

Competition at the range boundary in the slimy salamander: using reciprocal transplants for studies on the role of biotic interactions in spatial distributions

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Summary

1. Determining the factors that influence the distribution of species has been a longstanding goal in the field of ecology. New techniques such as ecological niche modelling have the potential to aid in addressing many broad questions in ecology, evolutionary biology, and behavioural ecology.
2. This study combines broad-scale ecological niche models with fine-scaled studies of biotic interactions to examine how abiotic and biotic interactions affect the spatial distribution of the terrestrial salamander species *Plethodon glutinosus* (northern slimy salamander), in a potential contact zone shared with *Plethodon mississippi* (Mississippi slimy salamander).
3. The core habitat in the interior portion of the range of *P. glutinosus* and the contact zone are distributed in unique environmental niche space.
4. The form of competition, inter- or intraspecific, significantly affected mass loss of adult salamanders. Salamanders lost more mass when interacting with a heterospecific.
5. Abiotic conditions strongly influenced the impact of competition on salamanders. Under stressful environmental conditions at the field site located in the contact zone, salamanders lost more mass than at the field site located in the interior of the range.
6. Furthermore, adult salamanders from range-edge populations and core populations (from the interior of the range) differed in their respective abilities to compete under the abiotic conditions in the contact zone.

Keywords: amphibians, contact zone, geographical distributions, Maxent, Plethodontidae

Introduction

The mechanisms driving the distribution of species have been of interest in the field of biology for over 150 years. Darwin (1859) placed emphasis on the importance of behavioural interactions, competition, and its potential influence in limiting the distributions of species (McDonald 2003). Disentangling the factors that determine species distributions has been and continues to be a central goal of ecology and evolutionary biology (Brown 1984; Krebs 1985; Brown & Lomolino 1998; Gaston 2003; Case *et al.* 2005; Holt & Keitt 2005; Parmesan *et al.* 2005) especially as modern climate change and increasing anthropogenic pressure are currently reshaping the geographical distributions of many plants and animals (Parmesan & Yohe 2003; Hampe & Petit 2005). In fact, ecologists are now being called upon to predict changes in species distributions in response to exotic invasions, habitat alteration and loss, land-use change, and pollution

(Parmesan *et al.* 2005); therefore, it is of utmost importance that we further our understanding of the influence of abiotic and biotic factors and their interplay on species distributions.

Climate has long been considered the dominant abiotic factor that influences the distribution of species (Hutchinson 1918; MacArthur 1958). Species range limits often coincide with particular combinations of climate variables (Rogers & Randolph 1986; Caughley *et al.* 1987; Gaston 2003; Parmesan *et al.* 2005) and shift in synchrony with changing climate (Parmesan & Yohe 2003). Climate can impose boundaries directly by causing mortality, or preventing successful reproduction or completion of life cycles (Hutchins 1947; Strathdee & Bale 1995; Spicer & Gaston 1999; Gaston 2003). However, climate conditions can also set a species' range limit indirectly by causing increases in the number of competitors or predators (Gross & Price 2000). Additionally, the southern range margins of many Northern Hemisphere species are thought to be delineated by competitive interactions while the northern limits are set by physiological tolerances (MacArthur 1972; Root 1988; for review see Gaston 2003).

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Many studies have demonstrated that biotic interactions, such as interspecific competition, have the capacity to produce abrupt range limits (Jaeger 1970; Connell 1983; Letcher *et al.* 1994; Jenkinson *et al.* 1996; Davis *et al.* 1998; Bullock *et al.* 2000; Gaston 2003; Case *et al.* 2005). In fact, competitive interactions influence the distribution of species in almost every major group of living organism (Jaeger 1970; Letcher *et al.* 1994; Davis *et al.* 1998; Bullock *et al.* 2000). Despite a rich history of research in the field of competitive interactions, the fundamental question of how biotic interactions vary across geographical space under differing abiotic conditions remains largely unanswered.

A wide-ranging species will experience a myriad of abiotic conditions and biotic interactions imposed by heterogeneous environments (Dunson & Travis 1991; Gómez-Mestre & Tejedo 2002). As the outcome of competitive interactions is frequently regulated by abiotic factors, the relative importance of competition in limiting populations, and subsequently distribution, will vary depending on the location within the range (Huffaker 1958; Randall 1982; Dunson & Travis 1991; Bullock *et al.* 2000; Gross & Price 2000). This interplay between physiological tolerances, set by abiotic factors, and species interactions can alter population density and the spatial distribution of a species, especially at the range margin (Westman 1980; Schaffer, Ellner & Kot 1986; Guo *et al.* 2005).

If competition between parapatric species at range margins affects the geographical distribution of one or both species, then ecologically suitable areas for both species in a contact zone should be especially important for investigating the dynamics of species interactions. However, contact zone studies still suffer from the inherent difficulty of determining the relative influence of abiotic conditions on biotic interactions (Anderson, Peterson & Gómez-Laverde 2002). That is, abiotic conditions may be biased towards the ecological requirements of one species over the other. Therefore, we suggest that with the ever-increasing use of ecological niche modelling techniques that combine spatially explicit environmental data and locality information of specimens (e.g. Elith *et al.* 2006), researchers will be able to accurately disentangle the effects of the environment from biotic interactions. Many niche modelling techniques implicitly include the effects of species interactions because a species' current location is a result of both abiotic and biotic interactions (Araújo & Guisan 2006). Therefore, niche modelling cannot be used in isolation; additional experimental and manipulative studies should be used to assess the relative roles of biotic and abiotic factors on populations. In this study, we combine the use of broad-scale ecological niche models with fine-scaled studies of biotic interactions in order to examine how abiotic and biotic factors interact at contact zones.

Ecological niche modelling uses climate data associated with museum occurrence localities to generate a model of habitat suitability (high or low probability of species occurrence) which provides an objective way to help control for climate as a random variable in experimental design. Field studies are often limited to 'ideal' reciprocal transplant situations, such as obvious steep climatic clines found in montane regions (e.g.

Berven 1981; Waser & Price 1985; Wang *et al.* 1997; Link *et al.* 2003; Angert & Schemske 2005; Iraeta *et al.* 2006). Unfortunately for ecologists, the majority of species do not interact at such narrow or easily defined contact zones. Therefore, in order to study how competitive interactions shape present-day distributions of wide-ranging species, ecological niche modelling can provide an a priori framework, allowing one to define areas that contain a habitable suite of climatic variables for both interacting species or to differentiate between climatic zones found across a species' range.

In this study, we examine the influence of environmental conditions on intra- and interspecific competition at the southern range margin of the terrestrial salamander species *Plethodon glutinosus* Green 1818 (northern slimy salamander). For amphibians, the environment is known to drive broad-scale patterns of diversity (e.g. Buckley & Jetz 2007), and in salamanders, intraspecific and interspecific interactions have been found to shape the distributions of species in nature (Hairston 1987; Walls 1990; Jaeger & Forester 1993; Marshall, Camp & Jaeger 2004). Within the family Plethodontidae (over 70% of known salamanders), the social behaviour of members of the genus *Plethodon* has been extensively studied, and territoriality is believed to be common and mediate inter- and intraspecific competition (Hairston 1987; Jaeger & Forester 1993; Mathis *et al.* 1995; Marvin 1998a,b; Maerz & Madison 2000). The occurrence of competitive interactions between salamander species that share parapatric or narrowly overlapping ranges has been extensively documented in salamanders of this genus (e.g. Jaeger 1970; Hairston 1980a,b). Within plethodontid salamander assemblages, interactions can range from interference competition to outright competitive exclusion, all of which can influence spatial distributions (Hairston 1987; Jaeger & Forester 1993; Mathis *et al.* 1995; Marvin 1998a,b; Maerz & Madison 2000). At its southern range limit, *P. glutinosus* shares a contact boundary in western Kentucky, Tennessee, and west-central Alabama with the closely related *Plethodon mississippi* Highton 1989 (Mississippi slimy salamander) (Fig. 1). Specifically, we ask (i) Are climate conditions at the contact zone significantly different than conditions in the interior or core area of the range of *P. glutinosus*? (ii) Do abiotic conditions at the range boundary influence competitive interactions among these salamanders? and (iii) Do individuals from core and edge populations show regional adaptation in regards to competition?

Materials and methods

SPECIES OF INTEREST

P. glutinosus and *P. mississippi* are members of the lungless, terrestrial salamander family Plethodontidae. *P. mississippi* is one of 16 species that was synonymized with *P. glutinosus* until electrophoretic analyses of 22 protein loci and albumin immunological assays revealed cryptic lineages within the *P. glutinosus* species (Highton, Maha & Maxson 1989). Currently, all 16 species are recognized as taxonomic species and are collectively referred to as the *P. glutinosus* salamander complex.

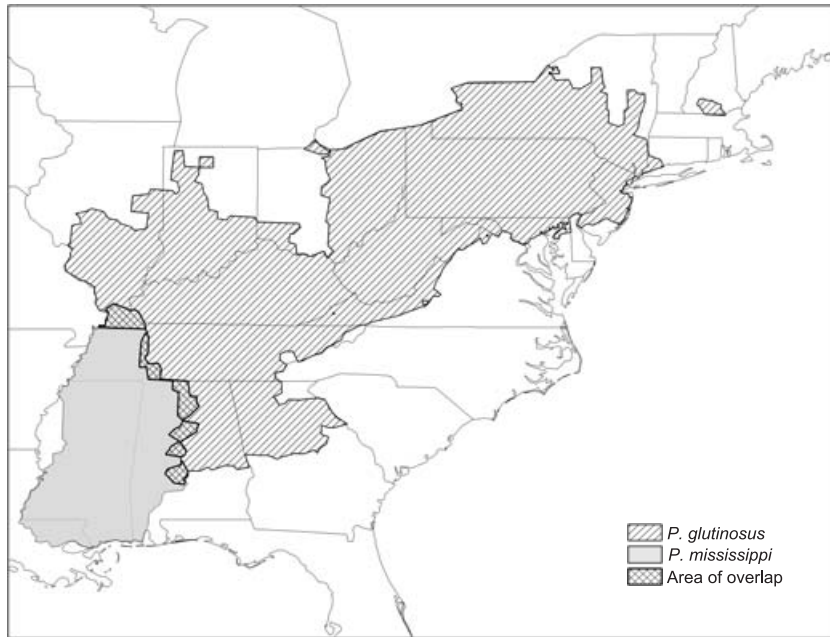


Fig. 1. The distribution of *Plethodon glutinosus* and *Plethodon mississippi*, and the area of range overlap based on Lannoo (2005). The range of *P. glutinosus* is shown with hatching; the range of *P. mississippi* is shown shaded in grey, and the area of range overlap is shown crosshatched.

Adults of both species are black with small, scattered white dorsal spots and range in size from 11.5–20 cm. Due to the morphological similarity of these species, identification is frequently based on locality rather than morphological characters. *P. glutinosus* is widely distributed in the eastern USA concurrent with the Appalachian Uplands; whereas, *P. mississippi* is an upland Gulf Coastal Plain species inhabiting southern temperate forests (Means 2000) (Fig. 1). These species share a parapatric boundary and potential contact zone near the Fall Line in Alabama. The Fall Line is the physiographic region separating the Gulf Coastal Plain and Appalachian Highlands and is characterized by multiple hybrid zones, phylogeographical breaks, and contact zones (Swenson & Howard 2005).

Due to their close genetic relationship, *P. glutinosus* and *P. mississippi* share a number of ecological and life-history traits. Moist, cool burrows are essential to the survival of these salamanders and are used as refuges to avoid desiccation and predation, and as brooding sites for females (Rissler *et al.* 2000). These salamanders are generalized predators, eating a wide variety of small arthropods.

RANGE MAPS AND AREA OF OVERLAP

Range maps were created for *P. glutinosus* and *P. mississippi* using those from Lannoo (2005). Range maps were based on presence records at the county level. The ranges of *P. glutinosus* and *P. mississippi* overlap in central Alabama; we defined this area as 'area of overlap' which we later used to identify the potential contact zone (CZ).

BIOCLIMATIC MODELLING

To more accurately identify the southern range limit of *P. glutinosus* and the CZ in terms of suitable habitat, we developed ecological niche models (ENM) for *P. glutinosus* and *P. mississippi* using Maxent version 2.0 (Phillips, Dudík & Schapire 2004). Maxent creates species distributional models by combining presence-only data with ecological layers using a machine-learning approach known as maximum entropy. The maximum entropy approach

estimates a species' ecological niche by finding a probability distribution that is based on a distribution of maximum entropy (with reference to a set of environmental variables). This method is equivalent to finding the maximum-likelihood distribution of a species (Phillips *et al.* 2004). The logical assumption regarding the resulting probability distribution is the higher the probability of species occurrence, the more suitable the environment is for the species of interest.

The purpose of ecological niche modelling in this study was to further refine the location of the southern range limit of *P. glutinosus*, identify areas of potential geographical contact (CZ), and select field sites. Although the range map, created from Lannoo (2005), for *P. glutinosus* placed the southern range edge in central Alabama, it did not define the location of the range edge to the resolution we desired in this study. The range maps were based on presence records at the county level; however, by using the ENMs that were generated using climate files with a resolution of ~1 km, we could work at a much finer scale. We also used ENMs to identify areas of potential geographical contact by identifying areas predicted to be suitable for both species. This information was then used to define the CZ.

Maxent was run using the point locality information from historical specimens in two Natural History Collection (NHC) data portals, HerpNet (www.herpnet.org) and Global Biodiversity Information Facility (GBIF; www.gbif.org), combined with climate layers that were downloaded from the WorldClim data base (Hijmans *et al.* 2005). The WorldClim bioclimatic layers are biologically relevant temperature and precipitation layers at a 1-km resolution based on the 30-year period from 1960–90 (Hijmans *et al.* 2005).

To ensure that we did not overparameterize our ENMs with redundant climate information, we followed the procedures of Rissler & Apodaca (2007). Eleven variables were chosen and used in all analyses. These included BIO2, mean diurnal range in temperature; BIO4, temperature seasonality; BIO5, maximum temperature of warmest month; BIO6, minimum temperature of coldest month; BIO7, annual range in temperature; BIO8, mean temperature of wettest quarter of year; BIO12, annual precipitation; BIO15, precipitation seasonality (coefficient variation); BIO16, precipitation of wettest quarter of year; BIO17, precipitation of driest quarter of

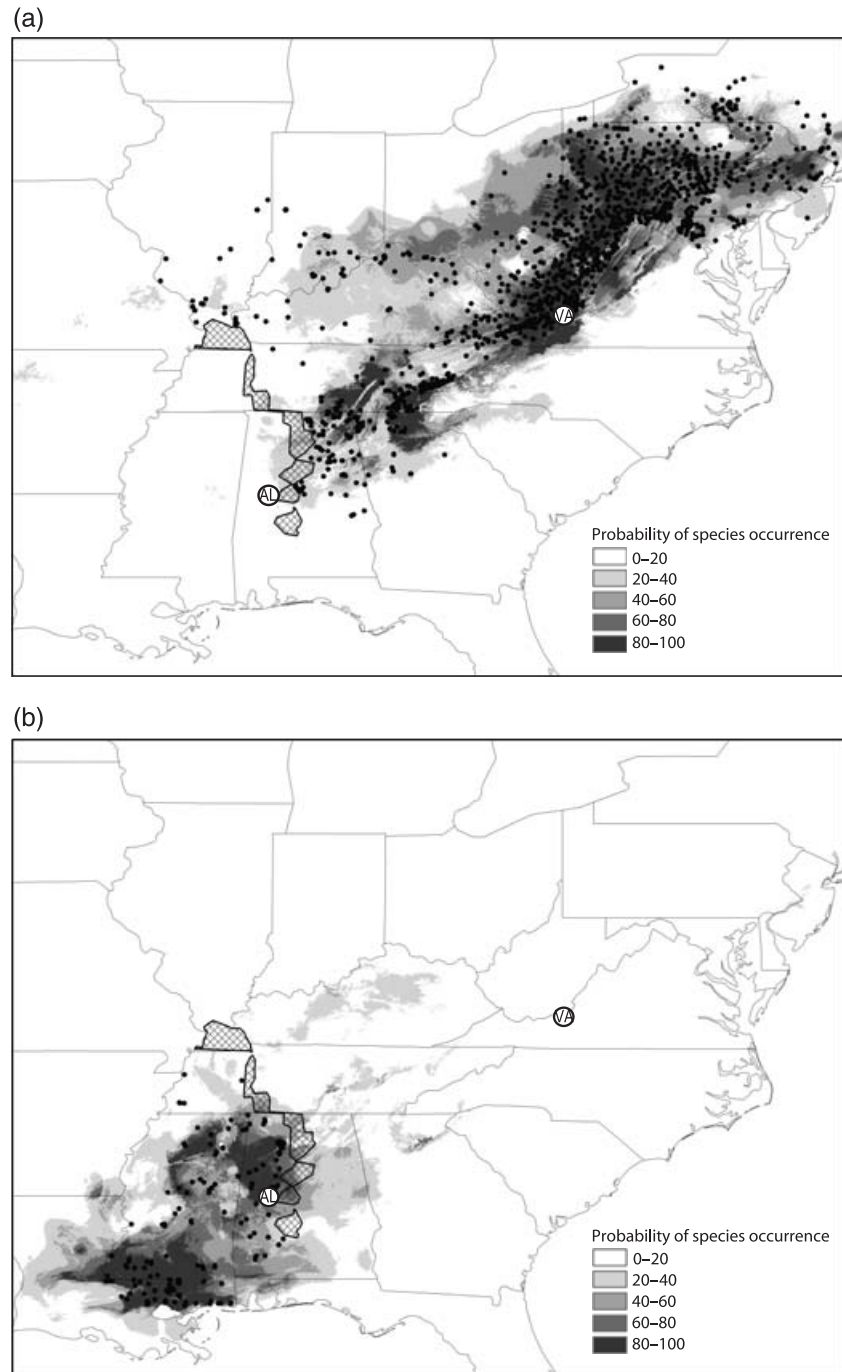


Fig. 2. The ecological niche models (ENMs) of (a) *Plethodon glutinosus* and (b) *Plethodon mississippi* are shown in a graded series from white to dark grey with low probabilities of occurrence in light colours and higher probabilities of occurrence in dark colours. The area of range overlap based on Lannoo (2005) is shown crosshatched. Black circles as NHC localities. The location of the Alabama (AL) and Virginia (VA) field sites are shown with open circles and state abbreviations. (a) ENM of *P. glutinosus*, and (b) ENM of *P. mississippi*.

year; BIO18, precipitation of warmest quarter of year; BIO19, precipitation of coldest quarter of year. Each climate layer was entered into Maxent as an ASCII raster grid.

Models for *P. glutinosus* and *P. mississippi* were created using 1335 and 190 unique locality records, respectively (Fig. 2). We did not include any point localities from the area of overlap in the models (Fig. 1). The default settings for Maxent were used to create each model. The jackknife option in Maxent was used to determine which variables contributed to the models the most. Twenty per cent of the data was used for training the models. The resulting files were viewed by converting the resultant ASCII file into raster format using ARCVIEW 9.1.

IDENTIFYING THE CONTACT ZONE

The range maps created by Lannoo (2005) identified an area of overlap in central Alabama (Fig. 1). However, the ENMs for *P. glutinosus* and *P. mississippi* (Fig. 2) predicted suitable areas beyond the range overlap for the two species. Therefore, to define the potential CZ for the two species, we included counties in the area of overlap and adjacent counties in which the ENMs predicted 20–40% probability of either species occurrence (Fig. 3). We felt this would be a more conservative approach rather than ignoring those areas and only using the overlap region shown by the range maps.

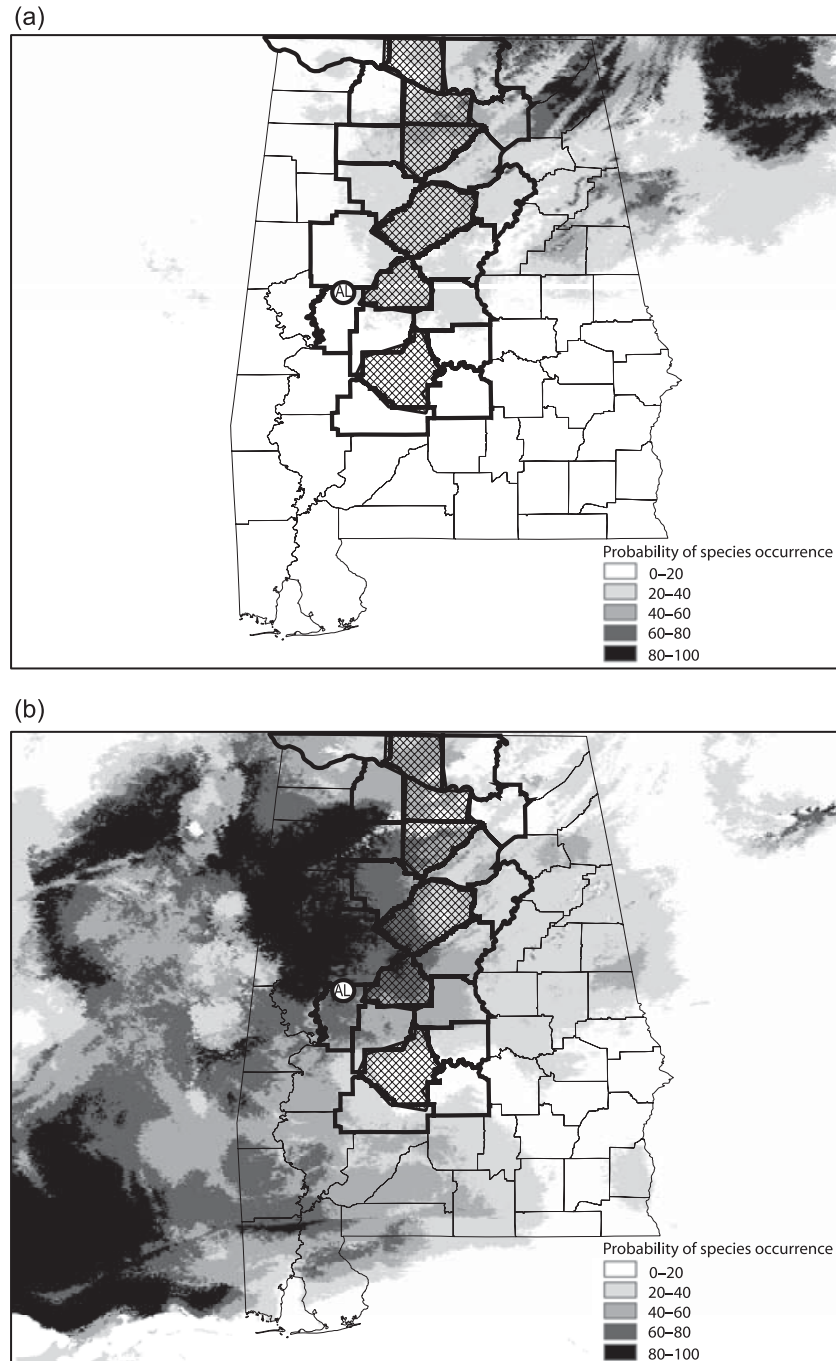


Fig. 3. The potential contact zone (CZ) and ENMs of (a) *Plethodon glutinosus* and (b) *Plethodon mississippi*. The CZ is shown with Alabama counties outlined in black (see text for details); the original area of range overlap based in Lannoo (2005) is shown crosshatched. The AL field site is shown with an open circle and the state abbreviation.

SELECTING FIELD SITES

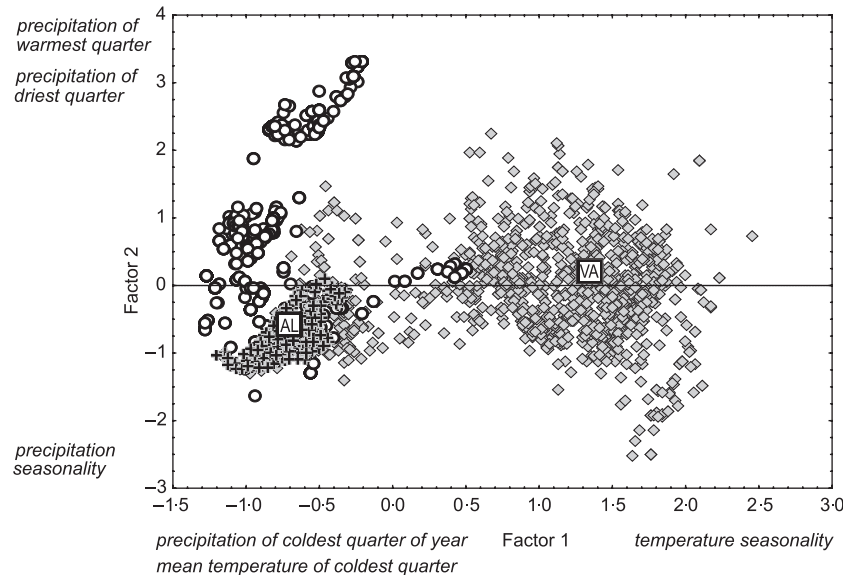
The ENMs for *P. glutinosus* and *P. mississippi* allowed us to identify areas predicted to have high and low environmental suitability for each species. To address the questions posed in this study, we identified two field sites: one site in an area that was predicted to be highly suitable for *P. glutinosus* and another site at the southern range edge of *P. glutinosus*, predicted to have low environmental suitability for *P. glutinosus* but also suitable for *P. mississippi*. The first site selected was within the range of *P. glutinosus* at Mountain Lake Biological Station in Giles County, Virginia (VA), hereafter referred to as the VA field site. Based on the ENM for *P. glutinosus*, this site was in an

area predicted to have high environmental suitability (Fig. 2a). The second site selected was in Hale County, Alabama (AL), hereafter referred to as the AL field site (Fig. 2). This site was located at the southern range edge of *P. glutinosus* and predicted to have low environmental suitability for *P. glutinosus* but suitable for *P. mississippi* (Fig. 3).

SPATIAL STATISTICAL ANALYSES

To examine overall differences in climate conditions, the environmental data were extracted for all 11 climate variables from WorldClim at NHC point localities for *P. glutinosus*, *P. mississippi*, and for

Fig. 4. The reciprocal transplant sites (white boxes) are distributed in the environmental centre of *Plethodon glutinosus* habitat (VA) and in the *P. glutinosus*-*P. mississippi* CZ (AL). The graph is the result of a principal components analysis (PCA) of the factor scores from the extracted environmental data at (a) *P. mississippi* Natural History Collection (NHC) localities (circles); (b) *P. glutinosus* NHC localities (grey diamonds); and (c) random points selected in the contact zone (pluses). Factor 1 and 2 explain a total of 75.48% of the variance.



500 random localities within the CZ. A principal component analysis (PCA) was run, and the factor scores for Factor 1 and Factor 2 were plotted. Our field sites were then plotted to confirm our choice of reciprocal transplant sites (Fig. 4). A multivariate analysis of variance (MANOVA) was carried out to determine if both species' ranges and the CZ differed climatically, and post-hoc tests were used to determine which groups differed significantly. Methods for climate extractions and analyses for the CZ were similar to those found in Rissler & Apodaca (2007). All statistical analyses were conducted using STATISTICA version 6.0 for Windows.

FIELD EXPERIMENT

Individuals of *P. glutinosus* were collected from the interior of the range in Giles and Montgomery Counties, Virginia, hereafter referred to as core populations. Individuals of *P. glutinosus* were also collected from populations near the range edge in Cleburne and Clay Counties, Alabama, hereafter referred to as range-edge populations. Individuals of *P. mississippi* were collected from areas near the CZ in western Hale, western Tuscaloosa, and Winston Counties, Alabama. Individuals were not collected from the area of range overlap for either species to ensure proper identification. Furthermore, individuals of *P. mississippi* that were collected from the CZ were from areas in the far western portion of the CZ beyond the range margin of *P. glutinosus* as predicted by the ENM.

Salamanders were collected from October 2004 through May 2005. The salamanders were housed individually in an environmental chamber at 15 °C under a 12L:12D photoperiod and fed one waxworm per week until the start of the experiment. Due to the similarity in coloration of these two species, we photographed each individual and wrote a description of their unique dorsal spot pattern for identification. Snout-vent length (SVL) from the tip of the snout to the posterior edge of the vent, tail length (TL) from the posterior edge of the vent to the tip of the tail, and total length (TTL) from the tip of the snout to the tip of the tail, of each individual was measured using digital calipers that read to 0.01 mm. The mass of each salamander was measured using an electronic balance that read to 0.001 g. All measurements were recorded within 1 week of the start of the experiment.

Table 1. Description of treatments replicated at the AL and VA field sites

Treatment	Competition	Description
1	Intraspecific	<i>Plethodon glutinosus</i> from Alabama (edge) × <i>P. glutinosus</i> from VA (core)
2	Interspecific	<i>P. glutinosus</i> from Alabama (edge) × <i>Plethodon mississippi</i> ; <i>P. glutinosus</i> from Virginia (core) × <i>P. mississippi</i>

A reciprocal transplant two-way fully factorial study was conducted at the VA (core range) and AL (range edge) field sites. Competition was the first factor with two levels: (i) intraspecific (*P. glutinosus* from core populations vs. *P. glutinosus* from range-edge populations), (ii) interspecific (*P. glutinosus* from both core and range-edge populations vs. *P. mississippi* from AL). Population was the second factor with two levels: (i) range-edge populations, and (ii) core populations (Table 1). Due to the inactivity of *P. glutinosus* in Virginia during the time salamanders were collected, we were unable to collect enough salamanders for intraspecific (between members of the same population) and no competition treatments.

At each field site, treatments were arranged in a randomized spatial block design with seven replicates for a total of 21 experimental mesocosms at each field site (AL and VA). Each block contained one replicate of each treatment. The mesocosms consisted of polyethylene tubs 53 × 43 × 30 cm with drain holes in the bottom and sides. Each mesocosm held two salamanders. To simulate a forest floor environment, soil, one cover-object, and fallen leaves collected at each field site were randomized and added to each unit. Soil was added to a depth of 20 cm in each mesocosm. Cover objects were constructed by cutting fallen tree branches into 30-cm sections, with 15-cm diameters, and then splitting the pieces in half lengthwise. Fallen leaves were gathered from the forest floor and added to each mesocosm to simulate natural cover. Before the start of the experiment, we added 20 waxworms to each mesocosm to ensure prey was available.

from the start of the study. We randomly assigned salamanders to appropriate treatments. To avoid confounding results from ecological interactions resulting from size disparity between competitors, salamanders in each pair were similarly sized. At the start of the experiment, the average SVL difference between two individuals in a pair was 2.38 mm. Fiberglass window screening was silicon-sealed over each mesocosm to prevent focal salamanders from escaping and the intrusion of nonfocal salamanders and predators.

The experiment ran 17 May–15 October 2005. Every 6 weeks, 10 waxworms were added to each mesocosm. However, invertebrates were observed in the units throughout the experiment. At the conclusion of the experiment SVL, TL, TTL, and mass of each salamander were recorded following the same protocol as the initial measurements. All response variables were calculated as percentages from initial and final measurements. There were few changes in SVL, TL, and TTL of salamanders over the course of the study; therefore, mass loss was the variable chosen for statistical analysis. Previous studies have shown that the presence of a competitor will reduce the mass of individuals of *P. glutinosus* (Price & Secki Shields 2002). Also, of the four variables, mass has been found to be the most sensitive to competitive effects in experiments with short duration times (Price & Secki Shields 2002).

The effects of AL and VA field site and competition on the mass loss in individuals of *P. glutinosus* from core and range-edge populations were determined using a factorial analysis of variance (ANOVA) under the general linear method (GLM) with type III sums of squares. Type III sums of squares was appropriate for our data as some salamanders did not survive the experiment resulting in unequal sample sizes in particular treatments (Quinn & Keough 2002). As our response variable was calculated as a percentage of mass lost, an arcsine transformation was used to meet the assumptions of ANOVA (Sokal & Rohlf 1995). All data were tested for normality using the Shapiro–Wilk test. Homogeneity of variance was tested using the Levene's test. The raw data are reported in the figures. For the intraspecific assays, the measurements of both salamanders in the treatment were analysed.

Results

BIOCLIMATIC MODELLING AND SPATIAL STATISTICAL ANALYSES

Maxent assigns each grid cell in the study area a probability of species occurrence; the darker colours (i.e., black) correspond to areas that have a high probability of species occurrence and the lighter colours (i.e., light grey) correspond to areas that have a low probability of species occurrence. A logical assumption with ENMs is that areas with high probabilities of species occurrence correspond to areas that have high environmental suitability of the species of interest. For *P. glutinosus*, the areas with the highest probability of species occurrence are located within the Appalachian Uplands; whereas, for *P. mississippi*, a Gulf Coastal Plain species, areas with the highest probability of species occurrence are located below the Fall Line in Alabama and in southern Mississippi (Fig. 2). The *P. glutinosus* and *P. mississippi* ENMs had some overprediction, meaning the models did predict beyond the species' range (Fig. 2). The *P. mississippi* ENM had more overprediction than the *P. glutinosus* model. However, the ENMs for both species predicted beyond the area of overlap

(defined from the range maps). Within the CZ, the probability of occurrence for *P. glutinosus* ranged from 0–40% and for *P. mississippi* the probability of occurrence ranged from 0–100% (Fig. 3). This indicates that there are areas in which the two species could potentially interact within the CZ.

The PCA scores differed significantly between the ranges of *P. glutinosus*, *P. mississippi*, and the CZ (Fig. 4). The overall MANOVA showed significant climatic differences across *P. glutinosus*, *P. mississippi*, and the CZ (Wilks' lambda = 0.123, $F_{16,6318} = 729.9817$, $P = 0.0000$). However, post-hoc tests showed that the CZ did not differ significantly from the climatic conditions in the *P. mississippi* range ($P = 0.673$). Although there is variation within the CZ and within the range of *P. glutinosus* and *P. mississippi*, the two reciprocal transplant sites were located in unique environmental niche spaces. A separate PCA using only variables that would have been 'active' at the time of the field study was carried out to confirm that the two sites and the CZ differed. The variables used in this analysis included BIO2, BIO5, BIO17, and BIO18. We found that the PCA did not change as a result of the exclusion of the other variables (data not shown).

Maxent analysis of variable importance for *P. glutinosus* and *P. mississippi* indicated that the environmental variables of importance for the ENMs for the two species differed. For *P. glutinosus*, BIO15 (precipitation seasonality (coefficient variation)) and BIO5 (maximum temperature of warmest month) were the variables that contributed the most to the ENM. For *P. mississippi* BIO19 (precipitation of coldest quarter of year) was the most informative variable for generation of the ENM. This suggests that although the two species are closely related, the environmental variables driving their distributions may be quite different.

FIELD STUDY

The effects of field site (AL vs. VA) and competition on the mass loss of adult salamanders were determined using a factorial ANOVA (Table 2). Individuals of *P. glutinosus* from range-edge and core populations lost more mass at the AL field site than the VA field site ($F_{1,23} = 104.38$, $P < 0.0000$; Table 2; Fig. 5) and over the course of the study, individuals of *P. glutinosus* from core populations suffered the highest mass loss ($F_{1,23} = 23.894$, $P < 0.0000$; Table 2; Fig. 5), suggesting that abiotic tolerances may vary between populations.

Although individuals of *P. glutinosus* sustained the highest mass loss in interspecific competition treatments versus intraspecific treatments ($F_{1,23} = 19.390$, $P < 0.0002$), it appears the effect of competition itself does not vary between populations ($F_{1,23} = 1.363$, $P < 0.2550$; Table 2). Abiotic conditions strongly impacted the influence of competitive interactions on individuals of *P. glutinosus* in this study ($F_{1,23} = 10.248$, $P = 0.0039$; Table 2). Similar mass loss was observed for salamanders engaged in inter- and intraspecific competition at the VA field site (Fig. 5). However, at the AL field site the mass loss increased significantly with the highest mass loss being sustained by individuals of *P. glutinosus* from core populations (Fig. 5). The influence of competition itself did not vary

Table 2. Results of factorial ANOVA of percentage of mass loss by individuals of *Plethodon glutinosus* from AL and VA populations across all treatments. Significant results are in boldface

Treatment	SS	DF	MS	F	P
Field site (AL vs. VA)	1944·3300	1	1944·3300	104·3760	0·0000
Competition (intraspecific vs. interspecific)	361·1900	1	361·1900	19·3900	0·0002
Population (range-edge vs. core)	445·0900	1	445·0900	23·8940	0·0000
Field site × competition	190·8900	1	190·8900	10·2480	0·0040
Field site × population	725·5000	1	725·5000	38·9470	0·0000
Competition × population	25·3900	1	25·3900	1·3630	0·2550
Field site × competition × population	81·5600	1	81·5600	4·3780	0·0476
Error	428·4500	23	18·6300		

SS = sum of squares; DF = degrees of freedom; MS = mean squares; F = F -value; P = P -value.

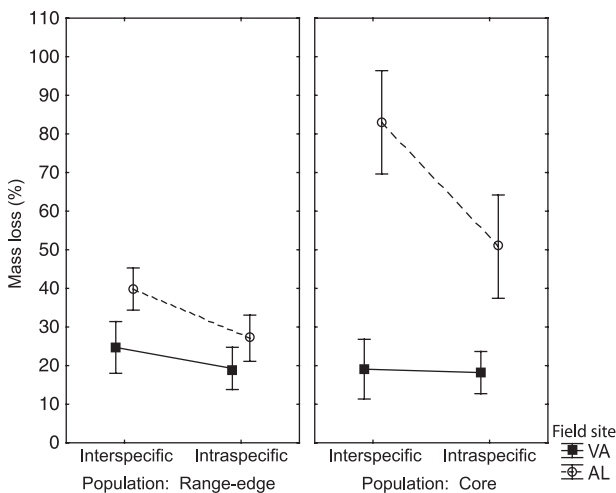


Fig. 5. Mean percentage of mass lost by *Plethodon glutinosus* salamanders from range-edge and core populations engaged in interspecific and intraspecific competition at the AL and VA field sites ($F_{1,23} = 4·3782$, $P < 0·0476$). Mass loss was calculated as percentage of mass loss using the beginning and ending mass of each individual of *P. glutinosus* (see text for details). Open circles and dotted lines indicate mass lost by salamanders at the AL field site and solid squares and solid lines indicate mass lost by salamanders at the VA site. Vertical bars denote 0·95 confidence intervals.

between populations and this suggests that abiotic tolerance may be shaping the extent of competition. In fact, we found that individuals of *P. glutinosus* from range-edge and core populations responded to competitive interactions at the AL and VA field sites differently ($F_{1,23} = 4·3782$, $P < 0·0476$; Fig. 5; Table 2). Individuals of *P. glutinosus* from range-edge populations lost significantly less mass in intra- and interspecific competition treatments at the AL field site versus salamanders from core populations (Fig. 5). Again, this suggests that abiotic tolerance may strongly regulate competition, and populations may have regional adaptation in regards to competition.

Discussion

It is frequently the case that the outcome of competitive interactions will be variable and environmentally specific (Dunson & Travis 1991; Gómez-Mestre & Tejedo 2002). In fact, differences in the competitive ability of plants and

insects from range-edge and interior populations have been observed in multiple species (Hoffman & Blows 1994). Yet, defining the mechanisms behind this remains a challenge due to the number of causative factors that could be responsible for differences in competitive ability. It has frequently been suggested that range-edge populations are more prone to extinction, exist at lower density, and are genetically less diverse than core populations because they persist under less favourable abiotic conditions (Lawton 1993; Vucetich & Waite 2003; Hampe & Petit 2005); therefore, individuals from range-edge populations may be locally adapted but perform poorly under different abiotic conditions (Hoffman & Blows 1994). However, this hypothesis has received little attention, largely due to the difficulty in quantifying the abiotic differences between core and edge habitats.

Frequently, environmental conditions at a species range margin are less favourable than conditions in the interior portion of the range (Whittaker 1956; Parsons 1991; Lawton 1993; Brown, Stevens & Kaufman 1996; Sagarin & Gaines 2002; Vucetich & Waite 2003). In our study, climate conditions at the CZ in Alabama were significantly different from those in the interior portion of the range of *P. glutinosus* (Fig. 4). These different selective environments are likely to drive patterns of resource use and the outcome of competitive interactions. As the CZ is suitable to varying degrees for *P. glutinosus* and *P. mississippi*, it is likely that the southern range limit of *P. glutinosus* is determined by the combined affect of environment and species interactions. Although it is hard to argue that two field sites can be broadly representative of conditions in the core and range-edge, our data suggest that abiotic tolerance may shape competitive interactions in this species.

In this study, individuals of *P. glutinosus* from both core and range-edge populations fared significantly worse under all competition treatments at the AL field site. However, salamanders from range-edge populations did better in their local conditions in Alabama than those from core populations (Fig. 5). Yet individuals of *P. glutinosus* from both populations did equally well in the VA field site, suggesting that those individuals from the CZ may be better adapted for the relatively more stressful conditions in that environment. It is possible that this could be a factor that contributes to the maintenance of this range limit. However, these findings are not surprising because populations of widespread species

often vary in their degree of specialization due to the different abiotic and biotic conditions found throughout their range (Gómez-Mestre & Tejedo 2002). By creating a more tangible abiotic niche (ENMs), we were able to disentangle the effect of regional variation in competitive ability with the effect that abiotic conditions have on species interactions.

The results from the factorial ANOVA indicated that salamanders from core and range-edge populations did not differ in their response to competition itself (Table 2). The percentages of mass lost by salamanders in inter- and intraspecific competition treatments were quite similar suggesting that the response to competition itself may not vary geographically. However, the differences in response to competition became apparent when abiotic factors (field site) were added (Fig. 5; Table 2). This suggests that abiotic factors can influence competitive interactions.

If salamanders show regional adaptation in terms of competition, then individuals of *P. glutinosus* from core and range-edge populations would be expected to perform best under native conditions. In this study, individuals of *P. glutinosus* did have significantly different responses (in terms of mass loss) to competition at the two field sites (Table 2; Fig. 5). Individuals of *P. glutinosus* from range-edge populations performed better than individuals from core populations at the AL field site (Fig. 5). Yet, at the VA field site, there was little difference in mass loss by individuals of *P. glutinosus* from both populations (Fig. 5). These results suggest that abiotic tolerance may shape competitive interactions (Fig. 5; Table 2). That said, because we only had two field sites in this study, we must be cautious in our inferences; the factors responsible for the observed differences are unclear at this time and could be the result of several factors. It is possible that individuals of *P. mississippi* discriminated between adult *P. glutinosus* from AL and VA, a type of dear enemy recognition, albeit at a broad geographical scale (Jaeger 1981). Dear enemy recognition (Fisher 1954; Wilson 1975) is the widespread phenomenon of reduced aggression between adjacent territorial neighbours in comparison to aggression directed towards intruding unfamiliar individuals. This has been observed in salamanders of the genus *Plethodon* (Jaeger 1981; Walls & Roudebush 1991). Also, previous studies have found that *P. glutinosus* individuals will respond aggressively towards heterospecifics (Nishikawa 1985; Marvin 1998a; Rissler *et al.* 2000; Price & Secki Shields 2002; Marshall *et al.* 2004) with the intensity of interspecific competition varying geographically with the highest intensity being in areas of narrow sympatry (Hairston 1980a,b; Nishikawa 1985). It is possible that what we observed was the result of a learned response by individuals of *P. glutinosus* from range-edge populations to frequent competitive interactions with *P. mississippi* in a narrow geographical area of favourable conditions in the CZ (Fig. 3). An alternative explanation is that individuals from range-edge and core populations have inherent behavioural differences that result in differences in competitive ability. It is possible that individuals of *P. glutinosus* from range-edge populations have behavioural adaptations to local conditions that decrease the cost of interspecific interactions; perhaps they

are more aggressive and win interspecific encounters more often than individuals from core populations.

The results of our study suggest that differences in abiotic tolerances between individuals from core and range-edge populations may shape competition; therefore, abiotic conditions may strongly influence competitive interactions. In order to determine how competitive abilities vary among individuals from core and range-edge populations, we encourage researchers to use ENMs to determine reciprocal transplant sites in core and edge environments. Future studies should incorporate additional field sites within the CZ and in the interior of the range to understand variation *within* core and edge areas. In addition, incorporating laboratory behavioural studies would also address if individuals from different populations have inherent behavioural differences. Much insight could also be gained by the incorporation of physiological studies to address the differences in abiotic tolerances of individuals from core and range-edge populations.

In summary, the geographical range of a species is influenced by a complex interplay of abiotic conditions and biotic interactions that operate at varying spatial scales across geographical space (Dunson & Travis 1991). A complication of disentangling these factors is that species interactions themselves can be affected by abiotic conditions (Coulson *et al.* 2001; Gaston 2003). The incorporation of ENMs and the analysis of spatially explicit climate data provide a novel method that can be used to help unravel the effects of abiotic factors on these interspecific interactions. It is likely that understanding the ecological dynamics of species boundaries will greatly enhance our understanding of a wide range of biological phenomena as range limits are entry points to understanding the ecological niche (Holt & Keitt 2005).

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