10	10	160	280
<i>Ophiogomphus carolus</i>		2.5	10	10	160	280
<i>Ophiogomphus howei</i>	2	2.0	10	10	200	350
<i>Ophiogomphus mainensis</i>		2.5	10	10	160	280
<i>Ophiogomphus rupinsulensis</i>		2.5	10	10	160	280
<i>Stylurus scudderi</i>		2.0		10	200	350
<i>Stylurus spiniceps</i>		2.0		10	200	350

<sup>1</sup> If voltinism varied with study, the median voltinism was used for dispersal calculations (Stettmer 1996, Hickling et al. 2005, Corbet et al. 2006, Hickling et al. 2006, Jaeschke et al. 2013)

Table 6.2. Lotic Odonata records were obtained from multiple sources, many of which are not publicly available because of data sensitivity concerns.

<b>Database</b>	<b>Years of survey data used in this study</b>	<b>Number of species records used</b>
Maine Damselfly and Dragonfly Survey (MDDS)	1991–2009	891
Maryland Department of Natural Resources & Maryland Biological Stream Survey	2004–2011	27
Maryland Natural Heritage Program	1995–2007	21
New Hampshire Dragonfly Survey (NHDS)	2007–2011	453
New York Dragonfly and Damselfly Survey (NYDDS)	2005–2009	48
OdonataCentral	1996–2010	82
Ohio Odonata Survey	1995–2009	32
Pennsylvania Natural Heritage Program	1998–2003	15
West Virginia Dragonfly and Damselfly Atlas	1997–2009	73
Virginia Natural Heritage Program (Virginia Department of Conservation and Recreation)	1994–2007	4
Vouchered observations that were not available in other databases (mostly PA records from Ben Coulter with additional MD and VA records from Steve Collins, Bill Hubick)	2005–2011	34

Table 6.3. The environmental variables used for modeling listed by scale (climatic, catchment or reach).

Reach	Mean Annual Water Velocity <sup>1</sup>	Climate	Annual Mean Temperature (BIO1) <sup>4</sup>
	Mean Reach Slope <sup>1</sup>		Mean Diurnal Temperature Range (BIO2) <sup>4</sup>
	Sinuosity of River Segment		Temperature Seasonality (BIO4) <sup>4</sup>
	Impounded (Boolean)		Maximum Temperature of Warmest Month (BIO5) <sup>4</sup>
	Majority Surficial Geology Unit within 100 m of River <sup>2</sup>		Minimum Temperature of Coldest Month (BIO6) <sup>4</sup>
	Area-weighted Percent Forest within 100 m of River <sup>2</sup>		Mean Temperature of Wettest Quarter (BIO8) <sup>4</sup>
	Area-weighted Percent Karst Geology within 100 m of River <sup>2</sup>		Mean Temperature of Driest Quarter (BIO9) <sup>4</sup>
	Mean Permeability (Soil L1 Horizon) within 100 m of River <sup>2</sup>		Annual Precipitation (BIO12) <sup>4</sup>
	Mean pH (Soil L1 Horizon) within 100 m of River <sup>2</sup>		Precipitation Coefficient of Variation (BIO15) <sup>4</sup>
	Weighted Average Sand Percentage (Soil L1 Horizon) within 100 m of River <sup>2</sup>		
Catchment	Upstream Drainage Area <sup>1</sup>		
	Area-weighted Percent Agriculture (2001 NLCD) <sup>1</sup>		
	Area-weighted Percent Forest & Wetland (2001 NLCD) <sup>1</sup>		
	Area-weighted Percent Open Water (2001 NLCD) <sup>1</sup>		
	Inverse Buffer Width from Agriculture Averaged Across Agriculture Cells <sup>3</sup>		
	Inverse Buffer Width from Developed Land Averaged Across Developed Cells <sup>3</sup>		
	Mean Human Population Density <sup>3</sup>		
	Area-weighted Percent Surficial Alluvium <sup>3</sup>		
Mean Permeability (Soil L1 Horizon) <sup>3</sup>			

<sup>1</sup> Variable as provided with NHDPlus ([http://www.horizon-systems.com/NHDPlus/NHDPlusV1\\_home.php](http://www.horizon-systems.com/NHDPlus/NHDPlusV1_home.php))<sup>2</sup> Summarized with Zonal Statistics function in ArcGIS<sup>3</sup> Accumulated with the CA3T NHDPlus Catchment Attribute Allocation and Accumulation Tool<sup>4</sup> Worldclim 30-arcsecond resolution climate data (<http://www.worldclim.org>)

Table 6.4. Current and projected habitat availability for 15 species of lotic Odonata within the northeastern U.S.

Species	Number of unique localities	Test AUC		Suitable present-day habitat in the focal extent (km)	Unavailable habitat restricted by non-climatic factors (km)	Suitable projected habitat (km)							
		NH	WV			Retained (no dispersal)				Newly available (unlimited dispersal)			
						CCSM4 RCP4.5	CCSM4 RCP8.5	HadGM3-ES RCP4.5	HadGM3-ES RCP8.5	CCSM4 RCP4.5	CCSM4 RCP8.5	HadGM3-ES RCP4.5	HadGM3-ES RCP8.5
<i>Boyeria grafiana</i>	162	0.949	0.894	50,153	100,590	17,378	10,333	8,800	3,827	479	793	636	2
<i>Calopteryx amata</i>	176	0.961	0.914	31,563	70,855	13,680	6,663	2,917	38	319	361	204	0
<i>Gomphus abbreviatus</i>	84	0.989		10,510	79,022	8,304	5,698	2,854	1,232	906	941	269	50
<i>Gomphus adelphus</i>	207	0.977		18,950	55,030	9,725	3,510	2,546	17	65	271	228	0
<i>Gomphus descriptus</i>	97	0.922		19,501	93,752	6,667	1,249	1,234	103	417	200	207	0
<i>Gomphus viridifrons</i>	27		0.934	19,834	99,983	12,352	7,804	6,593	1,883	1,775	2,771	437	68
<i>Lanthus parvulus</i>	77	0.950		67,665	58,114	7,732	180	857	20	4	5	9	0
<i>Neurocordulia yamaskanensis</i>	67	0.967		23,621	75,594	17,188	9,994	7,750	7,905	346	466	322	6
<i>Ophiogomphus aspersus</i>	124	0.984		21,064	71,547	11,455	6,104	4,739	1,521	74	513	436	7
<i>Ophiogomphus carolus</i>	166	0.974		20,084	82,751	7,332	2,964	3,218	149	28	152	232	0
<i>Ophiogomphus howei</i>	51	0.991		9,467	49,006	5,272	3,614	1,830	2,644	923	717	845	2,563
<i>Ophiogomphus mainensis</i>	171	0.978		21,239	72,562	11,390	5,221	4,964	1,459	288	599	555	200

Table 6.4. Continued.

Species	Number of unique localities	Test AUC		Suitable present-day habitat in the focal extent (km)	Unavailable habitat restricted by non-climatic factors (km)	Suitable projected habitat (km)							
		NH	WV			Retained (no dispersal)				Newly available (unlimited dispersal)			
						CCSM4 RCP4.5	CCSM4 RCP8.5	HadGM3-ES RCP4.5	HadGM3-ES RCP8.5	CCSM4 RCP4.5	CCSM4 RCP8.5	HadGM3-ES RCP4.5	HadGM3-ES RCP8.5
<i>Ophiogomphus rupinsulensis</i>	163	0.986		23,427	90,862	11,663	5,957	4,228	2,515	252	422	358	272
<i>Stylurus scudderi</i>	59	0.975		21,012	58,494	2,476	25	13	13	0	0	0	0
<i>Stylurus spiniceps</i>	74	0.988		18,484	103,248	3,140	1,082	686	120	355	143	24	0

Table 6.5. Climatic refugia, rivers where 20% or more study species will remain under the consensus of climate projections assuming no dispersal, are summarized by river name.

<b>State</b>	<b>River name</b>	<b>Length identified as refugia for 3 or more (of 15) species (km)</b>	<b>Richness in 2080 (no dispersal, consensus of 4 climate projections, max of all reaches)</b>	<b>Current predicted richness (max of all reaches)</b>
Maine	Allagash River	67.43	6	13
Maine	Aroostook River	46.61	4	14
Maine	Baker Branch Saint John River	18.14	3	12
Maine	Baskahegan Stream	20.64	4	14
Maine	Big Black River	26.24	4	9
Maine	Bowlin Brook	0.03	3	13
Maine	Chase Stream	0.61	3	10
Maine	Crooked River	10.11	3	12
Maine	Dead River	3.57	3	14
Maine	Dole Brook	4.77	3	10
Maine	East Branch Penobscot River	16.68	4	14
Maine	East Branch Umcolcus Stream	7.56	6	13
Maine	East Machias River	2.44	3	10
Maine	Fish River	13.55	4	14
Maine	Hancock Brook	0.04	3	13
Maine	Indian Stream	1.71	3	9
Maine	Kennebago River	8.24	3	12
Maine	Kennebec River	11.12	5	15
Maine	Little Black River	24.81	3	12
Maine	Little Madawaska River	29.53	5	12
Maine	Machias River	31.11	5	12
Maine	Magalloway River	22.14	4	13
Maine	Mattawamkeag River	38.51	6	13

Table 6.5. Climatic refugia, rivers where 20% or more study species will remain under  
 Table 6.5. Continued.

<b>State</b>	<b>River name</b>	<b>Length identified as refugia for 3 or more (of 15) species (km)</b>	<b>2080 (no dispersal, consensus of 4 climate projections, max of all reaches)</b>	<b>Current predicted richness (max of all reaches)</b>
Maine	McLean Brook	0.05	4	11
Maine	Molunkus Stream	6.84	3	13
Maine	Moose River	18.87	4	13
Maine	Mooseleuk Stream	10.55	5	13
Maine	Musquacook Stream	12.79	4	12
Maine	Narraguagus River	15.01	5	11
Maine	Nicatous Stream	0.17	3	9
Maine	North Branch Dead River	1.12	3	13
Maine	North Branch Penobscot River	10.14	3	13
Maine	Ossipee River	9.35	3	14
Maine	Passadumkeag River	18.05	4	14
Maine	Penobscot River	56.14	5	13
Maine	Pinette Brook	0.02	3	14
Maine	Pleasant River	2.42	3	3
Maine	Ragged Stream	3.20	3	11
Maine	Rapid River	6.14	5	13
Maine	Saco River	45.13	4	14
Maine	Saint John River	90.04	5	12
Maine	Seboeis River	14.01	5	13
Maine	Shields Branch	5.84	3	8
Maine	South Branch Penobscot River	5.32	3	12
Maine	Southwest Branch Saint John River	13.17	3	12
Maine	Spencer Stream	4.66	3	13
Maine	Stillwater River	7.45	3	14

Table 6.5. Climatic refugia, rivers where 20% or more study species will remain under the consensus of climate projections assuming no dispersal. are summarized by river  
 Table 6.5. Continued.

<b>State</b>	<b>River name</b>	<b>identified as refugia for 3 or more (of 15) species (km)</b>	<b>dispersal, consensus of 4 climate projections, max of all reaches)</b>	<b>predicted richness (max of all reaches)</b>
Maine	West Branch Mattawamkeag River	3.45	3	11
Maine	West Branch Penobscot River	19.03	5	15
Maine	West Branch Union River	8.58	4	11
Maine	Whetstone Brook	0.48	3	12
Maryland	North Branch Potomac River	11.07	3	7
Maryland	Potomac River	27.29	3	6
New Hampshire	Androscoggin River	31.85	4	14
New Hampshire	Connecticut River	1.14	3	13
New Hampshire	Flanders Brook	0.04	3	14
New Hampshire	Magalloway River	5.24	5	14
New Hampshire	Merrimack River	9.17	4	14
New Hampshire	Ossipee River	5.41	3	14
New Jersey	Delaware River	7.03	3	10
New York	Delaware River	5.62	3	8
New York	West Canada Creek	10.35	4	13
Pennsylvania	West Branch Susquehanna River	3.59	3	4
Vermont	Connecticut River	0.34	3	13
West Virginia	Anthony Creek	4.12	3	5
West Virginia	Ashcabin Run	0.03	3	5
West Virginia	Cheat River	5.74	3	7
West Virginia	Greenbrier River	10.88	3	10
West Virginia	North Branch Potomac River	0.58	3	5

Table 6.5. Climatic refugia, rivers where 20% or more study species will remain under the consensus of climate projections assuming no dispersal, are summarized by river name.

<b>State</b>	<b>River name</b>	<b>Length identified as refugia for 3 or more (of 15) species (km)</b>	<b>Richness in 2080 (no dispersal, consensus of 4 climate projections, max of all reaches)</b>	<b>Current predicted richness (max of all reaches)</b>
West Virginia	South Branch Potomac River	1.60	3	4

Table 6.6. Median values of selected environmental predictors for all rivers within the focal extent, those predicted to have high lotic Odonata richness in current climates, and those identified as climatic refugia.

<b>Environmental Predictor</b>	<b>Rivers with high richness under future climates (3 or more species)</b>	<b>Rivers with high richness under current climate (6 or more species)</b>	<b>All rivers within focal extent</b>
Drainage area (km <sup>2</sup> )	2,104	314	5
Agriculture in catchment (%)	0.1	2.8	14.2
Forest or wetlands in catchment (%)	87.6	89.3	69.5
Reach slope	0.0009	0.0017	0.0048
Forest or wetlands within 100 m (%)	81.3	77.5	60.1
Annual Mean Temperature (°C)	4.4	6.1	9.4
Temperature Seasonality (°C)	10.2	9.8	8.9
Max Average Temperature of Warmest Month (°C)	25.2	26.2	28.1
Min Average Temperature of Coldest Month (°C)	-17.3	-14.7	-8.8
Annual Precipitation (mm)	987	1,048	1,057
Precipitation Seasonality (%)	16	13	14

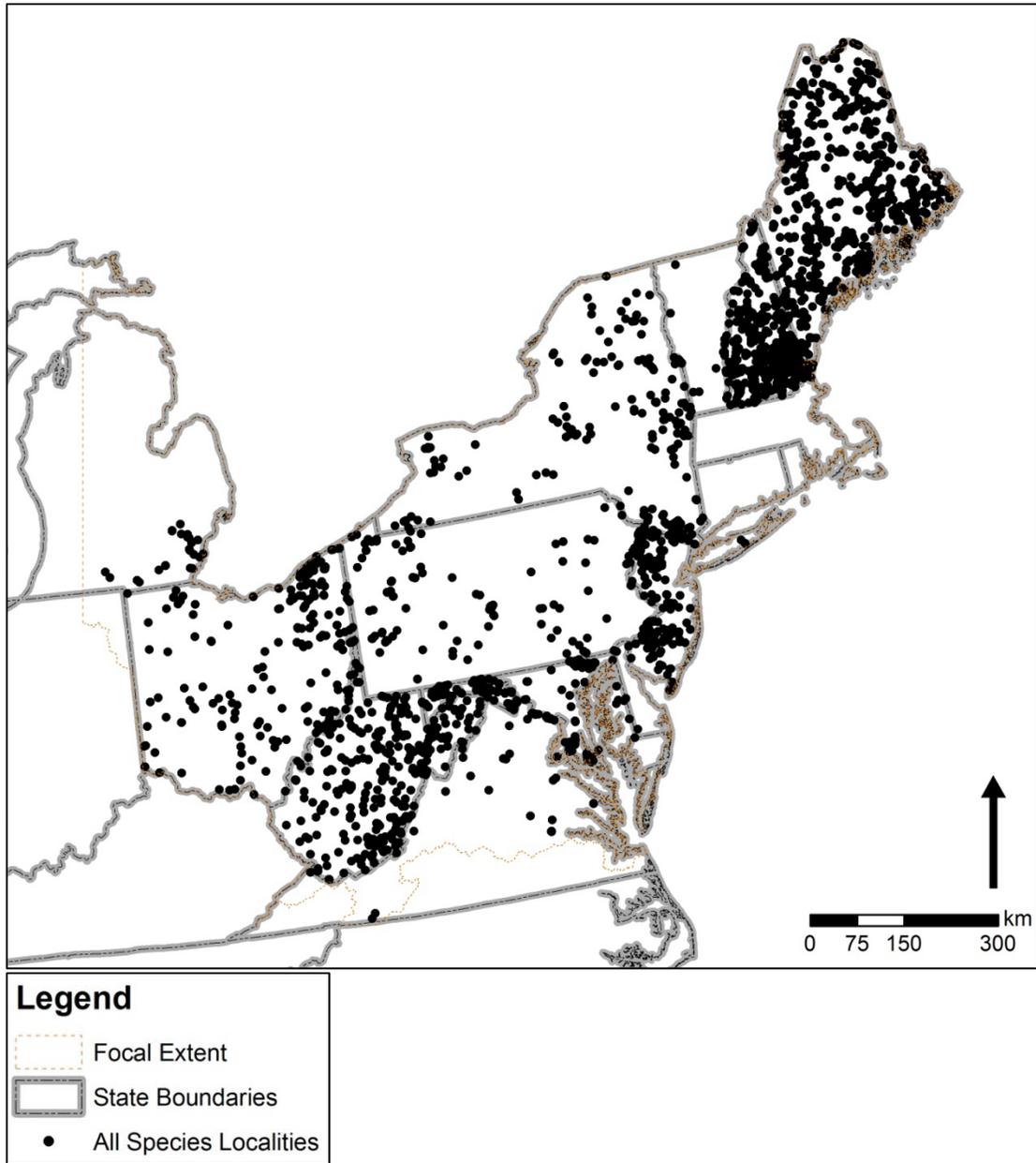


Figure 6.1. Lotic odonate data were obtained from several sources, with data density varying across the northeastern U.S. focal extent.

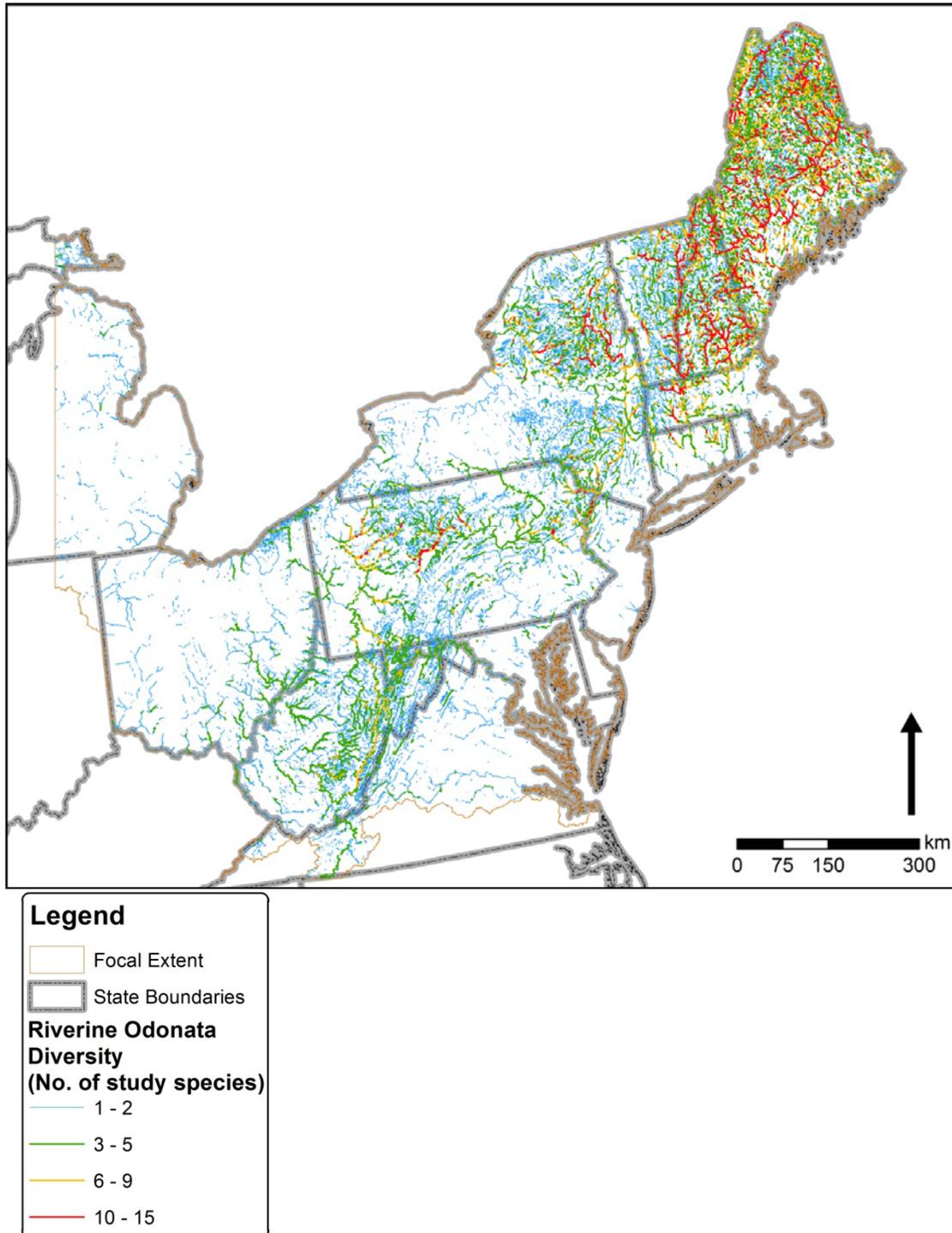


Figure 6.2. Current lotic odonate species richness for the 15 study species is clustered around major drainages within the Appalachian mountains.

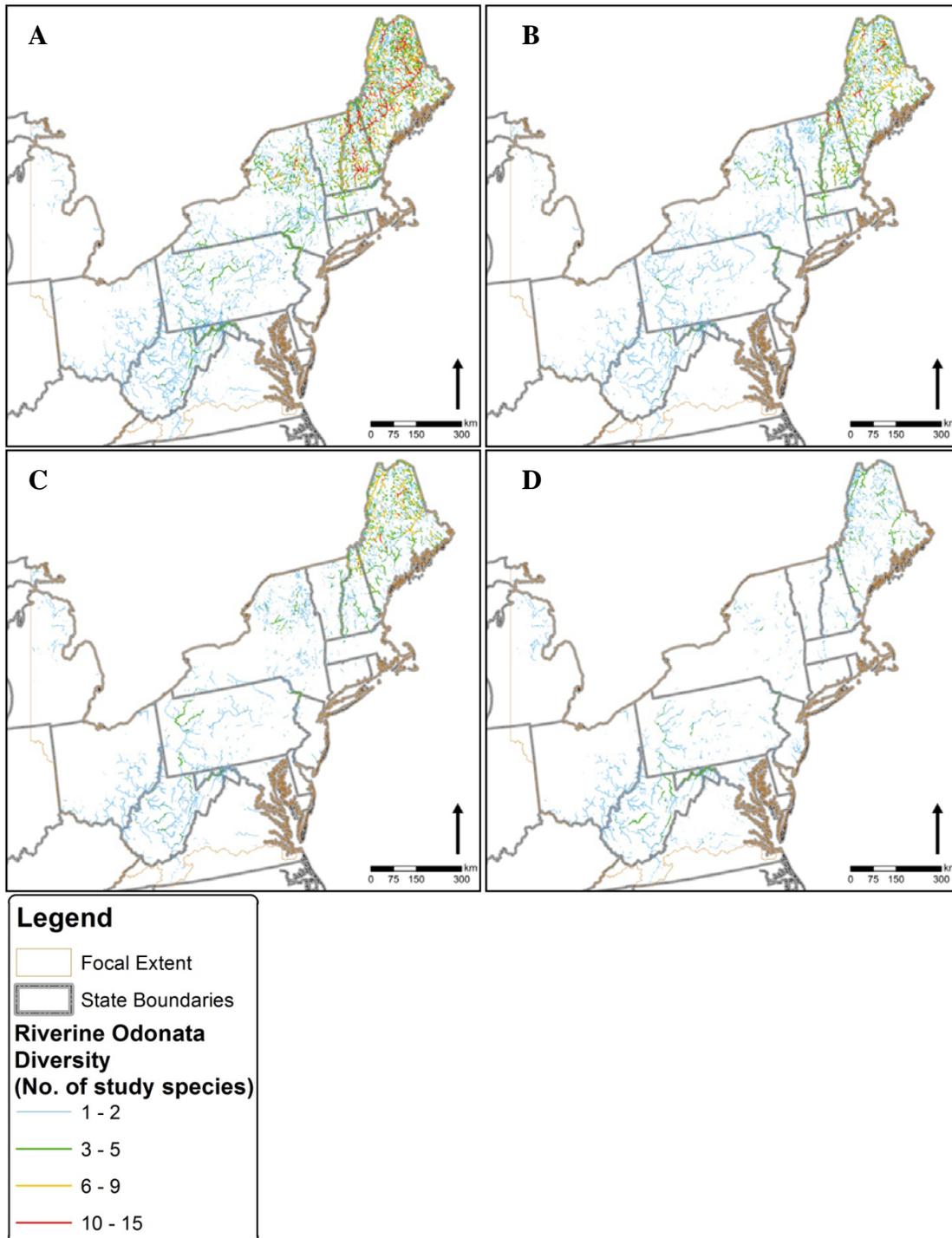


Figure 6.3. Projected lotic odonate richness will be reduced, but the magnitude of reduction varies with GCM and GEM. (A) CCSM4 RCP 4.5, (B) CCSM4 RCP 8.5, (C) HadCM3-ES RCP 4.5, (D) HadCM3-ES RCP 8.5.

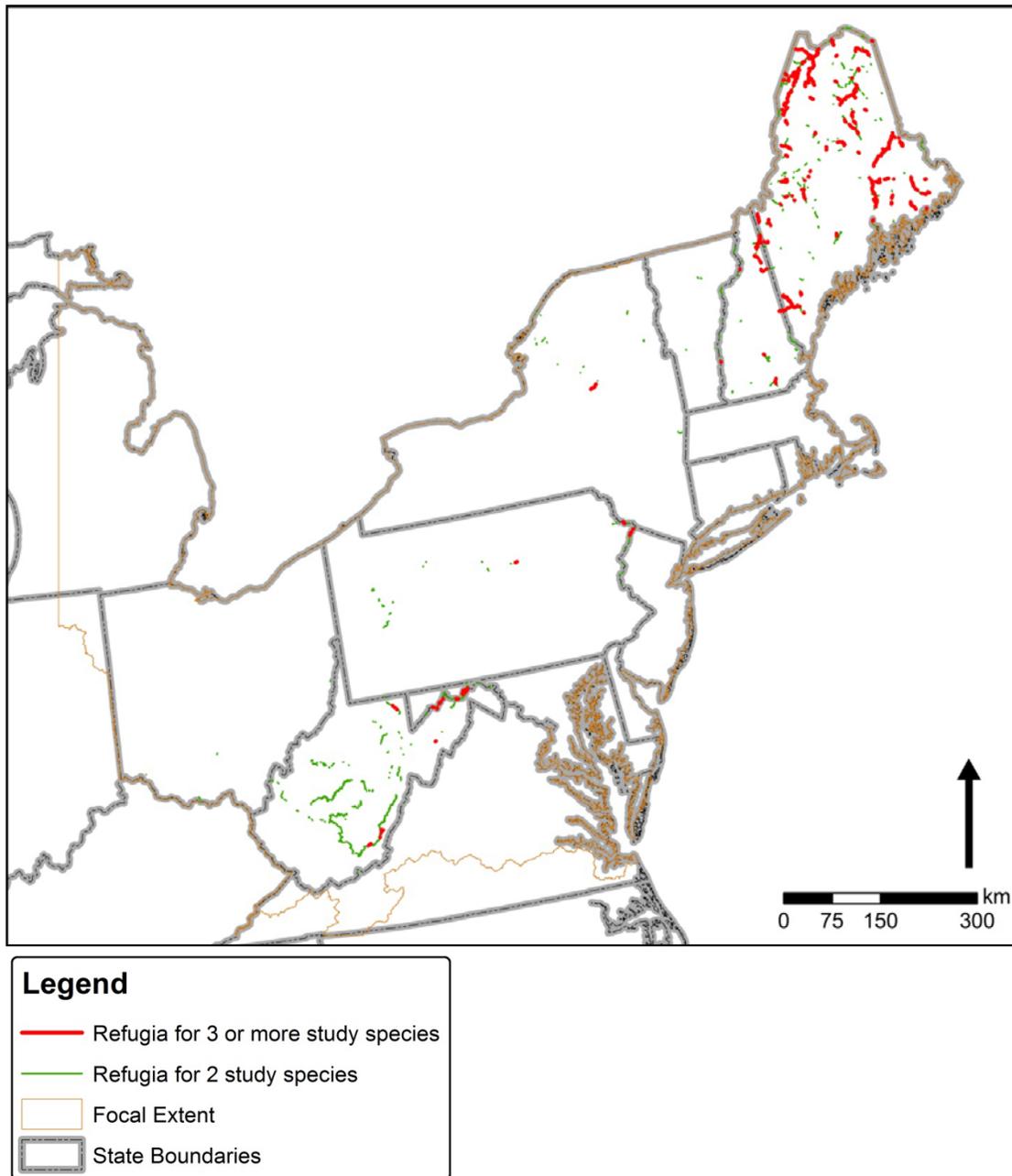


Figure 6.4. By only considering the ensemble of each climate projection and ignoring dispersal, the most certain climatic refugia for lotic odonate diversity can be identified.

## **CHAPTER VII**

### **CONCLUSIONS**

The species distribution modeling approach was reviewed with respect to Odonata and several modeling techniques were compared, revealing the approach to be a useful tool in understanding odonate-environment relations. Species locality data assigned only to U.S. county is prevalent in invertebrate databases, and it was found that using these data for modeling tends to overpredict the geographic distributions of both butterflies and Odonata within the U.S. Several techniques to compensate for geographic sampling bias, which is also a characteristic of these largely opportunisticly collected databases, were compared, though the optimum method (thinning data, biased background sampling, or no treatment) depended on the dataset, making a comprehensive recommendation impossible. It was found that using multi-state data with heterogeneous data density for model training resulted in greater predictive performance than models trained only with relatively dense data from a single state.

Watersheds and riparian zones are ecologically relevant for riverine organisms, and models with catchment- and local-scale predictors outperformed models based only on climate. This fine-scale modeling approach is appropriate for the conservation of freshwater diversity, because individual river segments containing suitable species habitat can be identified and prioritized. When modeling at the scale of individual river reaches, it was found that using river reaches, facilitated by the National Hydrography Dataset (NHD), as the unit for environmental background selection resulted in predictions that outperformed models built with a raster representation of river reaches. This is likely because the same number of background samples provides a more representative portrayal of all possible environmental conditions when taken from a smaller number of unique river reaches compared to a larger number of raster cells, many of which may represent identical stream conditions. Forgoing fine-scale rasters covering a large extent also allows for over 40-fold faster

model runs. When many species are modeled or  $k$ -fold partitioning techniques are used, the overall processing time may be reduced from several months using fine-scale rasters to several days using river reach tabular data.

The distributions of riverine dragonflies and damselflies were modeled at the scale of individual river segments across the northeastern United States, a 784,982 km<sup>2</sup> region spanning from Ohio, West Virginia, and Virginia northeast to Maine. Model performance varied by species, with poorer performance in widespread species (Table 7.1). This was not surprising, because previous studies have demonstrated that species with small geographic ranges or limited environmental tolerances can be modeled more accurately than other species (Hernandez et al. 2006, Grenouillet et al. 2011). Varying model performance between species also may be an indication that the selected environmental predictors more closely predict microhabitat for some species compared to others. Model performance was assessed by geographically partitioning the focal extent into training and testing regions, separately withholding the New Hampshire Dragonfly Survey (NHDS) or West Virginia Dragonfly and Damselfly Atlas (WVDDA) and those regions and then using those data and regions for model testing. Each regional dataset was collected independently, so it was assumed that the NHDS and WVDDA represented independent data. Some species did not have sufficient test data in New Hampshire or West Virginia, so models were also assessed through ten-fold cross-validation. The average cross-validated test AUC and the lowest test AUC from all folds is reported in Table 7.1, though the minimum score is based on one test record for some species with few available localities.

For the 48 species modeled within the northeastern U.S. focal extent, drainage area was the strongest predictor of species presence, followed by reach slope, minimum winter temperature, mean temperature of wettest quarter, stream water velocity, and catchment forest percentage. Predictor relevance varied with species, but models containing watershed and local-scale predictors outperformed models based only on climate. Predictors describing extreme events in the hydrological and

sediment regimes of particular rivers (e.g. peak discharge, minimum baseflow, bedload transport, shear stress) are likely to better represent the microhabitats important to lotic Odonata, and future work should attempt to quantify them.

The hotspots for species richness including all high-performing species models and species models with unknown performance ( $n = 41$ ) is similar to the richness in Figure 6.2, but it is a more comprehensive portrayal (Fig. 7.1). Species models determined to have poor predictive ability ( $n = 13$ ) were excluded from this figure. The prevalence of each species within the focal extent, as assessed by length of river determined to be suitable, also varied greatly between species (Table 7.1).

Climate change is expected to reduce the available habitat for riverine Odonata within the northeastern U.S. The future climate study focused on river-obligate species with ranges mostly within the northeastern U.S. focal extent, and many southern species were excluded. Rivers in the southern portion of the focal extent may remain suitable for southern taxa under future climates (Fig 7.2).

Dispersal ability may save some sensitive species from extinction or regional extirpation, but this ability is not documented for any of the studied species. Nymphs of *Ophiogomphus colubrinus*, a sister species to the *Ophiogomphus* dragonflies included in this study occupying rivers farther north, have only been recorded as dispersing downstream short distances related to discharge (Stout 1992), and adult dispersal is unknown. Overland dispersal is known in many lentic Odonata and several lotic Odonata (Stettmer 1996, Hickling et al. 2005, Corbet et al. 2006, Hof et al. 2006, Marten et al. 2006, Grewe et al. 2013, Jaeschke et al. 2013, May 2013), but the dispersal abilities and propensities for the study species are not known. High landscape resistance to dispersal reduces the ability of freshwater species to move freely across a landscape to establish new populations, reestablish local populations that have been extirpated, or respond to climate change (Strayer and Dudgeon 2010). Under the assumption of niche conservatism, if a species is unable to disperse under changing environmental conditions, it will perish (Cordellier et al. 2012). If dispersal

is largely restricted to dendritic networks, then denizens of cold, high gradient streams may be most imperiled by warming climates compared to denizens of low-gradient rivers, who may have the ability to occupy sites upstream of their current positions (Buisson et al. 2008b). Over 900 km of rivers that may serve as climatic refugia for lotic Odonata unable to disperse to track climate change were identified, and conservation of these rivers and their watersheds is essential.

Benthic macroinvertebrates perform several ecosystem services, including the recycling of nutrients, breakdown of organic matter, and transfer of energy to higher trophic levels such as fish. Conserving the native benthic fauna, which includes Odonata, is critical to maintaining the natural function and community structure of stream and river systems (Covich et al. 1999). This research provides a useful framework for aiding the conservation of river organisms. It expands an extant platform funded and updated by the USGS, the NHD, for use in conservation planning. The methods described within this dissertation can be applied to other river organisms and can be used to manage and promote river conservation efforts nationwide.

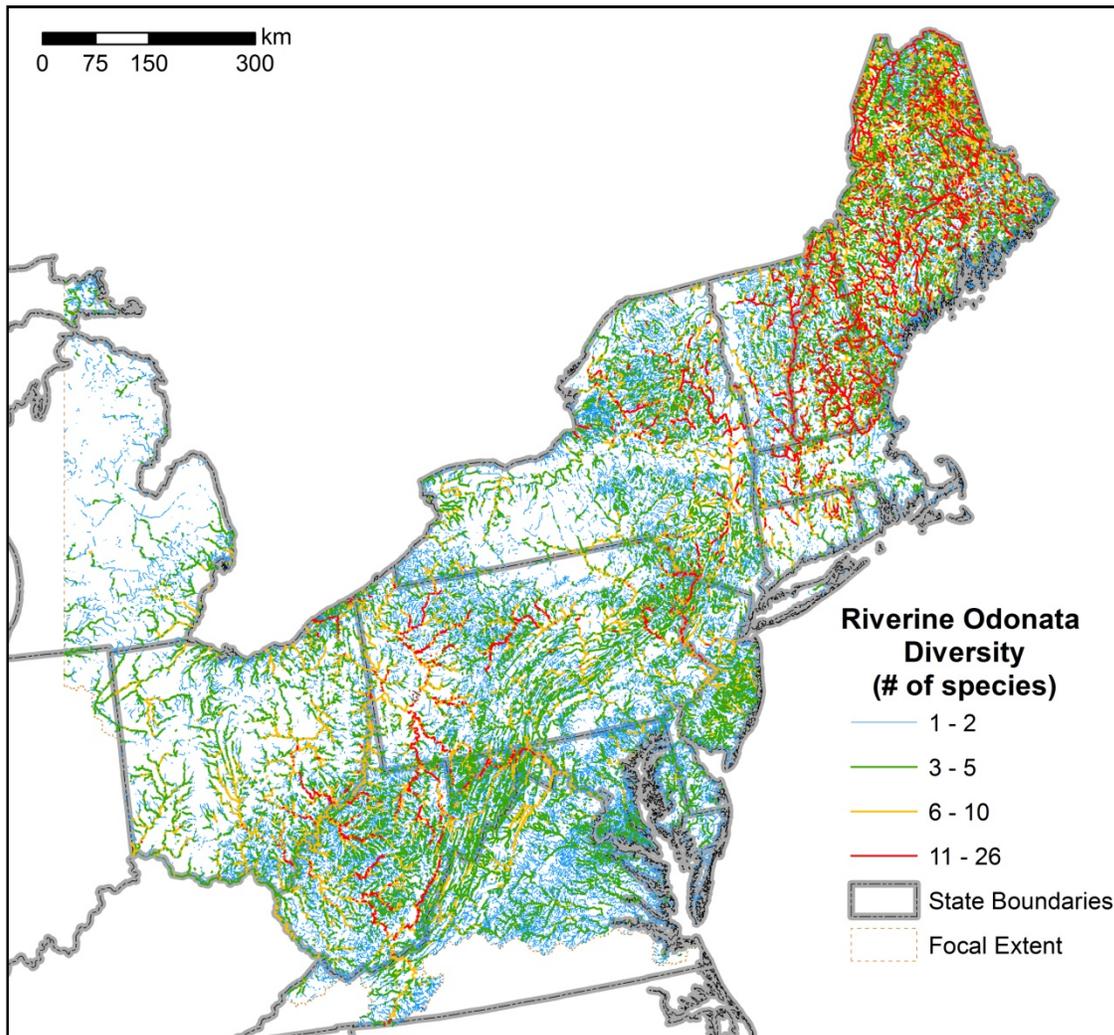
Table 7.1. Model performance and amount of predicted habitat varied between 48 species of lotic Odonata modeled in the northeastern U.S.

Species	Number of unique localities			Test AUC		Ten-fold cross-validation test AUC		Suitable present-day habitat in the focal extent (km)	Un-available habitat restricted by non-climatic factors (km)
	Focal extent	NH	WV	NH	WV	Avg	Min fold		
<i>Archilestes grandis</i> *	28		11		<b>0.481</b>	<b>0.765</b>	<b>0.477</b>	52,402	93,896
<i>Argia sedula</i>	46		22		0.911	0.940	0.886	36,161	93,733
<i>Argia tibialis</i>	87		25		0.878	0.946	0.836	38,544	114,867
<i>Argia translata</i>	127		75		0.913	0.939	0.857	40,560	89,640
<i>Boyeria grafiana</i>	162	21	12	0.949	0.894	0.939	0.894	50,153	100,590
<i>Boyeria vinosa</i> *	502	144	38	0.902	<b>0.676</b>	0.920	0.890	78,746	115,351
<i>Calopteryx amata</i>	176	47	17	0.961	0.914	0.973	0.958	31,563	70,855
<i>Calopteryx angustipennis</i>	12		6			0.977	0.837	50,840	42,582
<i>Calopteryx dimidiata</i>	24	10				0.988	0.954	10,356	94,227
<i>Calopteryx maculata</i> *	802	213		0.837	<b>0.570</b>	0.876	0.840	115,117	99,298
<i>Cordulegaster bilineata</i> *	8		1			<b>0.769</b>	<b>0.238</b>	81,266	127,528
<i>Cordulegaster diastatops</i>	72	1				0.899	0.804	63,028	68,075
<i>Didymops transversa</i> *	214	81	15	0.944	<b>0.752</b>	0.929	0.893	46,755	97,124
<i>Gomphus abbreviatus</i>	84	45		0.989		0.990	0.978	10,510	79,022
<i>Gomphus adelphus</i>	207	47	4	0.977		0.984	0.975	18,950	55,030
<i>Gomphus descriptus</i>	97	41	6	0.922		0.962	0.926	19,501	93,752
<i>Gomphus fraternus</i>	35		2			0.975	0.920	15,465	158,024
<i>Gomphus lineatifrons</i> *	11		4			0.881	<b>0.443</b>	94,331	97,447
<i>Gomphus lividus</i> *	136	17	48	<b>0.290</b>	0.996	0.889	0.861	59,662	141,957
<i>Gomphus quadricolor</i>	40	7	6			0.943	0.873	26,328	123,826
<i>Gomphus rogersi</i>	42		2			0.955	0.892	42,257	69,217
<i>Gomphus spicatus</i>	51					0.981	0.962	27,317	23,704
<i>Gomphus vastus</i>	67	23	11	0.993		0.993	0.977	7,107	105,354
<i>Gomphus viridifrons</i> *	27		13		0.934	0.938	<b>0.584</b>	19,834	99,983
<i>Helocordulia selysii</i>	20					0.985	0.943	2,756	18,151
<i>Helocordulia uhleri</i>	153	1				0.987	0.979	16,736	33,194
<i>Hetaerina americana</i>	147	16	46	0.876	0.919	0.941	0.911	44,381	151,023
<i>Hetaerina titia</i> *	7		1			<b>0.728</b>	<b>0.239</b>	49,063	128,545
<i>Lanthus parvulus</i>	77	21	6	0.950		0.936	0.894	67,665	58,114
<i>Lanthus vernalis</i> *	49	10	1	<b>0.728</b>		0.869	<b>0.735</b>	82,253	94,079
<i>Macromia illinoiensis</i>	302	64	23	0.961	0.917	0.966	0.911	32,885	115,543
<i>Macromia taeniolata</i>	21		5			0.987	0.970	10,861	145,085
<i>Neurocordulia michaeli</i>	75					0.993	0.974	7,331	39,793
<i>Neurocordulia obsoleta</i>	101	38		0.983		0.989	0.967	7,557	47,370
<i>Neurocordulia yamaskanensis</i>	67	16	4	0.967		0.982	0.956	23,621	75,594

Table 7.1. Continued.

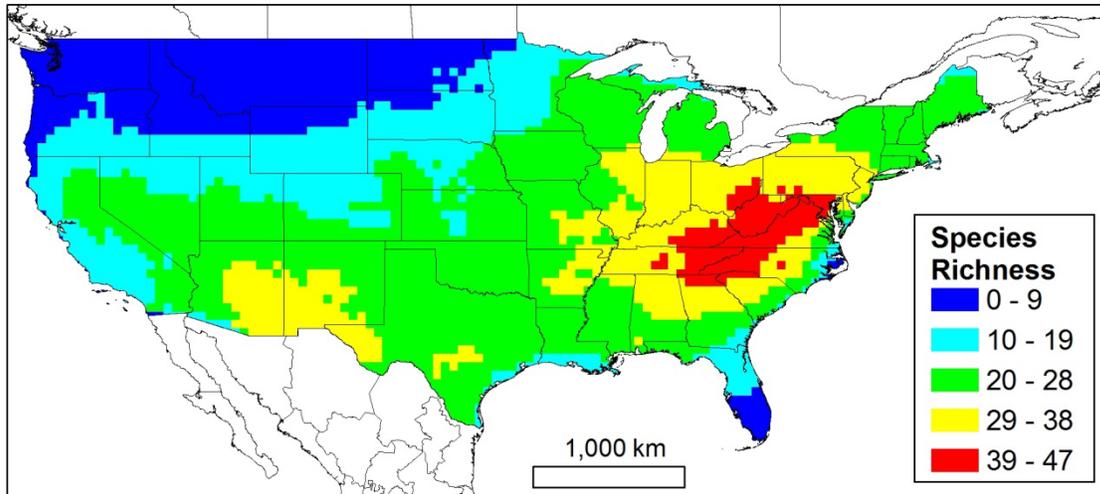
Species	Number of unique localities			Test AUC		Ten-fold cross-validation test AUC		Suitable present-day habitat in the focal extent (km)	Un-available habitat restricted by non-climatic factors (km)
	Focal extent	NH	WV	NH	WV	Avg	Min fold		
<i>Ophiogomphus anomalus</i>	112					0.992	0.975	5,393	36,286
<i>Ophiogomphus aspersus</i>	124	39		0.984		0.981	0.931	21,064	71,547
<i>Ophiogomphus carolus</i>	166	17	1	0.974		0.985	0.967	20,084	82,751
<i>Ophiogomphus howei</i>	51	14	1	0.991		0.986	0.926	9,467	49,006
<i>Ophiogomphus mainensis</i>	171	22	4	0.978		0.983	0.971	21,239	72,562
<i>Ophiogomphus rupinsulensis</i>	163	34	6	0.986		0.976	0.946	23,427	90,862
<i>Progomphus obscurus</i>	51	17		0.978		0.928	0.794	37,897	82,483
<i>Somatochlora linearis</i> *	41	1	8			0.797	<b>0.693</b>	98,096	119,890
<i>Stylogomphus albistylus</i> *	387	50	41	0.823	<b>0.746</b>	0.933	0.922	72,060	94,076
<i>Stylurus amnicola</i>	19	16				0.999	0.995	483	72,370
<i>Stylurus plagiatus</i> *	30					0.952	<b>0.658</b>	3,069	105,180
<i>Stylurus scudderi</i>	59	38		0.975		0.977	0.953	21,012	58,494
<i>Stylurus spiniceps</i>	74	35	2	0.988		0.985	0.966	18,484	103,248

Note: Models were assessed by withholding and testing with the NHDS and WVDDA datasets if there were more than 10 training and testing localities available. Not all species satisfied these criteria. Average and minimum test AUC from ten-fold cross-validation is also included for all species. Species with poor model performance (test AUC < 0.79) are marked with \* and lower scores are in bold. The test AUC of the minimum fold is based on one locality for some species.



Note: Using equal sensitivity/specificity threshold and only including well-performing species models (n = 35)

Figure 7.1. Hotspots for richness of riverine Odonata are located along major drainages centered on the Appalachian mountains.



Note: Convex hulls of known location records for every river-obligate odonate species in the U.S. were generated from OdonataCentral data, and the regions of overlap were counted.

Figure 7.2. Estimated species richness for river-obligate Odonata in the U.S. shows high species richness in the southern Appalachian mountains.

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## APPENDIX

Table A1: Change in predicted area within the contiguous United States for each modeled species (n = 230 butterflies, 283 Odonata) when county centroids are substituted for true localities. Predicted areas are defined as portion of scene using the minimum-training-presence and sensitivity-equals-specificity thresholds. Species selected for the western and eastern comparison and indicated with a “w” or “e,” and species selected for the lotic and lentic comparison are indicated with a “a” or “b,” respectively.

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<b>Butterflies from Butterflies and Moths of North America database</b>										
<i>Abaeis nicippe</i>	110	0.884	0.453	0.547	0.598	9.2%	0.618	0.191	0.191	-0.2%
<i>Achalarus lyciades</i>	47	0.937	0.767	0.233	0.196	-15.9%	0.702	0.149	0.135	-9.5%
<i>Adelpha californica</i> <sup>w</sup>	18	0.987	0.950	0.050	0.156	213.2%	0.895	0.050	0.092	84.6%
<i>Aglais milberti</i>	65	0.847	0.163	0.837	0.621	-25.8%	0.538	0.231	0.277	20.0%
<i>Agraulis vanillae</i>	166	0.910	0.459	0.541	0.484	-10.6%	0.663	0.169	0.175	3.6%
<i>Amblyscirtes aesculapius</i> <sup>e</sup>	16	0.929	0.816	0.184	0.151	-17.9%	0.750	0.125	0.125	0.0%
<i>Amblyscirtes hegon</i>	40	0.953	0.691	0.310	0.378	22.1%	0.790	0.110	0.128	15.7%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Amblyscirtes vialis</i>	45	0.830	0.145	0.855	0.692	-19.1%	0.511	0.244	0.289	18.2%
<i>Anaea andria</i>	59	0.904	0.489	0.511	0.481	-5.9%	0.627	0.186	0.183	-1.7%
<i>Anartia jatrophae</i> <sup>e</sup>	18	0.989	0.935	0.065	0.053	-19.4%	0.889	0.056	0.053	-5.2%
<i>Anatrytone logan</i>	67	0.874	0.519	0.481	0.428	-11.1%	0.552	0.224	0.194	-13.4%
<i>Ancyloxypha numitor</i>	126	0.885	0.328	0.672	0.717	6.8%	0.603	0.198	0.214	8.0%
<i>Anthanassa texana</i>	14	0.843	0.688	0.312	0.299	-4.1%	0.450	0.264	0.217	-17.9%
<i>Anthocharis midea</i>	60	0.916	0.702	0.298	0.318	6.9%	0.633	0.183	0.172	-6.1%
<i>Anthocharis sara</i>	11	0.988	0.962	0.038	0.055	46.3%	0.962	0.038	0.055	46.0%
<i>Anthocharis stella</i>	12	0.922	0.799	0.201	0.268	33.3%	0.806	0.111	0.219	96.9%
<i>Apodemia mormo</i> <sup>w</sup>	19	0.917	0.724	0.276	0.326	18.0%	0.677	0.165	0.194	17.6%
<i>Ascia monuste</i>	10	0.979	0.899	0.101	0.101	0.6%	0.800	0.100	0.100	0.0%
<i>Asterocampa celtis</i>	145	0.881	0.366	0.634	0.632	-0.2%	0.612	0.195	0.193	-0.8%
<i>Asterocampa clyton</i>	76	0.874	0.563	0.437	0.448	2.5%	0.584	0.205	0.223	8.6%
<i>Atalopedes campestris</i>	123	0.882	0.210	0.791	0.657	-16.8%	0.593	0.203	0.220	8.0%
<i>Atlides halesus</i>	54	0.858	0.336	0.664	0.634	-4.6%	0.563	0.215	0.225	4.8%
<i>Atrytonopsis hianna</i>	21	0.903	0.257	0.743	0.816	9.9%	0.619	0.191	0.213	11.8%
<i>Autochton cellus</i>	14	0.881	0.555	0.445	0.424	-4.7%	0.571	0.214	0.155	-27.7%
<i>Battus philenor</i>	157	0.862	0.263	0.737	0.706	-4.1%	0.541	0.229	0.210	-8.3%
<i>Battus polydamas</i>	13	0.976	0.909	0.091	0.094	2.4%	0.846	0.077	0.077	0.0%
<i>Boloria bellona</i>	48	0.936	0.716	0.284	0.286	0.8%	0.708	0.146	0.141	-3.2%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Boloria selene</i>	34	0.920	0.515	0.485	0.420	-13.5%	0.706	0.147	0.145	-1.4%
<i>Brephidium exilis</i>	32	0.883	0.526	0.474	0.409	-13.7%	0.553	0.228	0.219	-4.2%
<i>Callophrys augustinus</i>	43	0.884	0.230	0.770	0.675	-12.4%	0.620	0.194	0.233	19.8%
<i>Callophrys eryphon</i>	13	0.948	0.876	0.124	0.414	233.2%	0.723	0.123	0.134	9.2%
<i>Callophrys gryneus</i>	75	0.818	0.296	0.704	0.824	17.1%	0.440	0.281	0.277	-1.4%
<i>Callophrys henrici</i>	44	0.891	0.357	0.643	0.648	0.8%	0.636	0.182	0.182	0.0%
<i>Callophrys irus</i> <sup>e</sup>	17	0.955	0.831	0.169	0.196	15.7%	0.765	0.118	0.118	0.0%
<i>Callophrys johnsoni</i> <sup>w</sup>	27	0.979	0.901	0.099	0.125	26.5%	0.866	0.060	0.081	35.6%
<i>Callophrys niphon</i>	62	0.897	0.597	0.403	0.421	4.5%	0.613	0.194	0.205	5.7%
<i>Callophrys perplexa</i> <sup>w</sup>	16	0.990	0.967	0.034	0.059	74.6%	0.904	0.034	0.059	74.6%
<i>Callophrys sheridanii</i>	10	0.899	0.706	0.295	0.230	-22.0%	0.600	0.200	0.200	0.0%
<i>Callophrys spinetorum</i>	14	0.898	0.437	0.563	0.671	19.0%	0.714	0.143	0.143	0.0%
<i>Calpodetes ethlius</i>	14	0.913	0.721	0.279	0.300	7.6%	0.588	0.198	0.183	-7.6%
<i>Calycopis cecrops</i>	116	0.926	0.608	0.392	0.414	5.6%	0.703	0.151	0.161	7.0%
<i>Carterocephalus palaemon</i>	32	0.881	0.263	0.737	0.607	-17.6%	0.577	0.204	0.156	-23.3%
<i>Celastrina echo</i> <sup>w</sup>	29	0.932	0.780	0.220	0.265	20.3%	0.709	0.153	0.172	12.6%
<i>Celastrina ladon</i>	78	0.859	0.350	0.650	0.895	37.7%	0.513	0.244	0.244	0.0%
<i>Celastrina lucia</i>	29	0.928	0.298	0.702	0.510	-27.4%	0.724	0.138	0.138	0.0%
<i>Celastrina neglecta</i>	107	0.892	0.588	0.412	0.416	1.0%	0.589	0.206	0.176	-14.2%
<i>Celastrina serotina</i> <sup>e</sup>	21	0.980	0.953	0.047	0.041	-12.9%	0.906	0.047	0.041	-12.9%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Cercyonis oetus</i>	11	0.946	0.842	0.158	0.442	180.6%	0.818	0.091	0.173	89.8%
<i>Cercyonis pegala</i>	114	0.858	0.362	0.638	0.653	2.4%	0.512	0.242	0.209	-13.7%
<i>Cercyonis sthenele</i>	12	0.934	0.631	0.370	0.129	-65.0%	0.705	0.129	0.105	-18.9%
<i>Chlosyne acastus</i>	12	0.939	0.781	0.219	0.270	23.4%	0.701	0.132	0.167	26.4%
<i>Chlosyne gorgone</i>	16	0.837	0.402	0.598	0.680	13.6%	0.601	0.212	0.250	17.9%
<i>Chlosyne harrisii</i> <sup>e</sup>	26	0.982	0.920	0.081	0.150	86.3%	0.852	0.071	0.077	8.5%
<i>Chlosyne lacinia</i>	26	0.913	0.416	0.584	0.538	-7.9%	0.694	0.152	0.153	0.2%
<i>Chlosyne leanira</i>	13	0.938	0.591	0.409	0.312	-23.8%	0.711	0.135	0.094	-30.8%
<i>Chlosyne nycteis</i>	96	0.903	0.584	0.416	0.355	-14.7%	0.649	0.174	0.177	1.8%
<i>Chlosyne palla</i>	11	0.942	0.695	0.305	0.365	19.6%	0.818	0.091	0.118	30.0%
<i>Coenonympha tullia</i>	72	0.860	0.120	0.880	0.813	-7.6%	0.531	0.233	0.264	13.3%
<i>Colias alexandra</i>	12	0.899	0.651	0.349	0.316	-9.7%	0.683	0.151	0.167	10.7%
<i>Colias eurytheme</i>	173	0.825	0.180	0.820	0.855	4.3%	0.479	0.261	0.246	-5.7%
<i>Colias philodice</i>	114	0.884	0.342	0.658	0.593	-9.9%	0.631	0.185	0.191	3.0%
<i>Copaeodes aurantiaca</i>	18	0.962	0.792	0.208	0.174	-16.3%	0.781	0.108	0.098	-9.2%
<i>Copaeodes minima</i> <sup>e</sup>	20	0.951	0.869	0.132	0.115	-12.5%	0.802	0.098	0.089	-9.8%
<i>Cupido amyntula</i>	21	0.919	0.279	0.721	0.736	2.1%	0.714	0.143	0.141	-1.5%
<i>Cupido comyntas</i>	196	0.881	0.308	0.692	0.742	7.2%	0.623	0.188	0.189	0.6%
<i>Cyllopsis gemma</i>	59	0.925	0.664	0.336	0.324	-3.6%	0.695	0.153	0.136	-11.1%
<i>Danaus gilippus</i>	41	0.907	0.694	0.306	0.347	13.3%	0.622	0.183	0.198	8.0%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Danaus plexippus</i>	237	0.826	0.167	0.833	0.990	18.8%	0.494	0.253	0.259	2.3%
<i>Echinargus isola</i>	27	0.860	0.204	0.796	0.423	-46.9%	0.556	0.222	0.222	-0.2%
<i>Enodia anthedon</i>	111	0.910	0.607	0.393	0.444	12.8%	0.640	0.180	0.170	-5.8%
<i>Enodia creola</i> <sup>e</sup>	18	0.942	0.834	0.166	0.142	-14.2%	0.755	0.134	0.131	-2.6%
<i>Enodia portlandia</i> <sup>e</sup>	24	0.954	0.884	0.116	0.114	-1.6%	0.833	0.083	0.107	28.9%
<i>Epargyreus clarus</i>	232	0.855	0.242	0.758	0.945	24.7%	0.560	0.220	0.217	-1.5%
<i>Erynnis baptisiae</i>	102	0.931	0.629	0.372	0.391	5.3%	0.724	0.139	0.132	-5.0%
<i>Erynnis brizo</i>	54	0.869	0.276	0.725	0.807	11.3%	0.623	0.192	0.204	6.1%
<i>Erynnis funeralis</i>	36	0.871	0.553	0.447	0.443	-1.0%	0.566	0.211	0.222	5.1%
<i>Erynnis horatius</i>	92	0.906	0.527	0.473	0.444	-6.1%	0.670	0.167	0.188	12.6%
<i>Erynnis icelus</i>	40	0.913	0.464	0.536	0.775	44.5%	0.700	0.150	0.150	0.0%
<i>Erynnis juvenalis</i>	89	0.914	0.588	0.412	0.480	16.5%	0.663	0.169	0.169	0.0%
<i>Erynnis persius</i>	13	0.890	0.764	0.236	0.600	153.9%	0.662	0.184	0.154	-16.5%
<i>Erynnis tristis</i>	11	0.984	0.934	0.066	0.074	12.9%	0.843	0.066	0.074	12.9%
<i>Erynnis zarucco</i> <sup>e</sup>	14	0.954	0.901	0.099	0.087	-11.8%	0.845	0.084	0.084	0.1%
<i>Euchloe ausonides</i> <sup>w</sup>	15	0.953	0.853	0.148	0.277	87.6%	0.734	0.133	0.105	-21.0%
<i>Euphilotes battoides</i>	11	0.926	0.753	0.247	0.207	-16.5%	0.779	0.131	0.091	-30.3%
<i>Euphilotes enoptes</i>	12	0.989	0.976	0.024	0.053	118.7%	0.976	0.024	0.053	118.7%
<i>Euphydryas anicia</i> <sup>w</sup>	17	0.930	0.597	0.403	0.263	-34.8%	0.765	0.118	0.172	46.1%
<i>Euphydryas chalcedona</i> <sup>w</sup>	20	0.980	0.931	0.069	0.169	142.8%	0.884	0.066	0.077	16.6%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
				Minimum-training-presence threshold				Sensitivity-equals-specificity threshold		
<i>Euphydryas colon</i>	10	0.937	0.842	0.158	0.235	48.9%	0.765	0.135	0.130	-3.7%
<i>Euphydryas editha</i> <sup>w</sup>	22	0.974	0.839	0.161	0.287	78.4%	0.891	0.064	0.109	69.7%
<i>Euphydryas phaeton</i>	45	0.940	0.760	0.240	0.262	8.9%	0.733	0.133	0.156	16.7%
<i>Euphyes bimacula</i>	10	0.895	0.289	0.711	0.537	-24.5%	0.776	0.124	0.117	-5.5%
<i>Euphyes conspicua</i> <sup>e</sup>	14	0.966	0.853	0.147	0.244	66.2%	0.717	0.140	0.084	-40.2%
<i>Euphyes dion</i> <sup>e</sup>	24	0.853	0.534	0.466	0.433	-7.2%	0.496	0.254	0.250	-1.7%
<i>Euphyes vestris</i>	107	0.871	0.025	0.976	0.804	-17.6%	0.556	0.220	0.197	-10.6%
<i>Euptoieta claudia</i>	180	0.850	0.284	0.716	0.682	-4.7%	0.511	0.244	0.228	-6.8%
<i>Eurytides marcellus</i>	116	0.931	0.452	0.548	0.527	-3.7%	0.724	0.138	0.154	11.8%
<i>Feniseca tarquinius</i>	59	0.879	0.655	0.345	0.344	-0.3%	0.564	0.216	0.240	11.3%
<i>Glaucopsyche lygdamus</i>	49	0.838	0.173	0.827	0.778	-5.9%	0.503	0.252	0.245	-2.8%
<i>Glaucopsyche piasus</i>	13	0.926	0.733	0.267	0.305	14.3%	0.692	0.154	0.154	0.0%
<i>Heliconius charithonia</i>	19	0.954	0.695	0.305	0.357	17.3%	0.789	0.105	0.105	0.0%
<i>Hemiargus ceraunus</i>	27	0.884	0.519	0.481	0.486	1.0%	0.628	0.187	0.222	18.8%
<i>Hermeuptychia sosybius</i>	72	0.928	0.703	0.297	0.291	-2.0%	0.722	0.139	0.136	-1.9%
<i>Hesperia colorado</i> <sup>w</sup>	18	0.943	0.791	0.209	0.196	-5.9%	0.777	0.112	0.119	6.2%
<i>Hesperia juba</i>	11	0.941	0.742	0.259	0.274	5.9%	0.818	0.091	0.095	5.0%
<i>Hesperia leonardus</i> <sup>e</sup>	34	0.944	0.684	0.316	0.317	0.3%	0.765	0.118	0.152	29.3%
<i>Hesperia metea</i> <sup>e</sup>	22	0.942	0.789	0.211	0.220	3.8%	0.727	0.136	0.157	14.8%
<i>Hesperia sassacus</i> <sup>e</sup>	25	0.978	0.883	0.117	0.118	0.4%	0.840	0.080	0.080	0.0%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Hylephila phyleus</i>	186	0.830	0.270	0.730	0.763	4.5%	0.482	0.260	0.266	2.4%
<i>Junonia coenia</i>	315	0.831	0.066	0.934	0.930	-0.5%	0.479	0.260	0.265	1.7%
<i>Leptotes cassius</i> <sup>e</sup>	13	0.964	0.715	0.285	0.324	13.9%	0.846	0.077	0.077	0.0%
<i>Leptotes marina</i>	23	0.886	0.206	0.794	0.564	-29.0%	0.636	0.190	0.217	14.5%
<i>Lerema accius</i>	83	0.934	0.609	0.391	0.371	-5.2%	0.711	0.145	0.141	-2.6%
<i>Lerodea eufala</i>	50	0.879	0.622	0.378	0.393	4.0%	0.592	0.208	0.200	-3.7%
<i>Libytheana carinenta</i>	116	0.865	0.402	0.598	0.651	8.9%	0.552	0.224	0.224	0.0%
<i>Limenitis archippus</i>	140	0.844	0.222	0.778	0.825	6.1%	0.502	0.248	0.236	-5.1%
<i>Limenitis arthemis</i>	95	0.917	0.577	0.423	0.423	0.0%	0.661	0.171	0.158	-7.7%
<i>Limenitis arthemis arthemis</i>	39	0.950	0.620	0.380	0.281	-26.1%	0.795	0.103	0.128	25.0%
<i>Limenitis arthemis astyanax</i>	150	0.890	0.535	0.465	0.505	8.5%	0.615	0.192	0.185	-3.5%
<i>Limenitis lorquini</i> <sup>w</sup>	29	0.962	0.778	0.222	0.207	-7.1%	0.803	0.093	0.104	11.6%
<i>Limenitis weidemeyerii</i> <sup>w</sup>	15	0.966	0.855	0.145	0.211	45.4%	0.841	0.092	0.168	81.4%
<i>Lycaena cupreus</i>	10	0.939	0.716	0.284	0.259	-8.8%	0.627	0.173	0.200	15.8%
<i>Lycaena epixanthe</i> <sup>e</sup>	14	0.968	0.852	0.149	0.179	20.6%	0.857	0.071	0.071	0.0%
<i>Lycaena helloides</i>	24	0.919	0.667	0.334	0.386	15.7%	0.589	0.203	0.167	-17.7%
<i>Lycaena heteronea</i>	11	0.939	0.763	0.237	0.254	7.1%	0.662	0.157	0.172	9.6%
<i>Lycaena hyllus</i>	44	0.877	0.332	0.669	0.549	-17.9%	0.600	0.195	0.185	-5.3%
<i>Lycaena phlaeas</i>	79	0.901	0.308	0.692	0.871	25.9%	0.644	0.179	0.177	-1.0%
<i>Megathymus yuccae</i>	13	0.881	0.546	0.454	0.587	29.4%	0.662	0.184	0.231	25.6%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Megisto cymela</i>	119	0.890	0.596	0.404	0.398	-1.3%	0.613	0.193	0.202	4.3%
<i>Nastra lherminier</i> <sup>e</sup>	24	0.927	0.737	0.263	0.294	11.9%	0.735	0.140	0.167	19.3%
<i>Nathalis iole</i>	98	0.859	0.112	0.888	0.910	2.5%	0.532	0.233	0.245	5.0%
<i>Neophasia menapia</i> <sup>w</sup>	16	0.941	0.777	0.223	0.170	-23.6%	0.750	0.125	0.149	19.1%
<i>Nymphalis antiopa</i>	210	0.795	0.067	0.933	0.919	-1.5%	0.429	0.286	0.293	2.6%
<i>Nymphalis californica</i>	16	0.887	0.272	0.728	0.632	-13.1%	0.631	0.181	0.188	3.4%
<i>Nymphalis vaualbum</i>	28	0.946	0.433	0.567	0.468	-17.5%	0.786	0.107	0.102	-4.9%
<i>Ochlodes sylvanoides</i> <sup>w</sup>	20	0.911	0.507	0.493	0.518	5.0%	0.617	0.183	0.180	-1.9%
<i>Oeneis chryxus</i>	10	0.973	0.920	0.080	0.258	223.3%	0.820	0.080	0.157	97.0%
<i>Panoquina ocola</i>	50	0.921	0.701	0.300	0.281	-6.3%	0.671	0.169	0.161	-5.1%
<i>Papilio canadensis</i>	29	0.962	0.525	0.476	0.416	-12.5%	0.862	0.069	0.098	42.6%
<i>Papilio cresphontes</i>	182	0.858	0.260	0.740	0.701	-5.3%	0.538	0.231	0.247	6.8%
<i>Papilio eurymedon</i> <sup>w</sup>	26	0.948	0.746	0.254	0.222	-12.4%	0.699	0.147	0.141	-4.0%
<i>Papilio glaucus</i>	311	0.865	0.459	0.541	0.558	3.1%	0.556	0.222	0.222	0.0%
<i>Papilio indra</i> <sup>w</sup>	16	0.898	0.678	0.322	0.287	-11.0%	0.603	0.210	0.188	-10.6%
<i>Papilio multicaudata</i>	33	0.825	0.393	0.607	0.649	6.9%	0.465	0.263	0.303	15.4%
<i>Papilio palamedes</i> <sup>e</sup>	31	0.958	0.861	0.139	0.146	4.8%	0.799	0.105	0.096	-8.2%
<i>Papilio polyxenes</i>	241	0.847	0.242	0.758	0.780	2.9%	0.527	0.237	0.237	0.2%
<i>Papilio rutulus</i> <sup>w</sup>	36	0.936	0.694	0.306	0.416	35.6%	0.679	0.155	0.167	7.8%
<i>Papilio troilus</i>	169	0.899	0.530	0.470	0.446	-5.1%	0.622	0.188	0.172	-8.9%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Papilio zelicaon</i> <sup>w</sup>	23	0.920	0.643	0.357	0.401	12.5%	0.719	0.151	0.130	-13.5%
<i>Parnassius clodius</i> <sup>w</sup>	18	0.962	0.856	0.144	0.184	28.1%	0.778	0.111	0.090	-19.1%
<i>Parnassius smintheus</i>	10	0.961	0.864	0.136	0.249	82.8%	0.800	0.100	0.200	100.0%
<i>Parrhasius m album</i>	39	0.879	0.615	0.385	0.390	1.4%	0.590	0.205	0.214	4.2%
<i>Philotes sonorensis</i>	11	0.984	0.966	0.034	0.062	82.6%	0.966	0.034	0.062	82.6%
<i>Phoebis philea</i>	11	0.959	0.763	0.237	0.177	-25.3%	0.818	0.091	0.091	0.0%
<i>Phoebis sennae</i>	122	0.893	0.035	0.965	0.673	-30.2%	0.642	0.177	0.205	15.6%
<i>Pholisora catullus</i>	68	0.807	0.050	0.950	0.957	0.7%	0.523	0.242	0.252	4.0%
<i>Phyciodes cocyta</i>	42	0.912	0.454	0.547	0.476	-12.8%	0.714	0.143	0.143	0.1%
<i>Phyciodes mylitta</i> <sup>w</sup>	21	0.943	0.717	0.284	0.278	-2.1%	0.718	0.140	0.158	13.1%
<i>Phyciodes phaon</i>	34	0.895	0.747	0.254	0.302	19.1%	0.639	0.185	0.193	4.3%
<i>Phyciodes pulchella</i> <sup>w</sup>	23	0.895	0.342	0.658	0.373	-43.3%	0.574	0.209	0.203	-3.2%
<i>Phyciodes tharos</i>	231	0.844	0.183	0.817	0.731	-10.5%	0.515	0.243	0.237	-2.3%
<i>Pieris marginalis</i> <sup>w</sup>	17	0.933	0.771	0.229	0.373	62.7%	0.739	0.143	0.122	-15.1%
<i>Pieris oleracea</i> <sup>e</sup>	16	0.983	0.894	0.106	0.101	-4.4%	0.848	0.089	0.095	6.4%
<i>Pieris rapae</i>	177	0.858	0.135	0.865	0.928	7.3%	0.571	0.215	0.232	7.9%
<i>Pieris virginiensis</i> <sup>e</sup>	33	0.935	0.754	0.246	0.251	2.0%	0.754	0.124	0.133	6.8%
<i>Plebejus acmon</i> <sup>w</sup>	18	0.951	0.802	0.198	0.273	37.8%	0.772	0.117	0.143	22.3%
<i>Plebejus icarioides</i> <sup>w</sup>	26	0.946	0.771	0.229	0.315	37.6%	0.696	0.150	0.154	2.3%
<i>Plebejus lupini</i> <sup>w</sup>	19	0.938	0.641	0.359	0.329	-8.5%	0.779	0.116	0.158	36.7%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Plebejus melissa</i>	23	0.822	0.455	0.545	0.620	13.7%	0.496	0.243	0.261	7.3%
<i>Plebejus saepiolus</i>	13	0.917	0.650	0.350	0.202	-42.2%	0.692	0.154	0.183	19.1%
<i>Poanes hobomok</i>	83	0.917	0.261	0.739	0.646	-12.5%	0.665	0.167	0.164	-1.9%
<i>Poanes massasoit</i> <sup>e</sup>	12	0.973	0.873	0.127	0.125	-1.5%	0.833	0.083	0.111	33.5%
<i>Poanes viator</i> <sup>e</sup>	17	0.955	0.745	0.255	0.230	-9.7%	0.765	0.118	0.122	3.5%
<i>Poanes zabulon</i>	122	0.926	0.646	0.354	0.350	-1.0%	0.692	0.152	0.143	-6.3%
<i>Polites mystic</i>	31	0.918	0.241	0.759	0.661	-12.9%	0.742	0.129	0.129	0.0%
<i>Polites origenes</i>	47	0.889	0.659	0.342	0.346	1.3%	0.569	0.218	0.199	-9.0%
<i>Polites peckius</i>	117	0.921	0.295	0.706	0.698	-1.1%	0.678	0.160	0.147	-8.1%
<i>Polites themistocles</i>	94	0.908	0.486	0.514	0.489	-4.9%	0.639	0.180	0.159	-12.0%
<i>Polites vibex</i> <sup>e</sup>	29	0.924	0.284	0.716	0.623	-13.0%	0.724	0.138	0.138	0.0%
<i>Polygonia comma</i>	124	0.913	0.570	0.430	0.435	1.2%	0.676	0.162	0.177	9.3%
<i>Polygonia faunus</i>	27	0.945	0.678	0.322	0.647	100.9%	0.704	0.148	0.201	36.0%
<i>Polygonia gracilis</i>	24	0.906	0.439	0.561	0.709	26.5%	0.667	0.167	0.170	1.9%
<i>Polygonia interrogationis</i>	219	0.861	0.427	0.573	0.758	32.2%	0.563	0.218	0.228	4.7%
<i>Polygonia progne</i>	41	0.929	0.736	0.264	0.524	98.6%	0.659	0.171	0.170	-0.6%
<i>Polygonia satyrus</i> <sup>w</sup>	19	0.949	0.748	0.252	0.324	28.5%	0.784	0.111	0.164	47.6%
<i>Pompeius verna</i>	69	0.892	0.628	0.372	0.356	-4.3%	0.618	0.194	0.188	-2.7%
<i>Pontia occidentalis</i> <sup>w</sup>	16	0.937	0.701	0.299	0.255	-14.7%	0.642	0.171	0.188	9.6%
<i>Pontia protodice</i>	106	0.871	0.135	0.865	0.876	1.3%	0.604	0.198	0.208	4.7%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Pontia sisymbrii</i>	11	0.908	0.657	0.343	0.421	22.6%	0.478	0.250	0.144	-42.2%
<i>Pyrgus communis</i>	119	0.849	0.012	0.988	0.900	-8.9%	0.563	0.219	0.235	7.7%
<i>Pyrgus oileus</i>	37	0.970	0.896	0.104	0.099	-5.1%	0.843	0.076	0.081	7.4%
<i>Pyrisitia lisa</i>	87	0.858	0.462	0.538	0.520	-3.4%	0.520	0.239	0.228	-4.7%
<i>Satyrium acadica</i> <sup>e</sup>	23	0.965	0.813	0.187	0.162	-13.6%	0.809	0.104	0.087	-16.5%
<i>Satyrium calanus</i>	90	0.902	0.303	0.697	0.588	-15.6%	0.647	0.176	0.197	12.1%
<i>Satyrium californica</i>	10	0.977	0.895	0.105	0.165	57.0%	0.800	0.100	0.100	0.0%
<i>Satyrium caryaevorus</i> <sup>e</sup>	19	0.954	0.759	0.241	0.266	10.4%	0.789	0.105	0.105	0.0%
<i>Satyrium edwardsii</i> <sup>e</sup>	20	0.895	0.581	0.419	0.427	1.9%	0.597	0.203	0.184	-9.4%
<i>Satyrium favonius</i>	16	0.911	0.620	0.380	0.468	23.1%	0.622	0.190	0.188	-1.4%
<i>Satyrium favonius ontario</i>	14	0.886	0.707	0.294	0.279	-5.0%	0.579	0.207	0.211	1.8%
<i>Satyrium liparops</i>	43	0.880	0.369	0.632	0.601	-4.8%	0.619	0.195	0.198	1.2%
<i>Satyrium saepium</i> <sup>w</sup>	17	0.965	0.845	0.155	0.285	84.0%	0.793	0.090	0.142	58.2%
<i>Satyrium sylvinus</i>	12	0.957	0.824	0.176	0.132	-24.8%	0.828	0.088	0.089	0.6%
<i>Satyrium titus</i>	55	0.867	0.278	0.722	0.750	3.9%	0.561	0.221	0.182	-17.6%
<i>Satyroides appalachia</i>	44	0.890	0.610	0.390	0.416	6.6%	0.630	0.188	0.195	3.7%
<i>Satyroides eurydice</i> <sup>e</sup>	33	0.957	0.838	0.162	0.159	-1.7%	0.758	0.121	0.102	-15.9%
<i>Speyeria aphrodite</i>	49	0.936	0.695	0.305	0.526	72.7%	0.754	0.123	0.163	32.4%
<i>Speyeria atlantis</i>	24	0.962	0.569	0.431	0.279	-35.2%	0.834	0.082	0.144	74.2%
<i>Speyeria callippe</i> <sup>w</sup>	16	0.970	0.904	0.096	0.112	16.8%	0.855	0.083	0.072	-13.3%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Speyeria coronis</i>	11	0.940	0.699	0.301	0.366	21.6%	0.636	0.182	0.182	0.0%
<i>Speyeria cybele</i>	184	0.900	0.442	0.558	0.824	47.7%	0.620	0.190	0.194	2.2%
<i>Speyeria diana</i> <sup>e</sup>	21	0.942	0.648	0.353	0.329	-6.6%	0.725	0.132	0.107	-19.1%
<i>Speyeria hesperis</i>	14	0.934	0.795	0.206	0.274	33.4%	0.714	0.143	0.169	18.3%
<i>Speyeria hydaspe</i>	12	0.954	0.856	0.144	0.124	-14.3%	0.695	0.138	0.097	-30.2%
<i>Speyeria idalia</i> <sup>e</sup>	18	0.957	0.852	0.148	0.113	-23.3%	0.778	0.111	0.100	-9.7%
<i>Speyeria mormonia</i>	10	0.943	0.812	0.188	0.202	7.0%	0.615	0.185	0.145	-21.6%
<i>Speyeria zerene</i>	11	0.942	0.799	0.201	0.169	-15.8%	0.818	0.091	0.132	45.7%
<i>Staphylus hayhurstii</i> <sup>e</sup>	25	0.916	0.756	0.244	0.232	-4.7%	0.680	0.160	0.160	0.0%
<i>Strymon melinus</i>	189	0.817	0.105	0.896	0.969	8.2%	0.479	0.261	0.271	3.5%
<i>Thorybes bathyllus</i>	45	0.902	0.702	0.298	0.280	-6.0%	0.643	0.180	0.174	-3.4%
<i>Thorybes pylades</i>	73	0.865	0.253	0.747	0.851	13.9%	0.534	0.233	0.219	-5.9%
<i>Thymelicus lineola</i>	53	0.909	0.416	0.584	0.479	-18.0%	0.660	0.170	0.170	0.0%
<i>Urbanus dorantes</i>	11	0.949	0.824	0.176	0.157	-11.1%	0.664	0.155	0.140	-9.3%
<i>Urbanus proteus</i>	100	0.926	0.687	0.313	0.305	-2.4%	0.680	0.160	0.150	-6.3%
<i>Vanessa annabella</i> <sup>w</sup>	21	0.922	0.423	0.577	0.387	-32.9%	0.712	0.145	0.143	-1.3%
<i>Vanessa atalanta</i>	301	0.820	0.200	0.800	0.733	-8.4%	0.462	0.269	0.273	1.5%
<i>Vanessa cardui</i>	204	0.814	0.110	0.890	0.940	5.6%	0.471	0.265	0.282	6.5%
<i>Vanessa virginiensis</i>	204	0.846	0.277	0.723	0.915	26.4%	0.511	0.244	0.241	-1.3%
<i>Wallengrenia egeremet</i>	57	0.899	0.618	0.382	0.365	-4.2%	0.646	0.178	0.178	-0.4%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Wallengrenia otho</i>	36	0.900	0.701	0.299	0.309	3.4%	0.568	0.210	0.194	-7.5%
<i>Zerene cesonia</i>	25	0.821	0.386	0.614	0.764	24.4%	0.510	0.250	0.240	-4.1%
<i>Zerene eurydice</i>	11	0.991	0.975	0.025	0.050	99.2%	0.975	0.025	0.050	99.2%
Odonata from OdonataCentral										
<i>Acanthagrion quadratum</i> <sup>b</sup>	11	0.992	0.979	0.022	0.037	70.2%	0.979	0.022	0.037	70.2%
<i>Aeshna canadensis</i> <sup>b</sup>	56	0.893	0.641	0.359	0.716	99.3%	0.607	0.196	0.241	22.8%
<i>Aeshna clepsydra</i> <sup>b</sup>	15	0.956	0.747	0.253	0.303	19.4%	0.733	0.133	0.067	-50.0%
<i>Aeshna constricta</i> <sup>b</sup>	86	0.865	0.391	0.609	0.638	4.7%	0.535	0.233	0.236	1.6%
<i>Aeshna eremita</i> <sup>b</sup>	30	0.954	0.723	0.277	0.446	61.1%	0.800	0.100	0.167	66.7%
<i>Aeshna interrupta</i> <sup>b</sup>	122	0.861	0.410	0.590	0.580	-1.7%	0.525	0.238	0.208	-12.4%
<i>Aeshna juncea</i> <sup>wb</sup>	25	0.974	0.933	0.067	0.532	689.0%	0.858	0.062	0.088	41.3%
<i>Aeshna palmata</i> <sup>wb</sup>	120	0.900	0.556	0.444	0.494	11.3%	0.650	0.175	0.197	12.5%
<i>Aeshna sitchensis</i> <sup>b</sup>	16	0.974	0.916	0.084	0.340	307.2%	0.860	0.077	0.165	113.2%
<i>Aeshna subarctica</i> <sup>b</sup>	15	0.964	0.825	0.175	0.193	10.5%	0.733	0.133	0.133	0.0%
<i>Aeshna tuberculifera</i> <sup>b</sup>	30	0.881	0.623	0.377	0.796	111.2%	0.603	0.197	0.233	18.6%
<i>Aeshna umbrosa</i> <sup>b</sup>	144	0.807	0.237	0.763	0.810	6.1%	0.433	0.283	0.278	-1.7%
<i>Aeshna verticalis</i> <sup>b</sup>	18	0.943	0.797	0.203	0.203	-0.2%	0.667	0.167	0.111	-33.4%
<i>Aeshna walkeri</i> <sup>a</sup>	14	0.958	0.847	0.153	0.107	-30.3%	0.857	0.071	0.075	4.5%
<i>Amphiagrion abbreviatum</i> <sup>wb</sup>	59	0.902	0.583	0.417	0.467	12.2%	0.630	0.183	0.186	1.6%
<i>Amphiagrion saucium</i> <sup>b</sup>	26	0.917	0.685	0.315	0.326	3.6%	0.631	0.177	0.183	3.6%

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Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Anax junius</i> <sup>b</sup>	455	0.757	0.023	0.977	0.997	2.0%	0.363	0.319	0.326	2.4%
<i>Anax longipes</i> <sup>b</sup>	63	0.882	0.432	0.569	0.525	-7.6%	0.562	0.216	0.206	-4.5%
<i>Anax walsinghami</i> <sup>a</sup>	18	0.929	0.715	0.285	0.295	3.4%	0.667	0.167	0.222	33.3%
<i>Aphylla angustifolia</i> <sup>eb</sup>	30	0.982	0.918	0.082	0.094	14.3%	0.867	0.067	0.067	0.3%
<i>Aphylla williamsoni</i> <sup>b</sup>	72	0.946	0.826	0.174	0.173	-0.6%	0.778	0.111	0.117	5.4%
<i>Archilestes californicus</i> <sup>a</sup>	31	0.965	0.884	0.116	0.127	9.9%	0.810	0.094	0.078	-17.0%
<i>Archilestes grandis</i> <sup>a</sup>	120	0.861	0.206	0.795	0.977	22.9%	0.580	0.212	0.233	10.3%
<i>Argia agrioides</i> <sup>a</sup>	16	0.967	0.860	0.140	0.189	34.5%	0.770	0.105	0.114	8.9%
<i>Argia alberta</i> <sup>b</sup>	69	0.919	0.501	0.499	0.506	1.4%	0.652	0.174	0.182	4.4%
<i>Argia apicalis</i> <sup>b</sup>	356	0.841	0.316	0.684	0.830	21.3%	0.505	0.247	0.257	3.9%
<i>Argia bipunctulata</i> <sup>b</sup>	30	0.926	0.683	0.317	0.253	-20.1%	0.675	0.158	0.133	-15.6%
<i>Argia emma</i> <sup>wa</sup>	67	0.900	0.619	0.381	0.409	7.5%	0.666	0.170	0.178	4.8%
<i>Argia fumipennis</i> <sup>b</sup>	264	0.813	0.218	0.782	0.721	-7.9%	0.440	0.280	0.268	-4.3%
<i>Argia hinei</i> <sup>b</sup>	17	0.958	0.836	0.164	0.224	36.5%	0.765	0.118	0.135	14.6%
<i>Argia immunda</i> <sup>a</sup>	68	0.930	0.341	0.659	0.784	18.9%	0.765	0.118	0.125	6.1%
<i>Argia leonora</i> <sup>a</sup>	20	0.978	0.895	0.105	0.158	50.0%	0.890	0.060	0.062	4.0%
<i>Argia lugens</i> <sup>wa</sup>	37	0.943	0.704	0.296	0.238	-19.6%	0.730	0.135	0.162	20.1%
<i>Argia moesta</i> <sup>b</sup>	331	0.833	0.338	0.662	0.893	34.8%	0.517	0.242	0.270	11.5%
<i>Argia nahuana</i> <sup>a</sup>	89	0.930	0.545	0.455	0.454	-0.2%	0.727	0.139	0.138	-0.7%
<i>Argia plana</i> <sup>a</sup>	111	0.935	0.590	0.410	0.931	127.2%	0.748	0.126	0.150	18.7%

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Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Argia sedula</i> <sup>a</sup>	211	0.875	0.433	0.568	0.855	50.6%	0.564	0.218	0.218	-0.1%
<i>Argia tibialis</i> <sup>a</sup>	182	0.908	0.588	0.412	0.505	22.7%	0.647	0.178	0.191	7.7%
<i>Argia translata</i> <sup>a</sup>	119	0.939	0.596	0.404	0.506	25.1%	0.744	0.130	0.150	15.6%
<i>Argia vivida</i> <sup>wa</sup>	69	0.876	0.566	0.434	0.636	46.6%	0.619	0.193	0.182	-5.6%
<i>Arigomphus cornutus</i> <sup>b</sup>	30	0.941	0.761	0.239	0.256	7.4%	0.733	0.133	0.167	25.1%
<i>Arigomphus furcifer</i> <sup>b</sup>	17	0.950	0.852	0.148	0.148	0.1%	0.765	0.118	0.113	-4.2%
<i>Arigomphus lentulus</i> <sup>b</sup>	21	0.955	0.814	0.186	0.181	-2.6%	0.810	0.095	0.095	0.0%
<i>Arigomphus maxwelli</i> <sup>eb</sup>	22	0.983	0.924	0.076	0.073	-4.2%	0.903	0.052	0.071	37.1%
<i>Arigomphus pallidus</i> <sup>b</sup>	10	0.975	0.957	0.043	0.051	19.3%	0.957	0.043	0.051	19.3%
<i>Arigomphus submedianus</i> <sup>b</sup>	104	0.950	0.656	0.344	0.333	-3.0%	0.769	0.116	0.130	12.2%
<i>Arigomphus villosipes</i> <sup>b</sup>	65	0.937	0.793	0.207	0.220	6.4%	0.748	0.129	0.138	6.3%
<i>Basiaeschna janata</i> <sup>eb</sup>	86	0.910	0.592	0.408	0.444	9.0%	0.675	0.162	0.181	11.9%
<i>Boyeria graefiana</i> <sup>a</sup>	12	0.967	0.851	0.149	0.158	6.0%	0.833	0.083	0.083	0.0%
<i>Boyeria vinosa</i> <sup>a</sup>	48	0.908	0.629	0.372	0.389	4.7%	0.660	0.174	0.178	2.4%
<i>Brachymesia furcata</i> <sup>b</sup>	39	0.958	0.711	0.289	0.270	-6.7%	0.784	0.113	0.116	2.6%
<i>Brachymesia gravida</i> <sup>b</sup>	135	0.937	0.596	0.404	0.358	-11.4%	0.763	0.119	0.147	24.1%
<i>Brachymesia herbida</i> <sup>b</sup>	11	0.977	0.907	0.093	0.098	5.3%	0.818	0.091	0.091	0.0%
<i>Brechmorhoga mendax</i> <sup>a</sup>	55	0.941	0.635	0.365	0.395	8.1%	0.709	0.146	0.164	12.4%
<i>Calopteryx aequabilis</i> <sup>b</sup>	77	0.819	0.323	0.677	0.699	3.3%	0.481	0.260	0.269	3.7%
<i>Calopteryx angustipennis</i> <sup>a</sup>	16	0.960	0.873	0.127	0.136	6.7%	0.762	0.113	0.123	8.8%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Calopteryx dimidiata</i> <sup>ea</sup>	31	0.948	0.821	0.179	0.178	-0.8%	0.750	0.121	0.129	6.6%
<i>Calopteryx maculata</i> <sup>a</sup>	345	0.868	0.389	0.611	0.595	-2.6%	0.559	0.220	0.209	-5.3%
<i>Cannaphila insularis</i> <sup>b</sup>	11	0.977	0.874	0.126	0.080	-36.1%	0.818	0.091	0.080	-11.8%
<i>Celithemis amanda</i> <sup>b</sup>	13	0.953	0.871	0.129	0.133	2.6%	0.730	0.116	0.094	-19.1%
<i>Celithemis bertha</i> <sup>b</sup>	14	0.959	0.883	0.117	0.116	-0.5%	0.852	0.077	0.071	-7.2%
<i>Celithemis elisa</i> <sup>b</sup>	201	0.855	0.426	0.574	0.704	22.7%	0.495	0.252	0.247	-1.9%
<i>Celithemis eponina</i> <sup>b</sup>	358	0.828	0.333	0.667	0.808	21.2%	0.491	0.255	0.262	2.8%
<i>Celithemis fasciata</i> <sup>b</sup>	147	0.896	0.587	0.413	0.373	-9.5%	0.603	0.200	0.177	-11.6%
<i>Celithemis martha</i> <sup>b</sup>	14	0.987	0.974	0.026	0.073	185.5%	0.974	0.026	0.071	178.9%
<i>Celithemis ornata</i> <sup>b</sup>	21	0.957	0.825	0.175	0.093	-47.1%	0.810	0.095	0.089	-6.5%
<i>Celithemis verna</i> <sup>b</sup>	17	0.934	0.832	0.168	0.211	25.5%	0.676	0.147	0.139	-5.4%
<i>Chromagrion conditum</i> <sup>b</sup>	45	0.947	0.738	0.262	0.273	4.1%	0.732	0.135	0.133	-1.0%
<i>Coenagrion resolutum</i> <sup>b</sup>	44	0.929	0.681	0.319	0.600	88.0%	0.682	0.159	0.250	57.2%
<i>Cordulegaster bilineata</i> <sup>a</sup>	17	0.958	0.784	0.217	0.184	-14.8%	0.765	0.118	0.118	0.0%
<i>Cordulegaster diastatops</i> <sup>ea</sup>	23	0.979	0.934	0.066	0.091	36.9%	0.913	0.044	0.064	45.8%
<i>Cordulegaster dorsalis</i> <sup>wa</sup>	35	0.931	0.708	0.293	0.271	-7.3%	0.711	0.146	0.174	18.8%
<i>Cordulegaster erronea</i> <sup>a</sup>	19	0.966	0.865	0.135	0.296	119.8%	0.789	0.105	0.131	24.3%
<i>Cordulegaster maculata</i> <sup>a</sup>	41	0.911	0.554	0.446	0.419	-6.1%	0.659	0.171	0.186	8.9%
<i>Cordulegaster obliqua</i> <sup>a</sup>	64	0.879	0.521	0.479	0.543	13.2%	0.596	0.201	0.206	2.9%
<i>Cordulia shurtleffii</i> <sup>b</sup>	58	0.928	0.699	0.301	0.584	94.1%	0.720	0.143	0.204	42.9%

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Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Coryphaeschna adnexa</i> <sup>b</sup>	12	0.977	0.899	0.101	0.069	-31.2%	0.833	0.083	0.069	-16.9%
<i>Coryphaeschna ingens</i> <sup>b</sup>	27	0.952	0.861	0.140	0.152	9.0%	0.768	0.121	0.131	8.6%
<i>Crocothemis servilia</i> <sup>b</sup>	12	0.995	0.988	0.012	0.013	6.7%	0.988	0.012	0.013	6.7%
<i>Didymops transversa</i> <sup>a</sup>	95	0.916	0.665	0.335	0.351	4.7%	0.662	0.169	0.179	5.6%
<i>Dorocordulia libera</i> <sup>b</sup>	27	0.950	0.827	0.173	0.166	-3.9%	0.769	0.120	0.109	-9.4%
<i>Dromogomphus spinosus</i> <sup>b</sup>	121	0.906	0.373	0.627	0.469	-25.2%	0.653	0.174	0.175	0.7%
<i>Dromogomphus spoliatus</i> <sup>b</sup>	154	0.930	0.596	0.404	0.462	14.3%	0.714	0.143	0.136	-4.6%
<i>Dythemis fugax</i> <sup>b</sup>	95	0.962	0.803	0.197	0.238	20.9%	0.789	0.105	0.093	-11.7%
<i>Dythemis nigrescens</i> <sup>b</sup>	34	0.974	0.892	0.108	0.103	-4.0%	0.826	0.086	0.084	-2.6%
<i>Dythemis velox</i> <sup>b</sup>	124	0.924	0.605	0.395	0.480	21.3%	0.677	0.161	0.145	-10.0%
<i>Enallagma anna</i> <sup>a</sup>	69	0.892	0.316	0.684	0.662	-3.3%	0.657	0.169	0.200	18.1%
<i>Enallagma annexum</i> <sup>b</sup>	107	0.854	0.482	0.518	0.713	37.5%	0.551	0.224	0.229	2.2%
<i>Enallagma antennatum</i> <sup>b</sup>	101	0.927	0.518	0.482	0.595	23.3%	0.683	0.158	0.158	0.0%
<i>Enallagma aspersum</i> <sup>b</sup>	105	0.888	0.448	0.552	0.517	-6.3%	0.582	0.209	0.181	-13.3%
<i>Enallagma basidens</i> <sup>b</sup>	248	0.851	0.403	0.597	0.812	36.1%	0.534	0.233	0.249	7.1%
<i>Enallagma boreale</i> <sup>b</sup>	80	0.857	0.329	0.672	0.626	-6.8%	0.550	0.225	0.227	1.0%
<i>Enallagma carunculatum</i> <sup>b</sup>	166	0.844	0.288	0.712	0.855	20.1%	0.530	0.235	0.261	11.0%
<i>Enallagma civile</i> <sup>b</sup>	442	0.796	0.102	0.898	0.908	1.0%	0.448	0.276	0.286	3.6%
<i>Enallagma clausum</i> <sup>b</sup>	22	0.892	0.536	0.464	0.419	-9.7%	0.636	0.182	0.250	37.5%
<i>Enallagma concisum</i> <sup>b</sup>	11	0.978	0.950	0.050	0.055	10.9%	0.860	0.050	0.055	11.1%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Enallagma daeckii</i> <sup>b</sup>	22	0.968	0.833	0.167	0.156	-6.6%	0.840	0.069	0.119	72.9%
<i>Enallagma davisii</i> <sup>b</sup>	10	0.983	0.924	0.076	0.067	-11.9%	0.824	0.076	0.067	-12.0%
<i>Enallagma divagans</i> <sup>b</sup>	65	0.882	0.643	0.357	0.356	-0.3%	0.575	0.209	0.222	6.2%
<i>Enallagma doubledayi</i> <sup>b</sup>	18	0.946	0.846	0.154	0.130	-15.7%	0.789	0.100	0.111	11.5%
<i>Enallagma dubium</i> <sup>b</sup>	23	0.963	0.833	0.167	0.161	-3.6%	0.752	0.117	0.110	-6.0%
<i>Enallagma durum</i> <sup>b</sup>	28	0.939	0.725	0.275	0.279	1.5%	0.717	0.140	0.107	-23.4%
<i>Enallagma ebrium</i> <sup>b</sup>	40	0.871	0.627	0.373	0.422	13.3%	0.555	0.220	0.225	2.3%
<i>Enallagma exsulans</i> <sup>b</sup>	190	0.864	0.154	0.846	0.543	-35.8%	0.548	0.226	0.239	5.9%
<i>Enallagma geminatum</i> <sup>b</sup>	145	0.874	0.485	0.515	0.499	-3.1%	0.559	0.221	0.207	-6.3%
<i>Enallagma hageni</i> <sup>b</sup>	97	0.929	0.598	0.402	0.434	8.1%	0.711	0.144	0.144	0.0%
<i>Enallagma novaehispaniae</i> <sup>a</sup>	16	0.993	0.983	0.017	0.019	10.1%	0.983	0.017	0.019	10.1%
<i>Enallagma praevarum</i> <sup>b</sup>	64	0.896	0.544	0.456	0.642	41.0%	0.653	0.175	0.194	10.7%
<i>Enallagma signatum</i> <sup>b</sup>	242	0.859	0.304	0.696	0.830	19.2%	0.546	0.227	0.215	-5.2%
<i>Enallagma traviatum</i> <sup>b</sup>	90	0.891	0.613	0.387	0.394	1.7%	0.600	0.200	0.200	0.1%
<i>Enallagma vesperum</i> <sup>b</sup>	70	0.807	0.528	0.472	0.499	5.8%	0.423	0.291	0.262	-10.1%
<i>Enallagma weewa</i> <sup>b</sup>	10	0.963	0.911	0.089	0.092	2.8%	0.811	0.089	0.092	2.8%
<i>Epiaeschna heros</i> <sup>b</sup>	125	0.908	0.609	0.391	0.400	2.1%	0.648	0.176	0.184	4.5%
<i>Epitheca canis</i> <sup>b</sup>	23	0.929	0.742	0.258	0.273	5.9%	0.726	0.144	0.170	18.3%
<i>Epitheca costalis</i> <sup>eb</sup>	38	0.929	0.759	0.241	0.228	-5.4%	0.692	0.150	0.150	-0.1%
<i>Epitheca cynosura</i> <sup>b</sup>	130	0.906	0.541	0.459	0.501	9.2%	0.650	0.174	0.181	4.1%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Epitheca petechialis</i> <sup>b</sup>	58	0.914	0.523	0.477	0.585	22.7%	0.655	0.172	0.190	10.0%
<i>Epitheca princeps</i> <sup>b</sup>	193	0.880	0.486	0.514	0.520	1.2%	0.606	0.197	0.228	15.8%
<i>Epitheca semiaquea</i> <sup>b</sup>	44	0.928	0.716	0.284	0.375	31.9%	0.689	0.152	0.145	-5.0%
<i>Epitheca spinigera</i> <sup>b</sup>	24	0.874	0.397	0.603	0.419	-30.5%	0.583	0.208	0.214	2.8%
<i>Erpetogomphus compositus</i> <sup>wa</sup>	37	0.941	0.624	0.376	0.276	-26.5%	0.730	0.135	0.189	40.0%
<i>Erpetogomphus designatus</i> <sup>a</sup>	89	0.923	0.339	0.661	0.460	-30.5%	0.685	0.157	0.157	0.0%
<i>Erpetogomphus lampropeltis</i> <sup>a</sup>	13	0.970	0.781	0.219	0.186	-14.9%	0.846	0.077	0.138	79.3%
<i>Erythemis collocata</i> <sup>wb</sup>	82	0.931	0.627	0.373	0.453	21.4%	0.707	0.146	0.183	25.0%
<i>Erythemis plebeja</i> <sup>eb</sup>	22	0.981	0.946	0.054	0.068	26.1%	0.909	0.046	0.058	27.0%
<i>Erythemis simplicicollis</i> <sup>b</sup>	576	0.814	0.275	0.725	0.774	6.8%	0.458	0.271	0.269	-0.8%
<i>Erythemis vesiculosa</i> <sup>b</sup>	51	0.939	0.649	0.351	0.406	15.7%	0.730	0.132	0.153	15.9%
<i>Erythrodiplax berenice</i> <sup>b</sup>	43	0.967	0.180	0.820	0.699	-14.7%	0.860	0.070	0.078	12.0%
<i>Erythrodiplax minuscula</i> <sup>b</sup>	66	0.934	0.731	0.269	0.267	-0.6%	0.727	0.136	0.130	-4.5%
<i>Erythrodiplax umbrata</i> <sup>b</sup>	66	0.929	0.683	0.317	0.414	30.8%	0.697	0.152	0.151	-0.5%
<i>Gomphaeschna antilope</i> <sup>b</sup>	16	0.937	0.578	0.422	0.439	3.9%	0.750	0.125	0.139	11.1%
<i>Gomphaeschna furcillata</i> <sup>eb</sup>	48	0.910	0.622	0.378	0.451	19.2%	0.667	0.167	0.172	3.4%
<i>Gomphus apomyius</i> <sup>a</sup>	14	0.968	0.920	0.080	0.125	55.6%	0.857	0.071	0.117	63.2%
<i>Gomphus descriptus</i> <sup>a</sup>	11	0.970	0.939	0.061	0.071	15.7%	0.848	0.061	0.071	15.7%
<i>Gomphus dilatatus</i> <sup>a</sup>	19	0.950	0.836	0.164	0.140	-14.5%	0.789	0.105	0.112	6.7%
<i>Gomphus exilis</i> <sup>b</sup>	107	0.940	0.627	0.373	0.342	-8.1%	0.715	0.145	0.127	-12.4%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Gomphus externus</i> <sup>a</sup>	96	0.915	0.409	0.591	0.620	4.9%	0.690	0.154	0.163	5.8%
<i>Gomphus fraternus</i> <sup>b</sup>	19	0.920	0.724	0.276	0.277	0.7%	0.589	0.201	0.158	-21.4%
<i>Gomphus graslinellus</i> <sup>a</sup>	47	0.816	0.265	0.735	0.697	-5.2%	0.412	0.290	0.277	-4.7%
<i>Gomphus hybridus</i> <sup>ea</sup>	26	0.972	0.872	0.128	0.151	18.4%	0.783	0.101	0.114	12.5%
<i>Gomphus kurilis</i> <sup>b</sup>	13	0.975	0.943	0.057	0.053	-6.8%	0.866	0.057	0.053	-7.0%
<i>Gomphus lividus</i> <sup>a</sup>	76	0.914	0.665	0.335	0.342	1.9%	0.685	0.158	0.158	0.3%
<i>Gomphus militaris</i> <sup>b</sup>	119	0.927	0.665	0.335	0.449	34.0%	0.714	0.143	0.135	-5.9%
<i>Gomphus oklahomensis</i> <sup>eb</sup>	35	0.976	0.814	0.186	0.148	-20.4%	0.886	0.057	0.085	48.3%
<i>Gomphus quadricolor</i> <sup>a</sup>	19	0.947	0.713	0.287	0.262	-8.9%	0.765	0.130	0.158	21.5%
<i>Gomphus rogersi</i> <sup>a</sup>	12	0.971	0.934	0.066	0.075	12.3%	0.850	0.066	0.075	12.2%
<i>Gomphus spicatus</i> <sup>b</sup>	19	0.952	0.835	0.165	0.146	-11.2%	0.793	0.102	0.099	-2.6%
<i>Gomphus vastus</i> <sup>a</sup>	61	0.838	0.481	0.519	0.484	-6.8%	0.467	0.270	0.262	-3.0%
<i>Gomphus viridifrons</i> <sup>a</sup>	10	0.936	0.735	0.265	0.236	-10.7%	0.773	0.127	0.163	28.4%
<i>Hagenius brevistylus</i> <sup>b</sup>	112	0.904	0.507	0.493	0.527	6.9%	0.625	0.188	0.205	9.3%
<i>Helocordulia selysii</i> <sup>a</sup>	21	0.964	0.890	0.110	0.094	-14.9%	0.812	0.093	0.070	-25.4%
<i>Helocordulia uhleri</i> <sup>b</sup>	20	0.955	0.832	0.168	0.165	-1.4%	0.711	0.139	0.150	8.1%
<i>Hesperagrion heterodoxum</i> <sup>wa</sup>	15	0.977	0.923	0.077	0.065	-15.9%	0.865	0.068	0.065	-4.8%
<i>Hetaerina americana</i> <sup>a</sup>	324	0.835	0.216	0.784	0.872	11.2%	0.512	0.244	0.262	7.3%
<i>Hetaerina titia</i> <sup>a</sup>	74	0.872	0.612	0.389	0.432	11.1%	0.541	0.230	0.225	-2.1%
<i>Ischnura barberi</i> <sup>b</sup>	35	0.952	0.534	0.466	0.356	-23.6%	0.771	0.114	0.143	24.9%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Ischnura cervula</i> <sup>wb</sup>	66	0.897	0.399	0.601	0.687	14.3%	0.636	0.182	0.193	6.1%
<i>Ischnura damula</i> <sup>wb</sup>	60	0.936	0.774	0.226	0.287	27.0%	0.730	0.136	0.150	9.8%
<i>Ischnura demorsa</i> <sup>wb</sup>	31	0.954	0.868	0.133	0.239	80.3%	0.799	0.105	0.129	23.4%
<i>Ischnura denticollis</i> <sup>b</sup>	49	0.920	0.656	0.344	0.313	-9.2%	0.674	0.163	0.177	8.7%
<i>Ischnura erratica</i> <sup>b</sup>	23	0.979	0.914	0.086	0.060	-31.1%	0.906	0.051	0.054	5.7%
<i>Ischnura hastata</i> <sup>b</sup>	240	0.871	0.426	0.574	0.591	2.9%	0.582	0.209	0.218	4.2%
<i>Ischnura kellicotti</i> <sup>b</sup>	57	0.886	0.626	0.374	0.366	-2.1%	0.615	0.192	0.175	-8.5%
<i>Ischnura perparva</i> <sup>b</sup>	73	0.882	0.430	0.570	0.695	21.9%	0.617	0.191	0.192	0.4%
<i>Ischnura posita</i> <sup>b</sup>	395	0.872	0.448	0.552	0.584	5.9%	0.574	0.213	0.218	2.2%
<i>Ischnura prognata</i> <sup>b</sup>	11	0.960	0.903	0.097	0.090	-7.4%	0.818	0.091	0.090	-1.3%
<i>Ischnura ramburii</i> <sup>b</sup>	237	0.894	0.573	0.427	0.420	-1.7%	0.637	0.181	0.194	7.0%
<i>Ischnura verticalis</i> <sup>b</sup>	301	0.876	0.311	0.689	0.789	14.6%	0.595	0.203	0.217	7.2%
<i>Ladona deplanata</i> <sup>b</sup>	167	0.910	0.577	0.423	0.437	3.3%	0.652	0.174	0.175	0.3%
<i>Ladona exusta</i> <sup>b</sup>	11	0.984	0.951	0.049	0.040	-19.3%	0.860	0.049	0.040	-19.2%
<i>Ladona julia</i> <sup>b</sup>	61	0.918	0.601	0.399	0.866	116.9%	0.645	0.175	0.200	14.6%
<i>Lestes alacer</i> <sup>b</sup>	57	0.942	0.667	0.333	0.273	-18.0%	0.754	0.123	0.123	0.4%
<i>Lestes australis</i> <sup>b</sup>	187	0.889	0.471	0.529	0.604	14.2%	0.602	0.200	0.191	-4.8%
<i>Lestes congener</i> <sup>b</sup>	111	0.801	0.265	0.735	0.798	8.5%	0.407	0.296	0.252	-14.8%
<i>Lestes disjunctus</i> <sup>b</sup>	82	0.865	0.431	0.569	0.495	-13.1%	0.534	0.235	0.231	-1.4%
<i>Lestes dryas</i> <sup>b</sup>	99	0.842	0.273	0.727	0.689	-5.3%	0.535	0.232	0.231	-0.6%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Lestes eurinus</i> <sup>eb</sup>	34	0.910	0.688	0.312	0.375	20.2%	0.706	0.147	0.169	14.6%
<i>Lestes forcipatus</i> <sup>b</sup>	49	0.827	0.353	0.647	0.738	14.1%	0.506	0.249	0.247	-1.0%
<i>Lestes forcifcula</i> <sup>eb</sup>	14	0.961	0.749	0.251	0.269	7.3%	0.857	0.071	0.071	0.0%
<i>Lestes inaequalis</i> <sup>eb</sup>	69	0.840	0.599	0.401	0.434	8.3%	0.511	0.242	0.234	-3.7%
<i>Lestes rectangularis</i> <sup>b</sup>	171	0.913	0.450	0.550	0.624	13.5%	0.684	0.158	0.168	6.5%
<i>Lestes sigma</i> <sup>b</sup>	12	0.984	0.954	0.046	0.032	-31.9%	0.870	0.046	0.032	-31.7%
<i>Lestes unguiculatus</i> <sup>b</sup>	176	0.891	0.385	0.616	0.660	7.2%	0.625	0.188	0.193	3.1%
<i>Lestes vigilax</i> <sup>b</sup>	88	0.905	0.609	0.391	0.393	0.5%	0.661	0.169	0.205	21.1%
<i>Leucorrhinia borealis</i> <sup>b</sup>	12	0.967	0.875	0.126	0.082	-34.4%	0.804	0.113	0.082	-27.0%
<i>Leucorrhinia frigida</i> <sup>b</sup>	31	0.952	0.821	0.179	0.166	-7.6%	0.744	0.127	0.137	8.3%
<i>Leucorrhinia glacialis</i> <sup>b</sup>	29	0.929	0.268	0.732	0.532	-27.3%	0.724	0.138	0.183	32.9%
<i>Leucorrhinia hudsonica</i> <sup>b</sup>	39	0.945	0.710	0.290	0.746	157.4%	0.746	0.126	0.179	42.6%
<i>Leucorrhinia intacta</i> <sup>b</sup>	143	0.847	0.312	0.688	0.703	2.3%	0.510	0.245	0.250	2.0%
<i>Leucorrhinia proxima</i> <sup>b</sup>	33	0.933	0.616	0.384	0.521	35.7%	0.750	0.129	0.182	40.9%
<i>Libellula auripennis</i> <sup>b</sup>	58	0.905	0.601	0.400	0.401	0.4%	0.648	0.180	0.172	-4.1%
<i>Libellula axilena</i> <sup>b</sup>	49	0.941	0.765	0.235	0.250	6.3%	0.748	0.129	0.132	2.0%
<i>Libellula comanche</i> <sup>a</sup>	53	0.949	0.770	0.230	0.531	131.2%	0.769	0.118	0.113	-4.3%
<i>Libellula composita</i> <sup>b</sup>	29	0.941	0.792	0.208	0.743	257.9%	0.713	0.149	0.171	14.6%
<i>Libellula croceipennis</i> <sup>a</sup>	46	0.955	0.815	0.185	0.352	89.9%	0.793	0.099	0.130	32.4%
<i>Libellula cyanea</i> <sup>b</sup>	163	0.925	0.630	0.370	0.354	-4.3%	0.681	0.160	0.149	-6.6%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Libellula flavida</i> <sup>b</sup>	54	0.915	0.721	0.279	0.266	-4.6%	0.669	0.164	0.170	3.8%
<i>Libellula forensis</i> <sup>wb</sup>	114	0.920	0.561	0.439	0.388	-11.7%	0.702	0.149	0.196	31.1%
<i>Libellula incesta</i> <sup>b</sup>	304	0.889	0.517	0.483	0.509	5.3%	0.613	0.193	0.192	-0.5%
<i>Libellula luctuosa</i> <sup>b</sup>	497	0.794	0.154	0.846	0.915	8.1%	0.425	0.288	0.291	1.1%
<i>Libellula needhami</i> <sup>b</sup>	63	0.952	0.739	0.261	0.243	-6.8%	0.778	0.111	0.126	13.1%
<i>Libellula nodisticta</i> <sup>b</sup>	26	0.940	0.766	0.234	0.364	55.4%	0.769	0.115	0.170	47.1%
<i>Libellula pulchella</i> <sup>b</sup>	414	0.760	0.040	0.960	0.960	0.0%	0.382	0.309	0.337	9.1%
<i>Libellula quadrimaculata</i> <sup>b</sup>	148	0.848	0.438	0.562	0.615	9.5%	0.541	0.230	0.266	15.9%
<i>Libellula saturata</i> <sup>b</sup>	136	0.901	0.522	0.478	0.669	40.0%	0.632	0.184	0.230	24.9%
<i>Libellula semifasciata</i> <sup>b</sup>	69	0.899	0.622	0.378	0.365	-3.4%	0.623	0.188	0.187	-1.0%
<i>Libellula vibrans</i> <sup>b</sup>	231	0.906	0.458	0.542	0.562	3.6%	0.654	0.173	0.187	7.8%
<i>Macrodiplax balteata</i> <sup>b</sup>	53	0.958	0.790	0.210	0.837	298.1%	0.811	0.094	0.132	40.1%
<i>Macromia annulata</i> <sup>a</sup>	15	0.979	0.953	0.047	0.117	148.8%	0.886	0.047	0.067	41.6%
<i>Macromia illinoensis</i> <sup>a</sup>	62	0.820	0.472	0.528	0.521	-1.4%	0.455	0.270	0.279	3.2%
<i>Macromia magnifica</i> <sup>wa</sup>	21	0.956	0.715	0.285	0.385	35.1%	0.724	0.133	0.126	-5.0%
<i>Macromia pacifica</i> <sup>a</sup>	13	0.806	0.491	0.509	0.547	7.4%	0.385	0.308	0.231	-25.0%
<i>Macromia taeniolata</i> <sup>ea</sup>	61	0.877	0.575	0.425	0.411	-3.4%	0.571	0.216	0.230	6.3%
<i>Miathyria marcella</i> <sup>b</sup>	43	0.951	0.654	0.347	0.408	17.6%	0.804	0.103	0.116	13.4%
<i>Micrathyria hagenii</i> <sup>b</sup>	23	0.982	0.864	0.136	0.047	-65.3%	0.908	0.048	0.044	-9.8%
<i>Nannothemis bella</i> <sup>b</sup>	19	0.920	0.634	0.366	0.328	-10.3%	0.600	0.190	0.164	-13.5%

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Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Nasiaeschna pentacantha</i> <sup>b</sup>	83	0.898	0.460	0.540	0.523	-3.0%	0.619	0.188	0.205	8.9%
<i>Nehalennia gracilis</i> <sup>b</sup>	29	0.944	0.755	0.245	0.200	-18.5%	0.724	0.138	0.172	25.0%
<i>Nehalennia integricollis</i> <sup>eb</sup>	35	0.927	0.781	0.219	0.188	-14.5%	0.710	0.147	0.147	-0.1%
<i>Nehalennia irene</i> <sup>b</sup>	65	0.889	0.564	0.436	0.704	61.5%	0.633	0.182	0.231	26.8%
<i>Neoneura aaroni</i> <sup>ea</sup>	13	0.984	0.948	0.052	0.044	-14.9%	0.871	0.052	0.044	-14.9%
<i>Neurocordulia molesta</i> <sup>a</sup>	15	0.907	0.666	0.335	0.322	-3.8%	0.615	0.185	0.158	-14.4%
<i>Neurocordulia xanthosoma</i> <sup>b</sup>	20	0.968	0.926	0.074	0.134	79.9%	0.881	0.069	0.070	1.3%
<i>Neurocordulia yamaskanensis</i> <sup>ea</sup>	13	0.881	0.715	0.285	0.280	-1.9%	0.657	0.189	0.205	8.1%
<i>Octogomphus specularis</i> <sup>a</sup>	12	0.975	0.921	0.079	0.091	14.5%	0.838	0.079	0.083	5.3%
<i>Ophiogomphus occidentis</i> <sup>a</sup>	16	0.968	0.879	0.121	0.153	26.6%	0.780	0.095	0.105	11.1%
<i>Ophiogomphus rupinsulensis</i> <sup>a</sup>	21	0.911	0.764	0.236	0.297	25.8%	0.609	0.201	0.172	-14.3%
<i>Ophiogomphus severus</i> <sup>a</sup>	77	0.891	0.482	0.518	0.462	-10.9%	0.633	0.185	0.195	5.2%
<i>Orthemis discolor</i> <sup>b</sup>	28	0.983	0.843	0.157	0.173	10.0%	0.918	0.046	0.036	-22.9%
<i>Orthemis ferruginea</i> <sup>b</sup>	168	0.915	0.553	0.447	0.548	22.4%	0.680	0.160	0.167	4.4%
<i>Pachydiplax longipennis</i> <sup>b</sup>	619	0.771	0.035	0.965	0.884	-8.4%	0.395	0.303	0.313	3.3%
<i>Paltothemis lineatipes</i> <sup>a</sup>	25	0.940	0.803	0.197	0.213	8.3%	0.690	0.150	0.165	10.5%
<i>Pantala flavescens</i> <sup>b</sup>	246	0.815	0.237	0.763	0.897	17.5%	0.448	0.276	0.272	-1.2%
<i>Pantala hymenaea</i> <sup>b</sup>	199	0.841	0.181	0.819	0.907	10.7%	0.528	0.236	0.262	10.9%
<i>Perithemis domitia</i> <sup>b</sup>	16	0.989	0.959	0.041	0.057	40.1%	0.897	0.041	0.057	40.1%
<i>Perithemis tenera</i> <sup>b</sup>	497	0.817	0.084	0.916	0.861	-6.0%	0.472	0.264	0.263	-0.4%

Species	No. Training samples	Training AUC	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)	Training TSS	True Locality Model Predicted Area (Portion of Scene)	Centroid Model Predicted Area (Portion of Scene)	Change in Predicted Area (%)
Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Phyllogomphoides albrighti</i> <sup>a</sup>	23	0.988	0.971	0.029	0.031	7.3%	0.928	0.029	0.031	7.3%
<i>Phyllogomphoides stigmatus</i> <sup>b</sup>	48	0.961	0.875	0.126	0.138	10.0%	0.833	0.083	0.098	17.2%
<i>Plathemis lydia</i> <sup>b</sup>	571	0.772	0.056	0.944	0.997	5.6%	0.405	0.298	0.298	0.1%
<i>Plathemis subornata</i> <sup>wb</sup>	36	0.938	0.712	0.288	0.388	34.7%	0.722	0.139	0.167	20.0%
<i>Progomphus borealis</i> <sup>wa</sup>	23	0.972	0.824	0.176	0.334	89.4%	0.826	0.087	0.140	60.5%
<i>Progomphus obscurus</i> <sup>a</sup>	135	0.920	0.636	0.364	0.420	15.6%	0.686	0.158	0.193	21.9%
<i>Protoneura cara</i> <sup>a</sup>	14	0.977	0.951	0.050	0.060	20.4%	0.879	0.049	0.060	20.4%
<i>Pseudoleon superbus</i> <sup>a</sup>	30	0.957	0.858	0.142	0.160	12.9%	0.793	0.107	0.124	15.8%
<i>Rhionaeschna californica</i> <sup>wb</sup>	69	0.906	0.612	0.388	0.555	42.8%	0.630	0.182	0.169	-7.2%
<i>Rhionaeschna multicolor</i> <sup>b</sup>	220	0.839	0.040	0.960	0.842	-12.3%	0.500	0.250	0.270	8.2%
<i>Rhionaeschna mutata</i> <sup>b</sup>	22	0.964	0.905	0.095	0.123	28.9%	0.819	0.090	0.063	-30.2%
<i>Rhionaeschna psilus</i> <sup>b</sup>	12	0.933	0.700	0.300	0.258	-14.1%	0.682	0.152	0.167	10.0%
<i>Somatochlora albicincta</i> <sup>b</sup>	18	0.987	0.948	0.052	0.147	183.9%	0.893	0.052	0.111	115.3%
<i>Somatochlora ensigera</i> <sup>a</sup>	17	0.953	0.774	0.226	0.205	-9.2%	0.765	0.118	0.118	0.0%
<i>Somatochlora filosa</i> <sup>eb</sup>	10	0.950	0.777	0.223	0.203	-8.8%	0.800	0.100	0.100	0.0%
<i>Somatochlora linearis</i> <sup>ea</sup>	53	0.880	0.658	0.342	0.352	2.8%	0.585	0.208	0.220	6.1%
<i>Somatochlora minor</i> <sup>b</sup>	12	0.944	0.854	0.147	0.331	125.8%	0.804	0.113	0.167	48.2%
<i>Somatochlora semicircularis</i> <sup>wb</sup>	55	0.969	0.890	0.110	0.303	175.5%	0.851	0.076	0.164	115.0%
<i>Somatochlora tenebrosa</i> <sup>eb</sup>	37	0.932	0.791	0.209	0.216	3.1%	0.735	0.130	0.149	14.7%
<i>Somatochlora walshii</i> <sup>b</sup>	27	0.934	0.864	0.136	0.355	160.6%	0.773	0.116	0.155	34.4%

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Minimum-training-presence threshold							Sensitivity-equals-specificity threshold			
<i>Somatochlora williamsoni</i> <sup>b</sup>	10	0.973	0.920	0.080	0.091	13.7%	0.820	0.080	0.091	13.7%
<i>Stylogomphus albistylus</i> <sup>ea</sup>	23	0.954	0.738	0.262	0.271	3.2%	0.826	0.087	0.130	49.9%
<i>Stylurus intricatus</i> <sup>a</sup>	14	0.925	0.662	0.338	0.485	43.5%	0.736	0.121	0.286	136.5%
<i>Stylurus laurae</i> <sup>a</sup>	11	0.956	0.852	0.148	0.094	-36.2%	0.818	0.091	0.091	0.0%
<i>Stylurus olivaceus</i> <sup>a</sup>	23	0.955	0.760	0.240	0.204	-15.3%	0.749	0.121	0.111	-8.1%
<i>Stylurus plagiatus</i> <sup>a</sup>	98	0.927	0.637	0.363	0.627	72.9%	0.691	0.156	0.214	37.0%
<i>Sympetrum ambiguum</i> <sup>b</sup>	101	0.931	0.335	0.665	0.663	-0.4%	0.725	0.137	0.140	2.6%
<i>Sympetrum corruptum</i> <sup>b</sup>	394	0.765	0.011	0.989	0.925	-6.5%	0.412	0.294	0.319	8.6%
<i>Sympetrum costiferum</i> <sup>b</sup>	109	0.864	0.550	0.451	0.519	15.3%	0.561	0.218	0.210	-3.8%
<i>Sympetrum danae</i> <sup>wb</sup>	89	0.893	0.558	0.442	0.543	22.9%	0.619	0.190	0.214	12.4%
<i>Sympetrum illotum</i> <sup>b</sup>	38	0.949	0.316	0.684	0.462	-32.5%	0.842	0.079	0.079	0.0%
<i>Sympetrum internum</i> <sup>b</sup>	127	0.835	0.327	0.673	0.578	-14.1%	0.496	0.252	0.252	0.0%
<i>Sympetrum madidum</i> <sup>wb</sup>	53	0.878	0.564	0.436	0.389	-10.9%	0.593	0.200	0.189	-5.5%
<i>Sympetrum obrusum</i> <sup>b</sup>	191	0.864	0.346	0.654	0.736	12.5%	0.539	0.230	0.238	3.2%
<i>Sympetrum pallipes</i> <sup>wb</sup>	143	0.879	0.417	0.583	0.471	-19.4%	0.594	0.203	0.217	6.9%
<i>Sympetrum rubicundulum</i> <sup>b</sup>	77	0.909	0.479	0.521	0.513	-1.4%	0.662	0.169	0.167	-1.2%
<i>Sympetrum semicinctum</i> <sup>b</sup>	227	0.829	0.114	0.886	0.907	2.4%	0.480	0.260	0.279	7.3%
<i>Sympetrum vicinum</i> <sup>b</sup>	208	0.819	0.177	0.823	0.941	14.3%	0.490	0.255	0.262	2.8%
<i>Tachopteryx thoreyi</i> <sup>b</sup>	49	0.926	0.688	0.312	0.298	-4.4%	0.714	0.143	0.135	-5.2%
<i>Tanypteryx hageni</i> <sup>b</sup>	21	0.990	0.962	0.038	0.073	93.2%	0.914	0.038	0.058	52.4%

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				Minimum-training-presence threshold				Sensitivity-equals-specificity threshold		
<i>Telebasis byersi</i> <sup>eb</sup>	34	0.959	0.802	0.198	0.192	-3.1%	0.775	0.108	0.106	-1.0%
<i>Telebasis salva</i> <sup>b</sup>	80	0.956	0.783	0.217	0.211	-3.0%	0.800	0.100	0.113	12.5%
<i>Tramea calverti</i> <sup>b</sup>	40	0.855	0.508	0.492	0.552	12.0%	0.500	0.250	0.227	-9.4%
<i>Tramea carolina</i> <sup>b</sup>	101	0.913	0.678	0.322	0.342	6.1%	0.646	0.176	0.188	6.9%
<i>Tramea lacerata</i> <sup>b</sup>	387	0.780	0.080	0.920	0.943	2.5%	0.421	0.289	0.308	6.3%
<i>Tramea onusta</i> <sup>b</sup>	233	0.871	0.378	0.622	0.926	48.9%	0.588	0.206	0.234	13.5%
<i>Triacanthagyna trifida</i> <sup>b</sup>	11	0.991	0.973	0.027	0.028	2.2%	0.973	0.027	0.028	2.2%