INVASIVE RANGE EXPANSION: ENVIRONMENTAL TOLERANCE OF WIDESPREAD AND RESTRICTED CLONAL LINEAGES

By

JONATHAN ARTHUR FINGER

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To the Faculty of Washington State University:

The members of the Committee appointed to examine the thesis of JONATHAN ARTHUR FINGER find it satisfactory and recommend that it be accepted.

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Mark Dybdahl, Ph.D., Chair

____
Richard Gomulkiewicz, Ph.D.

____
Jeremiah Busch, Ph.D.

____
Erica Crespi, Ph.D.

INVASIVE RANGE EXPANSION: ENVIRONMENTAL TOLERANCE OF WIDESPREAD AND RESTRICTED CLONAL LINEAGES

Abstract

by Jonathan Arthur Finger, M.S.
Washington State University
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Chair: Mark Dybdahl

Widespread invaders must possess some capacity to disperse—either naturally or mediated by human activities, and dispersing genotypes need to tolerate novel environments for aggressive range expansion to occur once arriving. In this study, we tested the importance of environmental tolerance during invasive range expansion of the New Zealand freshwater snail (*Potamopyrgus antipodarum*). In North America, populations of *P. antipodarum* exist solely of one of two clonal genotypes: US1, a widespread genotype that dominates the western US, or US2, which is currently known only from the Great Lakes. We asked whether ten newly identified invasive populations near several Great Lakes states—WI, MD, MI, PA, and NY—were colonized by the US2 clone (with a shorter dispersal distance), or by US1 (the clone with a broader and more distant range but is an aggressive disperser). To do so, we constructed a *MAXENT* niche model based on the current range of each clone to predict habitat suitability of the

newly occupied range. Our model predicted higher habitat suitability for US2 than US1 at all ten sites—with much higher habitat suitability for US2 at two sites (NY). We then surveyed the clonal composition of each of the ten new populations. Our survey showed that eight of the new populations (from WI, MD MI, and PA) were comprised entirely of US1, and that the two NY populations were comprised entirely of US2. Thus, colonization of the NY sites by US2 is consistent with both habitat suitability and short dispersal distance. Colonization of the WI, MI and PA populations by US 1 suggests that human-mediated dispersal might be more important than dispersal distance and habitat suitability. Long-distance colonization by US1 might best be explained by human vectors of dispersal, which are perhaps more likely to move snails from distant streams than from deeper waters of the Great Lakes.

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INTRODUCTION

Invasion biologists and management officials have long sought to identify key biological features that associate with invasiveness—the ability of a species to colonize, establish in, spread across, and dominate novel environments (Baker 1965; Mack 1996; Tsutsui et al. 2000)**.** While species-specific traits can facilitate invasion, dispersal opportunities, often human-mediated (Meyerson and Mooney 2007; Perrings et al. 2005), also alter invasiveness by increasing propagule pressure in new habitats (Colautti, Grigorovich, and MacIsaac 2006). Persistence of insipient populations depends on matching the ecological niche (the sum biotic and abiotic conditions where an organism can grow and persist (Grinnell 1917; Hutchinson 1957))**,** of the arriving genotypes to the new environment (Peterson 2015). While post-establishment, invasive populations often aggressively expand their range further, which can also be influenced by variation in environmental tolerance and differential dispersal opportunities (Sexton et al. 2009; Lodge 1993). Widespread invasion is predicated then on not only the opportunity to invade but also suitable environmental tolerance during initial colonization and subsequent range expansion. However, support for general and ubiquitous biological traits that facilitate the invasive process, e.g. phenotypic plasticity, clonality, and weediness, is controversial or unclear (Matesanz, Horgan-Kobelski, and Sultan 2015; Lodge 1993). The sparsity of empirical work supporting models of invasion using key environmental variables is limiting progress towards better understanding of niche and range dynamics in invasion biology and ecology (Gaston 2009).

Testing steps of the invasion pathway presents a chance to study specific cases of broader ecological processes, such as range dynamics and limits (Crooks and Soulé 1999; Duckworth and Badyaev 2007). Studying specific invasive systems also offer real-world opportunities to test controversial and commonly invoked traits, such as human-mediated dispersal (Perrings et al. 2005; Meyerson and Mooney 2007; Shah, Reshi, and Rashid 2008). Free trade and increasing globalization alter the invasion landscape by allowing stowaway species a ride to areas that may be susceptible to invasion (Hulme 2009), for example. Moreover, while not all invaders are global hitchhikers, propagule pressure is consistently linked to establishment success of invaders (Lockwood, Cassey, and Blackburn 2005). Increased establishment via anthropogenic dispersal changes does not negate the importance of arriving individuals being able to tolerate the novel environmental (Pulliam 2000; Soberón and Peterson 2005; Jiménez-Valverde et al. 2011). The area dispersed into must contain the necessary biotic and abiotic components to population persistence. Broad tolerance then is expected to correlate with invasiveness, and while often explained that way, does not match all invasion histories (Lee 2002; Drown, Levri, and Dybdahl 2011).

The importance of dispersal and environmental tolerance in range expansion and invasion is also tied to issues of genetic variation. Newly established invasive populations often lack genetic diversity compared to their source populations (Amsellem et al. 2000; DeWalt and Hamrick 2004; Bossdorf et al. 2005; Dlugosch and Parker 2008; Marrs, Sforza, and Hufbauer 2008). It is historically thought only a few individuals actually succeed in colonizing and invading—resulting in a small sample of the original genetic variation. Additionally, that limited genetic variation can be reduced further via genetic drift due to small population size (Lee 2002). Genetic variation can be added back into the establishing invasive population from the reintroduction of new individuals (Lockwood, Cassey, and Blackburn 2005). The dynamics of dispersal, genetic variation, and niche-matching could be the explanation for the common 'lag period' seen after colonization but before aggressive range expansion occurs (Frankham 2005). Studying the paradox of genetically limited, but aggressively expanding, invaders can produce insight into the mechanisms of range dynamics not seen in other comparisons.

The invasion of *Potamopyrgus antipodarum* (the New Zealand freshwater snail; NZFS) across the U.S. offers a case-study for examining clonality, environmental tolerance, and dispersal in aggressive range expansion. In their native New Zealand, populations of this small freshwater snail can be entirely sexual, asexual, or mixed. However, invasive populations across Europe, Asia, Australia, and North America consist entirely of asexual females belonging to a limited number of multilocus genotypes (MLG) (Drown, Levri, and Dybdahl 2011). The invasion of Europe by *P. antipodarum* consists of only a few clonal lineages (Ponder 1988; Hauser et al. 1992; Weetman, Hauser, and Carvalho 2002; Dybdahl and Drown 2011). Similarly, only a limited number of clonal genotypes of *P. antipodarum* have invaded North America in the past thirty years, with the two dominant multilocus genotypes being US1 in the western U.S. and genotype US2 in the Great Lakes. While opportunistic specialists compared to native genotypes (Drown, Levri, and Dybdahl 2011), US1's distribution is broad in size and habitat type—covering Colorado to California and Washington to

Arizona. Populations of the rarer genotype, US2, remain restricted to the Great Lakes (**Figure 1**) since first being identified in 1991. Unlike its US1 counterpart, US2 likely dispersed from Europe as a secondary invasion. The invasion of the New Zealand freshwater snail across the US permits a test of the importance of genotype and dispersal in the invasion of novel habitat.

Here, we construct a predictive niche model for both US1 and US2 genotypes, and we sample and describe new invasive populations across the Great Lake states—testing the importance of dispersal, genotype, and environmental tolerance during the recent expansion of *P. antipodarum* into these areas**.** We surveyed and sampled individuals from ten newly-identified populations around the Great Lakes. We aim to explore questions of range expansion and invasion by measuring the frequency of both genotypes at each site and comparing it to predictions based on dispersal and environmental tolerance. Previous studies have identified environmental factors that may limit the distribution of *P. antipodarum* in North America, such as temperature, calcium, salinity, solar radiation, and conductivity (Loo, Nally, and Lake 2007; Herbst, Bogan, and Lusardi 2008; Cheng and LeClair 2011; Moffitt and James 2012; Vazquez, Ward, and Sepulveda 2016). If the current range of each clone represents its tolerance to climatic conditions, then what is the predicted habitat suitability of the unoccupied range—which clone is more suited? To get one estimate of environmental tolerance for each genotype we extracted the cumulative habitat suitability, how suitable a location is for a focal species based on climate and geography, from an environmental niche model. If proximity and dispersal influence invasion then we predict US2 to dominate populations across the ten new sites, as each new population sits just outside the edge of US2’s current distribution. However, it is also possible that niche breadth, the ability to persist in a variety of environmental conditions, may be just as important as dispersal during invasion. In this case, we expect US1 to be found more often than US2, despite a large dispersal distance, due to US1 being able to occupy a historically broader range of habitats.

METHODS

Niche model

In order to estimate the environmental breadth and tolerance, we built an environmental niche model to relate the current distribution of the two differentially invasive clones across the US. We assembled the current distribution of invasive *Potamopyrgus antipodarum* populations from the Global Biodiversity Information Facility (gbif.org) and recent publications regarding the invasion of the US (Zaranko, Farara, and Thompson 2011; Dybdahl and Drown 2011). We excluded points outside the U.S. and Canada and museum specimens without any genotypic or geographic context. Lastly, points were coded as either US1 or US2 based on the dominant genotype at that location (**Figure 1**). It should be reiterated that invasions in the western U.S. consist almost entirely of one genotype, US1, while the eastern U.S. is purely US2 populations. We used raster layers for climatic information from WORLDCLIM.org. Handling of GIS locations, climate layers, maps, and distributions was done with DIVA-GIS (v 7.5.0.0).

We constructed a niche model trained on the invasive distribution of each clone across the U.S. and forecast that model across the eastern U.S. Habitat suitability was modeled using the *MAXENT* program (v 3.3.3k). We used the *MAXENT* algorithm as it is the most popular choice for modeling, has been shown to be robust across limited sampling, and more conservative than other choices (Stockwell and Peterson 2002; Mainali et al. 2015). US1 sampling consisted of 380 sites across the known invasive range covering the western U.S. (Dybdahl and Drown 2011; USGS 2016; GBIF.org), while 44 known US2 occurrences (Zaranko, Farara, and Thompson 1997, GBIF.org) were assembled (**Figure 1**). For environmental predictors, we included all 19 climate layers available from WORLDCLIM (2.5 arcminute resolution; worldclim.org for more information) as environmental correlates. Both models were trained using a random 10% subset and replicated 50 times. We utilized settings recommended for small sampling size and for the biological context of our study system, such as cumulative habitat suitability calculations and a fixed 1.0 cumulative threshold (Elith et al. 2006; Pearson et al. 2007). Overall model robustness was evaluated using the Area Under the Curve (AUC) of a receiver operating characteristic plot. This is the recommended metric for testing predictive power, with scores nearing 1 being the most predictive (Guisan and Zimmermann 2000). We ranked the importance of each climatic variable using permutation importance, which has been shown to correlate with some fitness-related traits more than other *MAXENT* metrics (Searcy and Shaffer 2016). Lastly, we extracted average cumulative habitat suitability scores from each model projected across the seven new populations in DIVA-GIS (**Table 3**). Used this way, MAXENT provides a way of making simple estimates of habitat suitability for exploratory analysis (Merow, Smith, and Silander 2013; Searcy and Shaffer 2016).

Sample Collection and Genotyping

We collected individuals of *P. antipodarum* from ten newly established invasive populations across the Great Lakes region for allozyme multilocus genotyping (**Figure 1**; **Table 1.** Site ID, local name, general location, and GIS information for the seven sample populations of *Potamopyrgus antipodarum* across the Great Lakes states. . Invasive populations at each location have only recently established, and the clonal composition at each site has yet to be determined. WI, MI, and all three PA sites are local fishing spots, while the NY sites are isolated creeks that likely don’t experience the same fishing traffic. Individuals gathered at each site were shipped alive to Washington State University for multilocus genotype identification. We utilized a total of 202 samples from the seven different sites and obtained the MLG of each sample using cellulose acetate allozyme gel electrophoresis. Multilocus genotyping was based on up to six allozyme loci (PEPD, IDH, PGM, 6PGD, MPI and AAT) (Dybdahl and Lively 1995; Dybdahl and Lively 1996; Fox et al. 1996; Dybdahl and Lively 1998). Those that shared identical genotypes at all the six loci were considered members of the same clonal type, and by definition having the same MLG. Identification as US1 versus US2 clones was based on results for at least one of four diagnostic loci (IDH, PGM, 6PGD, AAT; **Table 2**; and Dybdahl and Drown 2011). To verify identity with US 1 and US 2 genotypes, each gel assay included "line-up" samples of US1 or US2 individuals.

We described the clonal composition of US2 and US1 individuals across the ten new populations. We calculated the frequency US1 and US2 genotypes at each site by dividing the number of individuals of each genotype by the total number collected (**Table 3**). This gives us an estimate of whether a population is entirely one clone or a mixture. In addition to estimating the frequency of both genotypes at each site, we estimated the minimum detectable frequency for the rarer genotype based on our sampling. We were interested to see—given our sample size and assuming the rarer clone is actually there—at what frequency could we get cases of detecting only one clone with 0.05 error. We calculated the average rate of occurrence for the scenario using a Poisson distributed binomial variable, where success was identifying the dominant clone and failure identifying the rare clone. We then solved for the average rate of success for a scenario where every individual sampled at each site identified as the common clone (zero successes across *n* samples with a Poisson probability of 0.05). This approach gives us an idea of the minimum frequency of the rarer clone that we were able to detect (**Table 3**).

RESULTS

Model Results

Our first aim was to build environmental niche models for both US1 (n = 380 presences) and US2 (n = 44 presences) genotypes across North America to estimate the environmental tolerance and importance of different climatic variables. Both models performed well ($AUC_{us1,\ us2}$ = 0.95) and were robust at discriminating background points from training sets with all 19 WORLDCLIM variables as predictors. We used permutation importance to determine the importance of each climatic predictor for both models (

Table 4). The top two variables of importance for the distribution of US1 genotypes were isothermality, the ratio of mean diurnal range to annual temperature range, and precipitation in the warmest month. In contrast, the top two variables differed with the US2 model, as mean diurnal range and average temperature of the coldest quarter were most important.

Cumulative habitat suitability scores from each model estimated the environmental tolerance and the likelihood of persistence for each clone at each of the seven new locations. The highest average suitability scores fall in areas of the western US for US1 (**Figure 2*a***). All ten sites are far (> 1,300 km) from the extent of their invasion of the western U.S., and have low cumulative habitat suitability scores (**Table 3**). US2's highest average cumulative habitat occurs around the Great Lakes US2 (**Figure 2*b***). Two of the new locations, Youngstown and Somerset, NY, have high cumulative habitat suitability (**Table 3**). However, the remaining sites are just outside the areas of high suitability predicted by the US2 model and have low cumulative habitat suitability scores.

Genotype Identification

Our second aim was to identify the frequencies of each multilocus genotype across all seven new populations. We found that eight of the ten sites consisted of entirely US1 while the remaining were solely US2 (**Table 3**). Two sites were completely dominated by US2, Youngstown, NY (n=31) and Somerset, NY (n=41). Both locations are small, isolated streams that drain into Lake Ontario, which is less than 10 km away. Sites with lower minimum frequencies, like Youngstown, show lower likelihood that we failed to detect the rarer clone. With this error rate and our sample sizes, we should detect at least one rare clone among our sampling as long as they occurred at least a frequency from 7%-10%. The other eight populations, Madison, WI (n=32); Badger Creek, WI (n=14); Lake County, MI (n=37), Au Sable River, MI (n=4); Wiseburg, MD (n=12) Bellfonte, PA (n=12), and State College, PA (n=48 ; n=31), consisted completely of US1. These locations—small creeks, rivers, and streams—are popular fishing spots in the Great Lakes region. While all seven sites are distant from the nearest known US1 source population in Colorado, these five sites are not directly adjacent to a Great Lake as seen the New York sites and Lake Ontario. With this error rate and our sampling, we should detect at least one US2 sample so long as they occur at least at a frequency from 6% -24% across these five populations (**Table 3**).

DISCUSSION

We modeled the niche of two genotypes of the clonal invasive snail *Potamopyrgus antipodarum*, one of which is widespread in the western US (US1) and one in the Great Lakes (US2). The two genotypes differed in habitat suitability—based on variation in climate between the two invaded ranges. We combined this effort with an assay of clonal composition across ten newly established populations in the Great Lakes region to test questions regarding dispersal, environmental tolerance, and invasive range expansion. Based on our sample and multilocus genotyping, all populations were comprised exclusively of either US1 or US2. The west coast invader (US1) was found in five populations across Michigan, Wisconsin, and Pennsylvania. This marks is the first time this multilocus genotype has been found outside its previous range extending from the Pacific Coast to Colorado. Genotyping results from the remaining two sites in New York indicated that they were established by the US2 clone. Based on our probability analysis, we concluded that all sites are either monoclonal or that the alternate clone is incredibly rare.

Colautti and MacIsaac (2004) suggested that every stage of the invasion pathway is affected by dispersal, environmental tolerance, or both. The importance of environmental tolerance is supported by the notion that intrinsic biological factors like phenotypic plasticity, weediness, and genetic variation affect the overall robustness of fitness to multiple environments (Lodge 1993). Therefore, the ability to survive and reproduce in the novel environment should be critically important in the capacity of different species or genotypes to expand their invasive range. Our ENM prediction, based on *MAXENT* data, showed that temperature and precipitation are generally the most important climatic correlates to *P. antipodarum* population persistence and invasion, based on variable permutation importance (**Table 4**). Our results are in broad agreement with the study by Loo, Nally, & Lake (2007), which also forecasted the extent of invasion of *P. antipodarum* in the US based on conditions across the invasive range. These climatic correlates are also supported by lab and field studies on the effects of temperature on physiology and persistence of *P. antipodarum* (Moffitt and James 2012; Cheng and LeClair 2011; Dybdahl and Kane 2005). Our niche model forecast and that of Loo et al. (2007) also predicted the invasive range to expand across the middle of the U.S. and outwards from the Great Lakes.

However, the two *P. antipodarum* genotypes found in the U.S. occupy drastically different ranges—in terms of size, climatic conditions, and habitat type. The differences might be due to variation in environmental tolerance, a conclusion which is supported by clone-specific differences measured in the ancestral and invasive range (Fox et al. 1996; Jokela, Dybdahl, and Lively 1999; Jokela et al. 2003; Drown, Levri, and Dybdahl 2011; Jacobsen and Forbes 1997). Consequently, we designed our niche model to predict range expansion and habitat suitability for the two clones separately. We found that US1 and US2 distributions are driven by different environmental conditions, suggesting different environmental tolerances. Specifically, for US1, isothermality (the ratio of monthly to yearly temperature change) and precipitation in the warmest quarter scored highest for variable importance in the model, while US2's model was impacted most by mean diurnal range and temperature in the coldest quarter. Based on these findings, the distribution of US2 seems more impacted by freezing temperature than that of US1, which is affected by both temperature range and necessary precipitation in warm months. The absence of precipitation in the US2 model is not necessarily surprising as the populations used to train the model were lake populations, where precipitation is less important.

While our model and that of Loo et al. (2007) predicted that the Great Lakes region is at high risk of invasion, it was not clear which genotype was most likely to invade at each location. The differences in climatic conditions in the region covered by our predictive model resulted in different habitat suitabilities and range size for the two genotypes. Our model predicted lower suitability for US1 compared to US2 across the entire Great Lakes region and eastern US. The low suitability for US1 in the Great Lakes area could be explained by differences in isothermality, which is higher in the western US, where US1 is found, and lower in the eastern US. Habitat suitability was particularly high for US2 in the New York sites, adjacent to Lake Ontario (**Figure 2** and **Table 3**). The high habitat suitability for US2 could be explained by mean diurnal range, which increases rapidly with distance from the shelter of the Great Lakes themselves. Consistent with these predictions, we discovered US2 only at the two New York sites. However, in contrast, we discovered only US1 at five locations across Wisconsin, Michigan, and Pennsylvania. If these five sites actually have lower habitat suitability, then perhaps US1 is sustained in the region by repeated dispersal and colonization over time.

Repeated dispersal leads to high propagule pressure, a strong predicator of both invasiveness and invasibility (Colautti, Grigorovich, and MacIsaac 2006), and we expected source populations far from newly established populations would be less likely to contribute colonists due to lower propagule pressure. Establishment success of distant indivuduals would be much lower than individuals already tolerating local sites (Lockwood, Cassey, and Blackburn 2005). Consequently, we expected that shorter dispersal distances for US2, along with higher habitat suitability, would have favored colonization of the Great Lakes region. The ten new populations are no more than 200 km from the US2 populations in the Great Lakes but at least 1,300 km away from the nearest known US1 source populations in Colorado. On the other hand, we might have expected US1 to be favored in colonizing of new sites, because US1 has exhibited a much greater range expansion than US2, which might represent differential dispersal capacity. One potential cause of greater dispersal by US1 than US2 to the Great Lake regions might be a greater likelihood of human-mediated dispersal.

Invasive and range expansion outcomes might depend more on occasional long-distance jump dispersal, especially vectored by humans, than on local movements that might be related to simple distance measures (Suarez, Holway, and Case 2001; Wichmann et al. 2009). In freshwater invaders, human-mediated dispersal has been cited as a major factor facilitating range expansion via movement of fish between hatcheries and streams by fisheries managers and recreational water users on vessels or fishing equipment (Hosea and Finlayson 2005; Alonso and Castro-Diez 2008). For the Great Lakes invasion by *P. antipodarum*, all of the US1 populations persist in small rivers or creeks that appear to be used for recreational fishing (J. Finger and E. P. Levri, Personal Observation). If human-mediated transport is more likely to connect streams in the western US to the Great Lakes region than compared to connecting the Great Lakes themselves to local streams, then colonization of this region by US1 might be more likely than by US2.

Supporting the notion of greater jump dispersal by US1 than local dispersal by US2 is a difference in the accessibility of different habitats to vectors of dispersal. In lakes Ontario and Erie the highest densities of US2 populations have been recorded at depths between 15 and 25 meters (Levri and Jacoby 2008; Levri, Kelly, and Love 2007; Zaranko, Farara, and Thompson 2011). It seems less likely that recreational water users would transport the snails from the deep-water lake habitats to local streams. On the other hand, the invasion of Great Lakes streams by US1 follows the pattern that has been responsible for aggressive range expansion among streams and rivers in the western United States, which is dispersal by recreational water users. The exception to this pattern is found in NY, where the two new invaded sites are found within 10 km of Lake Ontario, and where recreational water users would not likely visit (E. P. Levri personal observation). Here, local snail movements from shallow lake populations into adjacent tributary streams could explain the invasion and dispersal of US2.

Our study of the invasive range expansion of *P. antipodarum* across the Great Lake states emphasizes the importance of managing of sources of human-mediated dispersal to reduce further spread. Based on our range expansion prediction for each clone, it appears that human-mediated dispersal might be sufficient to overcome habitat suitability in determining the outcome of an invasion. Of course it remains possible, given the young age of the US1 populations they are either ephemeral and will go extinct, or will fail to spread in the region—consistent with ENM predictions. It also remains possible that US2 will now expand rapidly by human-mediated movement from one inland stream to another since they are now found in two New York streams. Our results suggest the importance of tracking both of these two genotypes in the Great Lakes region, and by doing so, further informing our knowledge of dispersal and environmental tolerance in the invasion process.

Figures and Tables

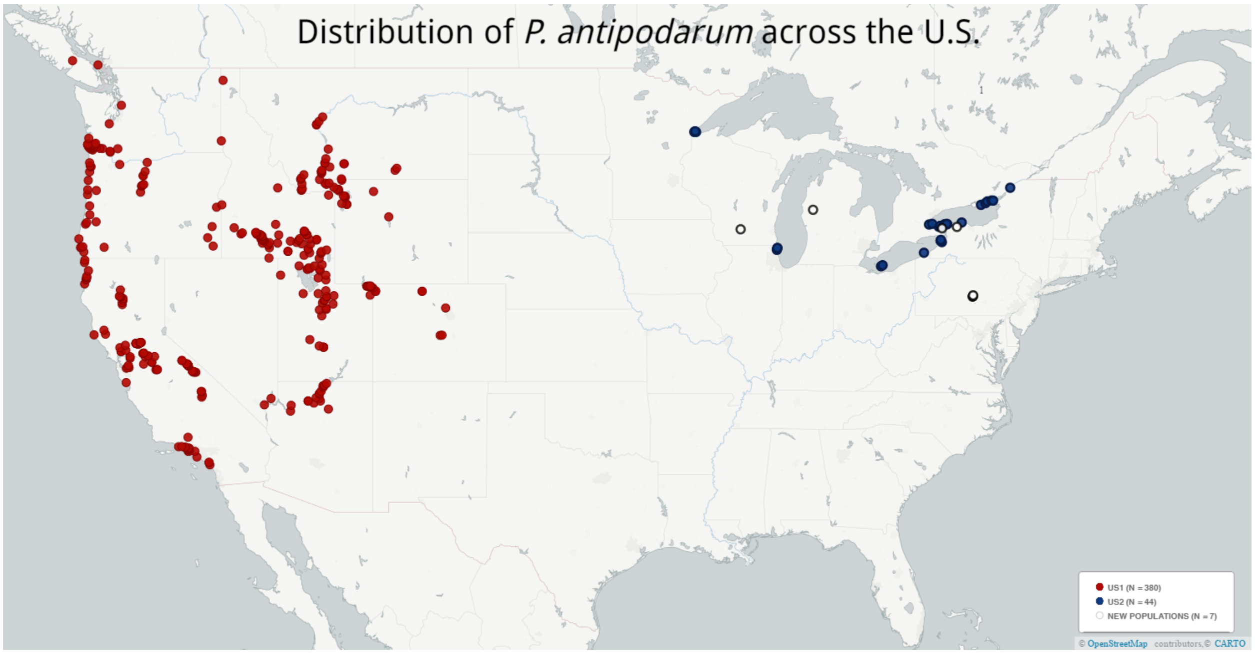

Figure 1. Map of invasive *Potamopyrgus antipodarum* genotypes across the U.S. Clonal genotype US1 (red) invaded Idaho in 1987 and has aggressively expanded its range across the western U.S. The Great Lakes populations were discovered twenty years ago, and US2 (blue) remains restricted to that region unlike its counterpart (Dybdahl and Drown 2011; Zaranko, Farara, and Thompson 1997). Newly established (white) invasive populations have also been discovered, but the genotype composition of these populations has yet to be described.

ID	Site	Location	Longitude	Latitude
WI 1	Black Earth Creek	Madison, WI	-89.7099	43.1249
MI 1	Pere Marquette River	Lake County, MI	-85.8993	43.8674
PA 001	Spring Creek	Bellfonte, PA	-77.5137	40.5394
PA 022	Spring Creek	State College, PA	-77.4859	40.5163
PA 043	Slab Cabin Run	State College, PA	-77.5033	40.4876
ONT 001	Unnamed Creek	Youngstown, NY	-79.0212	43.2711
ONT 029	Fish Creek	Somerset, NY	-78.5559	43.3600
WI 2	Badger Mill Creek	Verona, WI	-89.3149	42.5836
MI 2	Au Sable River	Frederic, Mi	-84.4519	44.4635
MD 1	Unnamed River	Wiseburg, MD	-76.3927	39.3719

Table 1. Site ID, local name, general location, and GIS information for the seven sample populations of *Potamopyrgus antipodarum* across the Great Lakes states.

Clonal Type	**Allozyme Genotypes**					
	PEPD	IDH	PGM	6PGD	MPI	AAT
US 1	bd	aab	abb	cc	aa	add
US 2	bd	aa	aa	bbc	aa	aab

Table 2. Allozyme multilocus genotype of the two predominant clones in the US. Western US states were colonized by US1, and Great Lakes were colonized by US2 (Dybdahl and Drown 2011).

Site ID	Location	Sample Size	US1 Frequency	US2 Frequency	US1 Model Suitability Score (Mean & Std. Dev)	US2 Model Suitability Score (Mean & Std. Dev)	Min. Frequency of Rarer Clone
WI 01	Madison, WI	32	1.00	0.00	$\mu = 0.132$; $\sigma = 0.063$	$\mu = 5.1$; $\sigma = 0.4$	0.138
MI 01	Lake County, MI	37	1.00	0.00	$\mu = 0.876$; $\sigma = 0.161$	$\mu = 6.50$; $\sigma = 0.2$	0.114
PA 01	Bellfonte, PA	12	1.00	0.00	$\mu = 0.420$; $\sigma = 0.098$	$\mu = 0.65$; $\sigma = 0.13$	0.326
PA 22	State College, PA	42	1.00	0.00	$\mu = 0.302$; $\sigma = 0.011$	$\mu = 0.77$; $\sigma = 0.03$	0.096
PA 43	State College, PA	48	1.00	0.00	$\mu = 0.297$; $\sigma = 0.015$	$\mu = 1.44$; $\sigma = 0.08$	0.072
NY 01	Youngstown, NY	31	0.00	1.00	$\mu = 0.309$; $\sigma = 0.101$	$\mu = 95.6$; $\sigma = 2.02$	0.144
NY 29	Somerset, NY	41	0.00	1.00	$\mu = 0.287$; $\sigma = 0.065$	$\mu = 49$; $\sigma = 1.9$	0.023
MI 02	Au Sable River, MI	12	1.00	0.00	$\mu = 0.842$; $\sigma = 0.124$	$\mu = 0.78$; $\sigma = 0.05$	0.327
WI 02	Badger Creek, WI	14	1.00	0.00	$\mu = 0.137$; $\sigma = 0.048$	$\mu = 6.23$; $\sigma = 0.06$	n/a
MD 01	Wiseburg, MD	16	1.00	0.00	$\mu = 0.162$; $\sigma = 0.056$	$\mu = 0.79$; $\sigma = 0.07$	n/a

Table 3. Sites, sample sizes, cumulative habitat suitability index, and the frequency of *P. antipodarum* clones based on allozyme multilocus genotypes (MLGs) in populations across the Great Lakes region. All sites were comprised of entirely one clone or the other. Both NY populations consist of 100% US2 individuals, while the remaining sites are entirely US1. We calculated the minimum detectable frequency of the rarer clone for each site, given our sampling effort and a 0.05 error rate. The lower the minimum frequency the more powerful our ability to have detected at least one of the rarer clone at that site.

Permutation Importance of BIOCLIM Variable	US1	US2
Isothermality	35.9753	0.2075
Precipitation of Warmest Quarter	29.392	0
Annual Mean Temperature	5.1159	0.0213
Precipitation of Coldest Quarter	4.9609	0
Temperature Seasonality	4.5723	0.0973
Precipitation of Wettest Month	3.0783	0.0114
Temperature Annual Range	3.0765	2.6255
Max Temperature of Warmest Month	2.6068	5.3545
Mean Temperature of Wettest Quarter	2.5024	0.1731
Precipitation of Wettest Quarter	1.8805	0
Mean Temperature of Driest Quarter	1.8095	0.1619
Precipitation Seasonality	1.4015	0.4489
Min Temperature of Coldest Month	0.937	0
Precipitation of Driest Month	0.8243	1.1836
Mean Temperature of Warmest Quarter	0.7696	0.112
Mean Diurnal Range	0.5186	35.8622
Mean Temperature of Coldest Quarter	0.4539	53.7409
Precipitation of Driest Quarter	0.0931	0
Annual Precipitation	0.0318	0

Table 4. Table of permutation importance for all 19 BIOCLIM variables for both US1 and US2 MAXENT models. US1 and US2 differed in most important climatic variables. The two most important variables for US1 were isothermality and precipitation in the warmest month, while mean diurnal range and mean temperature of the coldest quarter had the highest permutation importance for the US2 model.

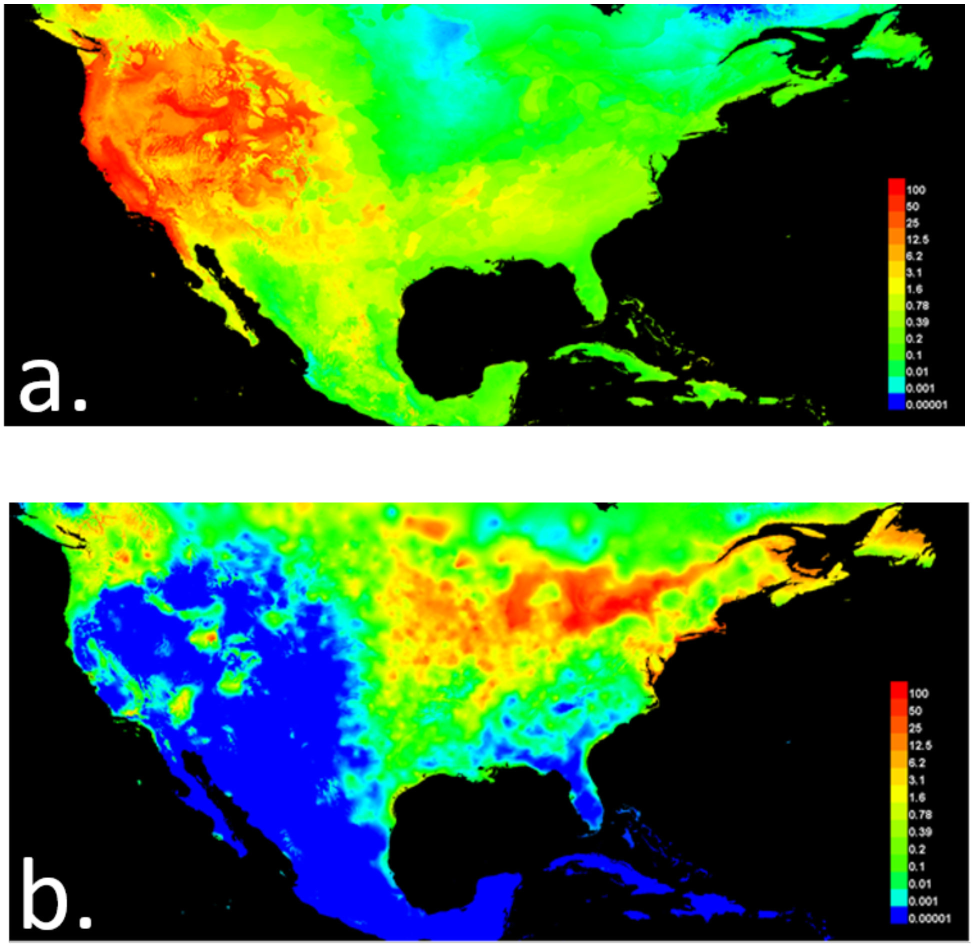

Figure 2. MAXENT habitat suitability model for a) US1, the western invasive clone, and b) US2, the restricted clone found in the Great Lakes. Colors on map represent average cumulative suitability across all replicates at 2.5m resolution.

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