

Evidence of a climatic niche shift following North American introductions of two crane flies (Diptera; genus *Tipula*)

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Abstract Ecological niche models assume a species niche should be conserved over space and time. Increasingly, studies have determined that niche shifts may occur during biological invasion events. The aim of this study is to examine niche conservation for two invasive crane flies, *Tipula oleracea* Linnaeus and *Tipula paludosa* Meigen, after introductions into North America. These species have broadly sympatric invasive distributions but differ in time since introduction and dispersal abilities. As these factors may impact the area accessible to dispersal, I examined the impact of background area delineation on conclusions of niche conservation. Results indicated that alternative delineations of accessible area (i.e., background area) had no effect on measures of niche equivalence. Neither *Tipula* species was found to be occupying invasive niche space equivalent to that of their native ranges. Niche dissimilarity was found for both species, with results strongly impacted by the choice of background area. *T. paludosa* introductions displayed a niche shift across both invasive introductions when the model area drew climatic information from an area that buffered occurrences by 40 km. The eastern *T. oleracea* introduction displayed a niche shift when background information was drawn from within a 400 km buffered area. This study suggests that

invasive populations may be displaying a niche shift when evaluated against one scale of background but conserved when evaluated against another scale. Dispersal limitations for *T. oleracea* in its eastern introduction and anthropogenic habitat associations for *T. paludosa* across both invasive introductions are indicated as causes for the observed niche shifts. The results of this study highlight the importance of carefully delineating the area accessible to invasive species in studies of niche conservation. Furthermore, it indicates that examining several spatial extents of background areas can be beneficial when examining niche conservation for species in non-equilibrium states.

Keywords Invasion biology · Ecological niche modeling · Maxent · *Tipula oleracea* · *Tipula paludosa* · Tipuloidea

Introduction

Predicting species distributions using occurrence-based ecological niche modeling (ENM), also called species distribution modeling (SDM), has emerged as an important tool for studying biological invasions (Peterson and Vieglais 2001; Peterson 2003; Thuiller et al. 2005). Predicting species occurrence with ENMs is based on the contention that ecological factors act as constraints on survival and ultimately determine a species' potential distribution (Hutchinson 1957;

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Pulliam 2000; Elith and Leathwick 2009). When applied to species with geographic expansion beyond their native ranges, ENMs can be used to identify areas suitable for establishment and predict the potential invasive range (Peterson 2003; Welk 2004; Martínez-Meyer and Peterson 2006; Mau–Crimmins et al. 2006).

An assumption of this application relies on the conservation of the species ecological niche; the ecological tolerances of the native populations should be maintained across invaded areas (Wiens and Graham 2005). While theory maintains a species' niche will remain unchanged or change only slowly over evolutionary time, certain conditions may cause a niche shift in ecological time (Pearman et al. 2008). While strongly debated, several studies provide evidence of a departure from niche stasis following biological invasion (Fitzpatrick et al. 2007; Broennimann et al. 2007; Loo et al. 2007; Beaumont et al. 2009; Da Mata et al. 2010; Medley 2010). Such changes are proposed to occur to the fundamental niche by evolutionary processes (genetic drift; selection in the invasive range) or to the realized niche through biotic release (removal of competition, pathogens and predators) (Ackerly 2003; Lavergne and Molofsky 2007; Pearman et al. 2008). Whether due to ecological or evolutionary factors, such a change may allow species to occupy geographic areas not predicted by the native niche. Transferring models trained solely on native occurrences would likely misrepresent the geography of these invasive distributions.

The present study examines niche conservation between the native and invasive ranges for two congener crane fly (Diptera: Tipuloidea) species, *Tipula oleracea* Linnaeus and *Tipula paludosa* Meigen. Both species have broadly overlapping native Western Palearctic ranges and similarly overlapping invasive North American ranges that are spread along the eastern and western coasts of the United States and Canada. The current North American invasive ranges for both species suggest that the east and west coasts distributions stem from independent introduction events (Fox 1957; Beirne 1971; Wilkinson and MacCarthy 1967; Jackson and Campbell 1975), with eastern and western occurrence records for either species being separated by 2,500 km.

While the species display a high degree of overlap in both their native and invasive distributions, they are known to differ in their environmental tolerances (Laughlin 1960; Meats 1975), dispersal capacity

(Blackshaw and Coll 1999) and invasion history (e.g. time since introduction). Therefore, the geographic areas available to either species since introduction, and current states of distributional equilibrium, are potentially different. This point is fundamentally important to ENM methods as they rely, in part, on contrasting the environmental conditions at known occurrences against the habitat available to the species. This available habitat, here termed the background area, is also known as the 'relative occurrence area' (Lobo 2008; Jiménez-Valverde et al. 2008) or 'dispersal area (M)' (Soberón and Peterson 2005; Barve et al. 2011) and is defined by the geographic area from which background or pseudo-absence data are extracted during model construction (Graham et al. 2004; Phillips et al. 2006; Elith et al. 2011). In establishing the background area one should consider the area actually available to a species, while omitting regions where absence is due to dispersal limitations or biotic interactions (Anderson and Raza 2010). Studies investigating alternative background area delineations in ENM approaches have found marked effects on model performance and predictions (Chefaui and Lobo 2008; Anderson and Raza 2010). However, defining the background area may present a challenge when faced with geographically dispersed occurrence records of invasive species that are in unknown states of equilibrium. The evaluation of invasive species niche conservation made from ENMs trained with alternative background areas has not been explicitly examined.

Herein I use maximum entropy niche modeling (Maxent) that considers available habitat (i.e., background area) during model construction to examine niche conservation between native and invasive populations of the two *Tipula* species. Climatic niche models were trained with species occurrences against alternative zones of (1) continental North America, (2) a 40 km zone buffering occurrences and (3) a 400 km zone buffering occurrences as background areas to evaluate niche overlap, niche equivalence and niche similarity using the methods of Warren et al. (2008). For this analysis I additionally examined the degree to which invasive introductions (i.e., eastern and western) would recover potential niche shifts that would not be found if ranges were combined as the North American invasive range (i.e., eastern and western occurrences combined). Niche evolution among populations can happen if species are maintaining genetically structured populations where the exchange of

genetic material is halted due to geographic separation (Pearman et al. 2008; Prentis et al. 2008; Schulte et al. 2012). I hypothesized that invasive introductions would recover niche shifts that would not be detected when all invasive occurrences were combined, and that the choice of background area would similarly impact these conclusions of niche conservation across invasive introductions. Therefore niche conservation comparisons were made for each species between the native range and (1) the invasive eastern introduction, (2) the invasive western introduction, and (3) combined North American invasive range that combined eastern and western occurrences, for each species, as composite units. Niche comparisons for each of the three invasive occurrence treatments were repeated three times, with each replicate having the invasive occurrence data trained against one of the three background areas, resulting in a total of 9 comparisons being made for each species. Results of model-based niche tests were then contrasted with an evaluation of niche conservation derived from a multivariate approach in environmental space that does not consider the habitat potentially available to a species. Finally, model-based and multivariate niche conservation results were interpreted against the predicted invasive geographic range for both species made from niche models trained with both native and all available occurrence data.

Methods

Study species

Both *Tipula* species are considered habitat generalists that inhabit moist organic soils and feed on numerous graminoid, ornamental and agricultural host plants; being most prominently pests of graminoids grown for turf and agriculture (Jackson and Campbell 1975; Blackshaw and Coll 1999; Peck et al. 2006). Dispersal abilities differ among species. *T. paludosa* has an annual life-cycle and is a weak flier as an adult, particularly the freshly eclosed gravid females (Blackshaw and Coll 1999). *T. oleracea* has two generations a year and is a relatively strong and active flier.

Native *T. oleracea* and *T. paludosa* ranges are broad and largely sympatric across Western Palearctic distributions (Theowald 1984), with *T. paludosa* displaying a more northerly distribution and *T. oleracea*

ranging south into northern Africa. Introduction of *T. paludosa* into eastern North America was attributed to dry soil ballast transport (Fox 1957; Lindroth 1957; Beirne 1971), and was first detected in eastern Newfoundland as early as 1909 (Alexander 1942) and again on Cape Breton Island in 1955 (Fox 1957; Beirne 1971). In western North America, *T. paludosa* was discovered near Vancouver, British Columbia in a second introduction originating from an unknown source (Wilkinson and MacCarthy 1967; Jackson and Campbell 1975). A third poorly described introduction has been reported from Iceland (Libungan 2006). *T. oleracea* shares a similar eastern and western North American distribution to *T. paludosa*, however the location and number of independent introductions are unknown. The first North American detection occurred in 1998 in Vancouver, British Columbia, however subsequent surveys indicate either rapid dispersal or an already widespread distribution at the time of detection (LaGasa and Antonelli 2000; Umble and Rao 2004). *T. oleracea* detection in eastern North America did not occur until 2003 in Quebec, Canada followed by U.S. detections in New York (2004) and Michigan (2005), and in Ontario, Canada in 2007 (Gelhaus 2006; Peck et al. 2006; Taschereau 2007). An isolated independent introduction of *T. oleracea* was detected in Ecuador, South America (Young et al. 1999).

A total of 479 *T. oleracea* (424 native; 55 invasive) and 323 *T. paludosa* (263 native; 60 invasive) georeferenced occurrences were used in this study. Records were obtained from the Entomology Collection of the Zoological Museum Amsterdam (ZMA) (<http://www.science.uva.nl/zma/>), Global Biodiversity Information Facility online database (GBIF; www.gbif.org), Bug Guide (<http://bugguide.net>), published literature (Simova 1959; Brodo 1994; McCracken et al. 1995; Salmela 2001; Umble and Rao 2004; Gelhaus 2006; Peck et al. 2006; Simard et al. 2006; Asche et al. 2007; Taschereau 2007), and regional collections (unpublished records, MJP). All occurrence records were checked for accuracy prior to use.

Climate variables

The WorldClim dataset (version 1.4; Hijmans et al. 2005), representing seasonal temperature and precipitation patterns, was used in niche modeling and in direct climate comparisons. To reduce potential multicollinearity among all available climate variables, I

eliminated grids for which Pearson correlations were greater than 0.85 (Elith et al. 2006), to a set of eight focal grids (“full set”: annual mean temperature [Bio 1], mean monthly temperature range [Bio 2], isothermality [Bio 3], temperature seasonality [Bio 4], maximum temperature warmest month [Bio 5], annual precipitation [Bio 12], precipitation driest month [Bio 14], precipitation seasonality [Bio 15]). This resulting set of factors matched environmental conditions known to regulate *Tipula* development and survival (Laughlin 1960, 1967; Meats 1975; Blackshaw and Perry 1994). As less conserved variables may lead to over-restrictive predictions (Rödder et al. 2010), a second dataset (“reduced set”; Bio 2, Bio 3, Bio 4, Bio 15) was derived from the “full set” by removing relaxed climate variables (i.e., those that include values beyond those found in the native range). All analyses were run with both datasets. All utilized grids were at a 0.08333 cell resolution (5 arc min).

Background areas

Across the native range, both species occupy similar habitats and occur as adults during a common time of the year. Therefore, detection of one *Tipula* species should result in a high probability of encountering the other *Tipula* species, if present. The native background area used in model calibration was established as a convex polygon inclusive of all native range occurrence points for both species.

Three study areas were delineated around invasive occurrences as alternative hypotheses of potentially accessible area. The first study area was bound at the continental scale (North America), a common ENM background delineation approach. It assumes that current distributions are in an equilibrium-state and unoccupied areas across North America are unsuitable. The second and third areas were established by first fitting a minimum convex hull to invasive eastern and western occurrences, respectively. Next, each convex hull was buffered by either a 40 or 400 km distance. The 40 km distance describes a species with assumed limited dispersal since introduction. This distance represents an estimate of the maximum geographic distance a wind-assisted adult fly may travel. The 400 km buffer describes a species that is assumed to have sufficiently dispersed across a broad regional area.

Ecological niche modeling

Models were developed through maximum entropy modeling using Maxent (version 3.3.2; Phillips et al. 2006; Phillips and Dudík 2008). Maxent is a machine learning method that fits a probability distribution from known species occurrences based on the constraints provided by each environmental variable (Phillips et al. 2006). Maximum entropy density estimation is then used to approximate the known distribution of environmental variables at each occurrence point. Output from Maxent provides each pixel with a non-negative measure of habitat suitability from unsuitable habitat (0) to optimal habitat (100); this measure indicates the probability of the cell to offer conditions suitable as defined by the environmental variables used in the analysis. Minimum habitat suitability below which habitat is determined as unsuitable was established as the minimum training presence logistic threshold. In tests comparing different distribution modeling techniques, Maxent performed equally well or better than alternative methods (Elith et al. 2006). Modeling was conducted largely under the program’s default conditions (10,000 random background points; conversion threshold 10^{-5} ; 500 maximum iterations; clamping activated). Model accuracy was evaluated by calculating the area under the receiver operating characteristic curve (AUC). The AUC offers an evaluation of model performance providing a global comparison of model fit to that of a random prediction. AUC values range from 0.0 to 1.0, with values over 0.7–0.9 regarded as useful models and excellent models producing values above 0.9.

Owing to the visible clustering of species occurrences within several geographic areas, I anticipated a potential collection bias due to collections made in areas of increased pest status or areas of taxonomic expertise. A bias may occur if occurrence locations do not present a random representation of a species’ actual distribution (Phillips 2008; Phillips et al. 2006). A bias grid was constructed to down weight occurrences with many geographic neighbors (*see* Elith et al. 2010). The bias grid was created for each species using ArcGIS (version 9.3). Estimation values were taken as inverse to density and rescaled to a range of values 1.0 (high density)–10.0 (low density). Bias grids were used in all Maxent applications.

Model-based niche comparisons

Maxent models were used to evaluate niche overlap, equivalency and similarity using ENMtools (version 1.3; Warren et al. 2008; Warren et al. 2010). Niche comparisons were based on two metrics, I of Warren et al. (2008) and Schoener's index of niche overlap (D) (Schoener 1968). Methods first compute a niche overlap value for two groups (i.e. native vs. invasive) based on ENM probability scores. Niche overlap is calculated with similarity values ranging from 0.0 (no overlap) to 1.0 (identical) for each comparison among pairs of models. To compare niche conservation in the strictest sense, that is whether niches are equivalent, an identity test was conducted. This randomization test compares the overlap score from actual species occurrences with a distribution of overlap scores produced by 100 pseudoreplicate datasets. Pseudoreplicate datasets are produced by randomly partitioning a pooled set of occurrences (i.e. native + invasive) into two datasets with sizes equal to that of the actual datasets. Values of D and I from the 100 pseudoreplicated datasets produce a null distribution against which the overlap score from actual occurrences are compared in a one-tailed test ($\alpha = 0.01$). Niche models are considered equivalent if the overlap scores from actual occurrences is no different than that produced from randomly drawn samples (Warren et al. 2010). Niche similarity tests alternatively take into account the background climatic conditions from which the occurrences used in model construction were drawn. Again a randomization test is used by to compare the overlap of models produced from actual occurrences against a null distribution of 100 pseudoreplicate overlap scores from random data. Here the distribution of random scores is produced by computing niche overlap between a model produced for a set of occurrences (i.e. native) to a model produced using the same occurrences (i.e. native) but with background data taken from the alternative range (i.e. invasive). Here the number of background occurrences is equal to that of actual occurrences from the alternative range (i.e. invasive). This procedure is then repeated with the alternative dataset (i.e. invasive occurrences with native background). Niche similarity is viewed as a two-tailed test ($\alpha = 0.01$), where the overlap of two ranges is viewed as being no different from, or more or less similar than expected by chance alone, with

chance defined by the range of scores produced by the pseudoreplicated data.

Niche comparisons in environmental space

Niche space was compared through a principal component analysis (PCA) using the *ade4* package (Romesburg 1985) in the R environment (version 2.8.1). Significance differences between ranges were determined by a between-class analysis, which yielded a between-class inertia percentage (Dolédec et al. 2000). Significance of between-class inertia percentages was tested with 999 Monte-Carlo randomizations.

Predicted North American distributions

Potential invasive distributions for either species were predicted by transferring niche models to North America that were trained on either native occurrence data only, or all available data (native + invasive). Several studies have suggested an advantage in considering all available data (native + invasive) when forecasting species invasions (Welk 2004; Mau-Crimmins et al. 2006; Broennimann and Guisan 2008; Beaumont et al. 2009). Doing so is thought to provide a better characterization of the species' fundamental niche by incorporating a greater range of conditions under which species' survival is possible. Background data for models trained on all available data were drawn from background areas combining the native range with the invasive range background area at which niche conservation was found.

Results

Ecological niche modeling

All ecological niche models resulted in AUC scores greater than 0.85, indicating strong predictive power. Native trained models for both species captured all occurrence data from the native range (Fig. 1) and predicted the potential for spread of both species across large regions of both eastern and western North America (Figs. 2A, B). Similar to the native geographic ranges of the two species, invasive predictions were broadly overlapping. However, native models failed to predict all invasive range occurrences for either species. Models

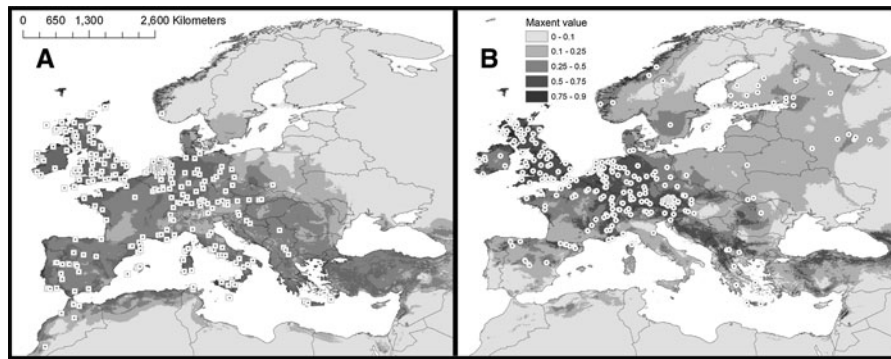


Fig. 1 Predicted native range of *Tipula oleracea* (A) and *Tipula paludosa* (B) based on models constructed with native range occurrences. The light grey coloration represents areas predicted below the minimum presence threshold, with

increasing color intensity showing higher probability habitat. Occurrences used in model training are marked with open squares (*T. oleracea*) and circles (*T. paludosa*)

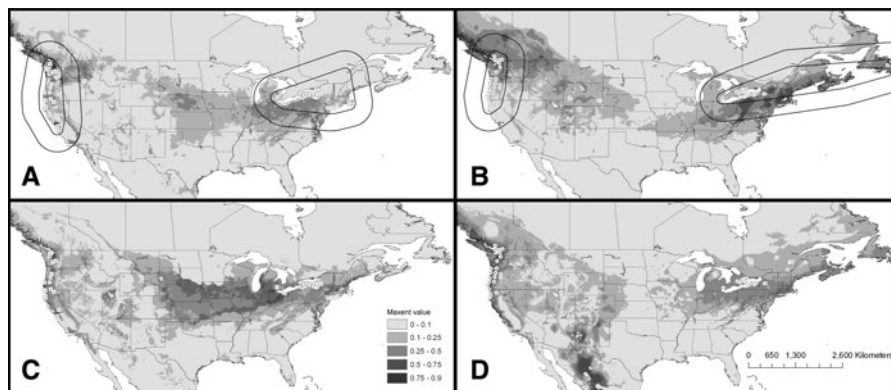


Fig. 2 Predicted introduced North American ranges of *T. oleracea* and *Tipula paludosa*. Maps A and B were trained with native range occurrences of *T. oleracea* and *T. paludosa*, respectively, and projected to North America. Solid lines indicate the 40 and 400 km background areas. Maps C and D were trained using on all available occurrence data for

trained with the “full” dataset, which contained all climate variables, generally had higher omission that models trained with the “reduced” dataset, which contained only climate variables within the range of native conditions. When evaluated at the minimum training threshold, *T. oleracea* (threshold = 0.027) predicted all occurrences across the invasive western introduction (“full”: 0 %, “reduced”: 0 %), but had high omission across the invasive eastern introduction (“full”: 65 %, “reduced”: 2 %). Conversely, *T. paludosa* (threshold = 0.083) had low omission across the invasive eastern introduction (“full”: 0 %, “reduced”: 8 %) but was higher across the invasive western introduction (“full”: 38 %, “reduced”: 8 %). Invasive range occurrences for both species were shown to have been collected

T. oleracea and *T. paludosa*, respectively, and projected to North America. The light grey coloration represents areas predicted below the minimum presence threshold, with increasing color intensity showing higher probability habitat. Occurrences are marked with open circles (*T. oleracea*) and squares (*T. paludosa*)

in only a small portion of the potential range predicted by native range models.

Model-based niche comparisons

Model-based niche equivalency tests were similar for both “full” (Table 1) and “reduced” (not shown) datasets, and did not differ qualitatively. For *T. oleracea* and *T. paludosa*, the climatic niche of native and invasive ranges, as the North American range (eastern + western introductions) or as individual eastern or western introductions, were not equivalent ($P < 0.01$). Furthermore, differences were significant regardless of the geometry of background area used during model construction.

Table 1 Tests of niche overlap, niche equivalency (identity) and niche similarity (background) for *Tipula oleracea* and *T. paludosa*

	Overlap		Equivalency		Similarity	
	D	I	D	I	D	I
<i>T. oleracea</i> (40 km)						
Invasive versus Native	0.618	0.786	0.862**	0.978**	0.357**, 0.228**	0.641**, 0.491**
West versus Native	0.421	0.706	0.787**	0.949**	0.151**, 0.216**	0.387**, 0.497**
East versus Native	0.202	0.462	0.867**	0.979**	0.106**, 0.088**	0.331**, 0.261**
<i>T. oleracea</i> (400 km)						
Invasive versus Native	0.685	0.878	0.845**	0.972**	0.210**, 0.298**	0.461**, 0.573**
West versus Native	0.308	0.599	0.782**	0.945**	0.169**, 0.337 ns	0.396**, 0.629 ns
East versus Native	0.030	0.128	0.836**	0.969**	0.099** , 0.106**	0.312** , 0.315**
<i>T. oleracea</i> (null)						
Invasive versus Native	0.676	0.872	0.834**	0.968**	0.362**, 0.112**	0.666**, 0.347**
West versus Native	0.410	0.686	0.688**	0.895**	0.200**, 0.139**	0.459**, 0.398**
East versus Native	0.262	0.491	0.771**	0.939**	0.124**, 0.131**	0.337**, 0.384**
<i>T. paludosa</i> (40 km)						
Invasive versus Native	0.675	0.891	0.840**	0.973**	0.199**, 0.304**	0.448**, 0.564**
West versus Native	0.189	0.391	0.839**	0.973**	0.213** , 0.701**	0.469** , 0.925**
East versus Native	0.159	0.364	0.844**	0.970**	0.160 ns , 0.194 ns	0.415** , 0.453 ns
<i>T. paludosa</i> (400 km)						
Invasive versus Native	0.688	0.893	0.851**	0.975**	0.337**, 0.330**	0.641**, 0.621**
West versus Native	0.486	0.778	0.813**	0.963**	0.210**, 0.370**	0.471 ns , 0.661**
East versus Native	0.649	0.860	0.829**	0.967**	0.133**, 0.229**	0.370**, 0.506**
<i>T. paludosa</i> (null)						
Invasive versus Native	0.452	0.700	0.817**	0.964**	0.332**, 0.182**	0.631**, 0.469**
West versus Native	0.344	0.598	0.820**	0.965**	0.257**, 0.200**	0.532**, 0.490**
East versus Native	0.297	0.547	0.819**	0.964**	0.144**, 0.129**	0.372**, 0.381**

Metrics of niche overlap (I and D; see Warren et al. 2008) are offered for comparisons among native ranges with the North American invasive range (Invasive), eastern introduction (East) and western introduction (West). Significant values are indicated with asterisks (ns: $P > 0.05$; ** $P < 0.01$) and indicate significant differences from the overlap score. Niche similarity values are given for comparisons of invasive to native, and native to invasive. Niche similarity results represent either significantly more similar (regular font) or not significantly different from and significantly less similar (bold font) than expected by chance

When niche comparisons were made with the niche similarity tests, the conclusions of niche conservation were more complicated and heavily influenced by the selection of background area (Table 1). When compared using ENMs trained with all invasive North American occurrences, and at all choices of background (i.e., continental, 40, 400 km), the invasive niches of *T. oleracea* and *T. paludosa* were found to be more similar to their corresponding native niches than expected by chance ($P > 0.01$). Niche similarity was also found for both species when comparisons were made between the native ranges and invasive eastern and invasive western introductions when models were trained with the continental scale background area.

Niche dissimilarity was found for both species when invasive occurrences were treated as eastern and western introductions. For *T. oleracea*, niche similarity was found between the native range and both eastern and western introductions when ENMs were trained against a 40 km study area, but was found to be dissimilar when ENMs were trained against the 400 km background area, though not reciprocally so in the western introduction. For *T. paludosa*, niche similarity was found when ENMs were trained against the 400 km study area, but dissimilar (western introduction) or not significantly different (eastern introduction) when trained against the 40 km background area. These results appear to indicate that the degree to

which the climatic niche of either species is conserved is dependant on the area of background area used during model construction.

Niche comparisons in environmental space

Ordination (PCA) results for the “full” (Fig. 3) and “reduced” (not shown) datasets were highly similar for both *Tipula* species and did not differ qualitatively. PCA indicated three axes explained a majority (81 %) of the variation in the climate data for *T. oleracea* and three axes explained a majority (89 %) of the variation for *T. paludosa* (Table 2).

Significant differences ($P < 0.001$) in climatic niches were found for both *Tipula* species between the native and the invasive occurrences, whether invasive occurrences were treated as separate eastern and western introductions or as combined invasive ranges. Invasive eastern and western introductions for both species were strongly divergent. When compared to native range climatic conditions, invasive western *T. oleracea* occurrences were found in warmer areas with lower temperature seasonality, while invasive eastern occurrences were in areas of greater temperature seasonality. Invasive *T. paludosa* occurrences were found in areas with higher temperatures and greater precipitation, with eastern and western introductions strongly

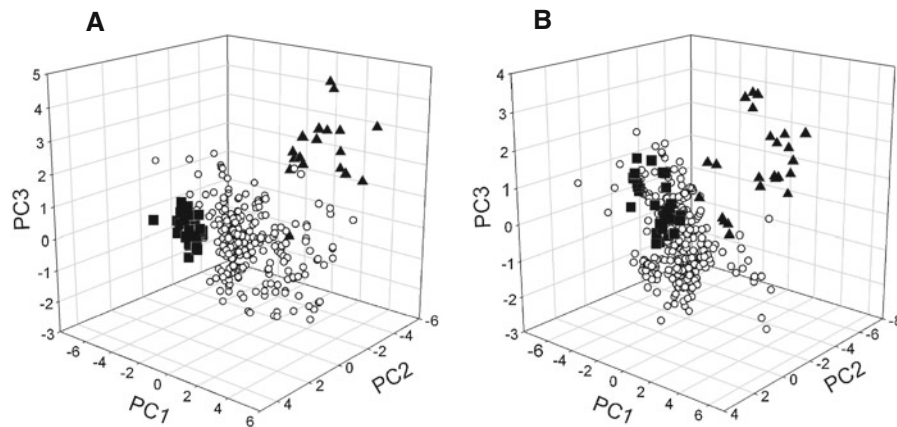


Fig. 3 Climate niche space based on the ‘full’ climatic variable dataset. Points indicate native (*open circle*) and invasive (*filled square* = eastern introduction, *filled triangle* = western introduction) occurrences of *T. oleracea* (A) and *Tipula paludosa* (B) plotted against the first three PCA axes. For *T. oleracea*, the

three PCA axes explained 81 % of the variation in the climate data (PC I: 35 %, PC II: 31 %, PC III: 15 %). For *T. paludosa*, the three PCA axes explained 89 % of the variation in the climate data (PC I: 50 %, PC II: 26 %, PC III: 13 %). Variable contributions to PCA axes are shown in Table 1

Table 2 Loadings of climate variables on three PCA axes for *Tipula oleracea* and *Tipula paludosa*

Climate variable descriptions		<i>Tipula oleracea</i>			<i>Tipula paludosa</i>		
		PC I	PC II	PC III	PC I	PC II	PC III
Bio 1	Annual mean temperature	0.583	-0.546	-0.282	0.865	-0.234	-0.258
Bio 2	Mean diurnal range	0.717	0.113	0.605	0.605	0.430	0.647
Bio 3	Isothermality	0.148	-0.907	0.147	0.390	-0.698	0.503
Bio 4	Temperature seasonality	0.344	0.878	0.276	0.099	0.962	0.159
Bio 5	Max. temp. of warmest month	0.902	0.243	0.157	0.895	0.368	0.055
Bio 12	Annual precipitation	-0.484	-0.465	0.683	-0.658	-0.313	0.477
Bio 14	Precipitation of driest month	-0.779	0.181	0.370	-0.934	0.108	0.186
Bio 15	Precipitation seasonality	0.424	-0.550	0.215	0.758	-0.415	0.076

Axes explained 81 % of variation for *T. oleracea* (PC I: 35 %, PC II: 31 %, PC III: 15 %) and 89 % for *T. paludosa* (PC I: 50 %, PC II: 26 %, PC III: 13 %)

diverging by patterns of low (western) or high (eastern) temperature seasonality.

North American distributions

When predicted at a minimum presence threshold (*T. oleracea*: 0.027; *T. paludosa*: 0.083), models trained on native range occurrences and projected onto North American indicated large geographic areas would offer climatic conditions suitable for either species (Figs. 2A, 2B). Niche differences were found between native and invasive occurrences that suggested climatic conditions (i.e., niche space) not found in the native range were being occupied by both species in the invasive ranges. Therefore model predictions made from all available data (native + invasive occurrences) were developed to predict the potential North American distribution. When all available data were included, at a minimum presence threshold (*T. oleracea*: 0.027; *T. paludosa*: 0.083), the areas predicted were similar to those based on native range occurrence trained models. While the geographic extent differed between native only and all data predictions, the consensus of both models is that both species are occupying only a small portion of predicted climate space (Figs. 2C, D).

Discussion

While the niche of a species is assumed to be conserved over space and time (Wiens and Graham 2005), several studies have detected niche shifts following invasion events (Fitzpatrick et al. 2007; Broennimann et al. 2007; Loo et al. 2007; Beaumont et al. 2009; Da Mata et al. 2010; Medley 2010). In the present study, strict tests of niche equivalence clearly illustrate a shift in the invasive introductions of *T. oleracea* and *T. paludosa*. In fact it was apparent that invasive occurrences for both species were being found in climatic conditions that represented novel combinations of climate factors not present in either of the species native ranges. Compared to native conditions, both species are currently occupying invasive North American climates that have higher maximum temperatures along eastern introductions and displaying either greater (western) or less (eastern) annual variation in annual temperatures. However, in the absence of climatic conditions identical to those of the

native range, both species were found to be occupying invasive niche space either more or less similar to native conditions that expected by chance alone. Specifically, *T. oleracea* is occupying dissimilar niche space across the eastern introductions, but only with the 400 km background area, while *T. paludosa* is occupying dissimilar niche space across both eastern and western introductions, but only with the 40 km background area.

The conflicting niche similarity results indicate that conclusions of similarity between native and invasive niches are strongly dependent on the invasive area determined to be available to species via dispersal. Niche similarity is a function of a species occurring in conditions, out of the area available to the species via dispersal, that are most similar to those of the native range (Anderson and Raza 2010; Václavik and Meentemeyer 2012). Previous work has shown that the delineations of background areas can significantly impact ENM performance and prediction (Soberón and Peterson 2005; Chefaoui and Lobo 2008; Anderson and Raza 2010; Barve et al. 2011). Here it is shown that alternative background areas can similarly impact conclusions of niche similarity, however conclusions of niche equivalence appear to be less impacted. The greatest discrepancy in these results occurred between the 40 and 400 km areas. More accurate measures of the realized niche can be made, even in early stages following introduction, if the background is carefully delineated to include only conditions that are actually available to the species (Soberón and Peterson 2005; Chefaoui and Lobo 2008; Barve et al. 2011). Therefore the niche dissimilarity for *T. paludosa* with the 40 km area is suggestive of an actual change, while niche similarity for *T. oleracea* with the 40 km indicates niche stasis. Niche dissimilarity for *T. oleracea* against the 400 km does however suggest factors other than climate are influencing its current distribution across the eastern introduction.

Niche shifts such as those found for *T. paludosa* could be due to changes to the species fundamental or realized niche. A genetic response influencing abiotic requirements may arise by founder effects leading to rapid adaptive change in invasive populations (Alexander and Edwards 2010). This change to the fundamental niche would lead to species occurrence in ecological conditions different from those of the native range. Invasive *T. paludosa* populations do show low genetic variation (Myers and Iyer 1981),

however this has not been definitively related to changes in environmental tolerances between native and invasive populations. Additionally, transplant experiments with related crane flies have shown developmental plasticity related to climate, but conservation of physiological tolerances over time (Hadley 1971; Coulson et al. 1976; Butterfield 1976). Changes to the species realized niche could occur by release from biotic interactions present in the native range, or the addition of biotic interactions present in the invasive range (Pearman et al. 2008; Prentis et al. 2008; Václavik et al. 2011). Several biological agents may limit *T. paludosa* populations numbers, however evidence does not support range limitation due to biotic interactions across either the native or introduced ranges (Myers and Iyer 1981; Blackshaw and Coll 1999).

An alternative explanation for the niche dissimilarity shown here may be due to distributional non-equilibrium. Recent work has shown that many documented niche shifts following biotic invasion may be better explained by ongoing colonization instead of a fundamental change to the species' niche requirements (Petitpierre et al. 2012). Such non-equilibrium states due to colonization time lag and dispersal limitations can be likely during stages of biological invasion (De Marco et al. 2008; Václavik and Meentemeyer 2012; Václavik et al. 2011). Both species have significant residence times in their respective invasive ranges, however models trained with either native occurrences or all occurrence data suggest that current invasive populations are occupying only a portion of the geographic areas predicted to support their survival. It is probable that factors other than climate, including anthropogenic habitats and other dispersal limitations, may be affecting species distributions in the invasive ranges and limiting them from occurring in all climatically suitable areas.

Invasive occurrences of *T. paludosa* are patchy in distribution and occurring largely in urban areas. Native records for the species may occur in areas of human habitation, but are somewhat equally spread through these and more natural areas (Blackshaw and Coll 1999). Particularly important across the invasive introductions is the distribution of habitat in the form of managed turf grass (e.g. lawns, parks). Evidence further suggests that the eastern and western occurrences of *T. paludosa* are influenced by human activity, including long distance dispersal along areas

of human habitation (Jackson and Campbell 1975; Peck et al. 2010; Petersen et al. 2011). Such biased records may result in a measured niche change when no such change has acutely occurred (Pearson and Dawson 2003). The location and connectivity of these habitats is likely influencing the dispersal patterns in the invasive range by the extent to which species are still spreading (Donald and Evens 2006), resulting in the shift to the realized niche of *T. paludosa*.

While non-climatic factors appear to be influencing the local distributions of *T. paludosa*, *T. oleracea* occurrences tended to the less biased towards human activities. Niche similarity further indicated occurrence in predicted climates across the areas available to dispersal in the 40 km background area. However, a restrictive distribution was particularly evident across the 400 km background area of the eastern introduction. Detected only 10 years, niche dissimilarity for this species may be indicating dispersal limitations are limiting its current distribution. This would explain why the large areas of suitable, but unfilled habitat in the 400 km background areas currently exists. Invasive range shifts west into Ohio and south into New Jersey have recently occurred and suggest future expansion within the 400 km study. Both native and all data models also predict a potential for a large expansion to the west from this current realized range.

These results demonstrate that conclusions of niche conservation, specifically niche similarity, between native and invasive ranges can be strongly affected by stage of biotic invasion and choice of background area delineation. When species are in non-equilibrium states, background information should be selected to limit areas where absence is due to non-environmental factors. However given the difficulties in establishing such an area, particularly for invasive species, establishing multiple areas may be more appropriate. This study advocates carefully examining the results of multiple background areas in studies of niche conservation across invasive introductions. Furthermore, niche equivalency tests have been criticized for being overly strict, recovering changes in available habitat rather than changes in a species niche (Godsoe 2010; Peterson 2011). Similar results are illustrated here. While not equivalent, the niche dissimilarities recovered here are best explained by ongoing invasive range expansion. Because it may not be possible to measure the full niche of a species while it is in early stages of invasion, future investigations into niche conservation

will be needed after both species have attained equilibrium across their invasive introductions.

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