

Decoupled conservatism of Grinnellian and Eltonian niches in an invasive arthropod

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Abstract. Whether a species niche is conserved or shifts across space and time is a question of heightened interest in ecology and evolution. Considerable scientific inquiry into this topic has used invasive species to evaluate conservatism of the Grinnellian climatic niche while generally neglecting the Eltonian functional niche. By contrast, we report here on the first simultaneous reciprocal comparison of both the Grinnellian and Eltonian niches for the globally invasive signal crayfish *Pacifastacus leniusculus* between its native (Pacific Northwest of North America) and non-native ranges (Japan). Using multivariate statistics and the Maxent machine-learning algorithm, we found strong evidence for a climatic niche shift between geographic regions for *P. leniusculus*. *Pacifastacus leniusculus* shifted from warmer temperatures with strong precipitation seasonality in western North America to cooler temperatures with less precipitation seasonality in Japan. However, analysis of stable isotopes of carbon and nitrogen revealed conservatism of the functional niche of *P. leniusculus* between multiple lakes in the native and non-native ranges. We found that trophic position and niche width of *P. leniusculus* were equivalent between regions, and that niche attributes including reliance on autochthonous or allochthonous energy sources and ontogenetic shifts were comparable regardless of origin. Our finding of functional niche conservatism contrasts with the results of some recent studies evaluating the Grinnellian niche for invasive species, as well as our own climatic niche comparison, and raises the question of whether Grinnellian or Eltonian niches are more prone to shifts or conservatism. We hypothesize that the Grinnellian niche may be more labile than the Eltonian niche in general, but argue that resolving this question will require more reciprocal comparisons of Eltonian niches to keep pace with the recent increase in Grinnellian niche studies.

Key words: invasive species; Japan; niche conservatism; North America; *Pacifastacus leniusculus*; reciprocal comparison; species distribution model; stable isotopes.

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INTRODUCTION

The ecological niche has been a central concept throughout the modern history of ecology, with broad relevance to species distributions, diversity, and coexistence (Colwell and Rangel 2009, Devictor et al. 2010). Substantial investigation has focused on the topic of niche conservatism, as ecologists and evolutionary biologists alike ques-

tion whether niches are conserved across space and time or whether niche shifts are observed (i.e., a change in position of either the fundamental or realized niche; Pearman et al. 2008). This line of inquiry has implications for characterizing the process of speciation, determining whether imperiled species are capable of adapting to rapid anthropogenic change, and understanding how some species are able to

successfully invade new habitats and regions (Wiens and Graham 2005).

Despite attempts at synthesis and unification of the concept (Hutchinson 1957, Chase and Leibold 2003), many ecologists continue to recognize two separate components of the niche (Devictor et al. 2010). The first is the Grinnellian (or scenopoetic) niche characterized by non-interactive environmental conditions that influence where an organism occurs, while the second is the Eltonian (or bionomic) niche that describes the functional role and biotic interactions of a species (reviewed in Soberón 2007, Colwell and Rangel 2009, Devictor et al. 2010). Increased availability of species distribution and environmental datasets combined with the development of sophisticated modeling approaches has resulted in many recent studies evaluating whether the Grinnellian niches of species are stable through time or across regions (Elith and Leathwick 2009). By contrast, considerably less research has explored similar reciprocal comparisons of the Eltonian niche (but see Lohrer et al. 2000, Pintor et al. 2008). This disparity of attention given to the Grinnellian over Eltonian niche has important limitations, as knowledge of where species may occur is less useful and reliable in the absence of knowledge about their ecological function (Schmitz et al. 2003, Elith and Leathwick 2009).

The niche conservatism hypothesis predicts that species should retain their niche attributes over space and time (Wiens and Graham 2005, Pearman et al. 2008). Species invasions provide a novel opportunity to test the niche conservatism hypothesis through comparisons of niche attributes between native and non-native ranges (Hierro et al. 2005, Sax et al. 2007). Many non-native species that establish and spread outside of their native range are ecological generalists exhibiting substantial breadth in their functional roles and habitat requirements (e.g., Jeschke and Strayer 2006, Snyder and Evans 2006). Yet, the paucity of studies examining invasive species in their native ranges prevents ecologists from knowing if the prevalence of generalist invaders represents conservatism of broad native range niches, or instead niche shifts as a result of mechanisms like rapid adaptation or ecological release from native range enemies and competitors (Liu and Stiling 2006, Lavergne and

Molofsky 2007). In addition, niche attributes like ontogenetic shifts or habitat-mediated reliance on different energy sources are poorly explored for generalist species, particularly in comparison to species with more discrete functional roles like top predators (Olson 1996, Post et al. 2000, Doi 2009). Generalist invaders offer the prospect of testing the niche conservatism hypothesis via reciprocal comparisons between native and non-native ranges, evaluating whether their niche breadth is an inherent trait conserved between populations in distant regions or is instead a result of the invasion process.

We report on the findings of an inter-continental comparison of both the Grinnellian and Eltonian niche of a generalist arthropod, the signal crayfish *Pacifastacus leniusculus*. Native to western North America, *P. leniusculus* has been introduced globally (Hobbs et al. 1989) and impacts aquatic communities as a polytrophic consumer on plants, animals, and detritus (e.g., Stenroth and Nyström 2003, Usio et al. 2009). We first made reciprocal comparisons of the Grinnellian niche for this species between its native range and a non-native region (Japan) using multivariate statistics and a machine-learning algorithm (i.e., species distributional modeling). We then evaluated Eltonian niche conservatism by using carbon and nitrogen stable isotopes to characterize the trophic function of *P. leniusculus* in both of these regions. We compared trophic position, diet breadth, and sought evidence for inter-range consistency in ontogenetic niche shifts and relationships between the niche and habitat attributes for *P. leniusculus*.

Our study provides a novel reciprocal comparison of both the Grinnellian and Eltonian niche of an invasive generalist and offers an empirical perspective on whether the Grinnellian or Eltonian niche is more prone to shifts or conservatism. We predicted that Grinnellian and Eltonian niches should behave synchronously, either shifting or exhibiting conservatism together, owing to their unification under Hutchinson's (1957) classic synthesis of the niche concept (Chase and Leibold 2003). As such, we provide among the first responses to Soberón's (2007) challenge to explore cross-correlations between Grinnellian and Eltonian niches and investigate the "more dynamic and more complex domain of the Eltonian niche" as related to niche conservatism.

METHODS

Grinnellian niche

Pacifastacus leniusculus is native to the Pacific Northwest region of Canada and the United States, occurring from coastal drainages of northern California to southern British Columbia and inland to the Pacific slope of the Rocky Mountains (Miller 1960, Bondar et al. 2005). *Pacifastacus leniusculus* was introduced from the Columbia River to Lake Mashu on Japan's northern island of Hokkaido in the late 1920s, and has since expanded its distribution on Hokkaido and isolated sites on the island of Honshu through subsequent illegal introductions and secondary spread (Usio et al. 2007). We evaluated Grinnellian niche conservatism between these native and non-native ranges using known species occurrences and bioclimatic variables analyzed with multivariate statistics and a machine-learning algorithm.

We used bioclimatic variables from the WorldClim dataset at a five arc-minute resolution for our analysis (Hijmans et al. 2005). These variables, composed of ecologically relevant temperature and precipitation attributes, have been recommended for and widely applied to species distribution modeling (Wiens and Graham 2005, Broennimann et al. 2007, Medley 2010). We first explored Grinnellian niche conservatism in *P. leniusculus* with a Principal Components Analysis (PCA) on the full WorldClim dataset (19 variables). This analysis allowed us to characterize climatic differences between the native and non-native ranges of *P. leniusculus* descriptively by plotting convex hulls and empirically by testing for differences using permutational multivariate linear models (Anderson 2001). To account for potential redundancies and correlations in the dataset, we used the PCA to visually assess relationships and removed highly correlated ($r > 0.80$) variables prior to species distribution modeling.

We next made reciprocal species distribution predictions between the native and non-native ranges using the Maxent (maximum entropy) machine-learning algorithm (Phillips et al. 2006). The Maxent algorithm uses presence-only species occurrence data and environmental variables to predict distributions. The Maxent algorithm is increasingly applied to Grinnellian niche studies

(e.g., Rödder and Lötters 2009, Medley 2010), and has been found to outperform similar machine-learning species distribution models (Elith et al. 2006, Phillips et al. 2006). We developed native and non-native range Maxent distribution models for *P. leniusculus* and then projected each model to the other geographic region. Models in the native range were based on 202 occurrences compiled from museum records and published accounts (Larson and Olden, *in press*), and models in the non-native range were based on 28 occurrences from Usio et al. (2007). Maxent has been found to be robust in modeling low numbers of occurrences comparable to and smaller than our non-native range dataset (Hernandez et al. 2006). The background extent used in species distribution modeling can influence model results, as backgrounds that are too small may produce inaccurate projections while background areas that are too large may over-predict distributions (Thuiller et al. 2004, VanDerWal 2009). We defined an intermediate background extent for our Maxent models as a compromise between the area needed to capture the accessible native range in North America, bounded by river drainages occupied by *P. leniusculus*, and the entirety of the non-native country for which we had data (Japan).

In both the native and non-native range, Maxent models were trained with half of the occurrence data and tested against the remainder. Model performance was assessed for the testing dataset with the area under the Receiver Operating Characteristic (ROC) curve (AUC) and one-tailed binary tests of omission based on minimum training presence as a threshold (Phillips et al. 2006). Native and non-native range models were then projected to the other geographic region and compared using the aforementioned tests. Niche conservatism was also evaluated using tests of niche equivalence and similarity proposed for this purpose by Warren et al. (2008). Equivalence defines niche conservatism as identical niches while similarity defines conservatism as niches that are no more different or similar than would be expected relative to background conditions. These definitions represent a continuum from strict (equivalence) to more flexible (similarity) interpretations of the niche conservatism hypothesis that may produce different results under different applications

(Warren et al. 2008).

We evaluated equivalence and similarity using a measure of niche overlap (D) adapted by Warren et al. (2008) from Schoener (1968), which scales from 0 (no overlap) to 1 (identical). A related measure (I) was also analyzed but not reported as its results did not differ from D . We calculated D for the native range Maxent model projected to the non-native range and the reciprocal comparison. We then tested for equivalence and similarity using randomization tests in the ENMTools package (Warren et al. 2010). Selection of appropriate background area is critical to niche similarity (Warren et al. 2008), and consequently we defined background area in Japan by the present invaded range and background area in North America by the geographic extent of river drainages occupied by *P. leniusculus*.

Eltonian niche

Field and laboratory.—During summer 2008 (5 July–30 July), we surveyed five Hokkaido lakes occupied by *P. leniusculus*: Kussyaro (Lat: 43.58, Long: 144.31), Mashu (43.61, 144.55), Oketo (43.61, 143.38), Shikaribetsu (43.27, 143.10), and Shikotsu (42.77, 141.40). These lakes range in size from 2.1 to 79.5 km², include four natural lakes and one artificial reservoir, and have watershed conditions with little anthropogenic disturbance due to containment in or close proximity to national parks. Study lakes in Hokkaido range from oligotrophic, with minimum chlorophyll-a of 0.08 mg/m³ and maximum Secchi disk depths of 25 m, to mesotrophic, with maximum chlorophyll-a of 5.40 mg/m³ and minimum Secchi disk depths of 2 m. In late summer 2008 (28 August–7 September), we surveyed four native range lakes of *P. leniusculus* in Washington State, USA: Crescent (Lat: 48.06, Long: –123.79), Pleasant (48.07, –124.33), Whatcom (48.76, –122.42), and Wynoochee (47.39, –123.60). Native range lakes vary in size from 2.0 to 20.3 km², include three natural lakes and one artificial reservoir, and have watersheds similarly protected by public land. Washington lakes range from oligotrophic, with minimum chlorophyll-a of 0.50 mg/m³ and maximum Secchi disk depths of 18 m, to mesotrophic, with maximum chlorophyll-a of 3.60 mg/m³ and minimum Secchi disk depths of 4.6 m. Although visits to native and non-native

range lakes were separated by as much as two months, Stenroth et al. (2006) found stable isotope signatures of *P. leniusculus* in small Swedish lakes to be consistent over a comparable time interval.

At each lake, we collected allochthonous (terrestrial detritus) and autochthonous (aquatic macrophytes, periphytic algae) basal resources, non-crayfish invertebrates, *P. leniusculus*, and fish from the littoral zone over several days using hand collection while snorkeling, an Ekman sediment grab, and trapping with gill nets, hoop nets, and baited Gee minnow traps deployed overnight. We kept 14–16 crayfish from each lake for stable isotope analysis, using individuals across the available range of sizes in a balanced male:female sex ratio. *Pacifastacus leniusculus* and fish were euthanized and abdominal muscle tissue dissected from each specimen. Basal resources, whole invertebrates, and muscle tissue from crayfish and fish were placed on ice, transported to the laboratory, and frozen until processing for stable isotope analysis.

Stable isotopes can be used to assess the functional role of species, as the ratio of ¹³C to ¹²C ($\delta^{13}\text{C}$) is fixed at photosynthesis and conserved up food chains, tracing the origin of an organisms' energy sources, while the ratio of ¹⁵N to ¹⁴N ($\delta^{15}\text{N}$) increases in a consistent manner (~3.4‰) with each step up a food chain, revealing an organisms' trophic position (Vander Zanden and Rasmussen 2001, Post 2002). Stable isotope sample preparation followed the recommendations of Stenroth et al. (2006) for crayfish. Samples were dried at 60°C for over 24 h and then homogenized using a mortar and pestle, excluding some small invertebrates that were analyzed as whole specimens. We placed approximately 1 mg of animal and 2–3 mg of plant tissue in tin capsules, which were sent to the University of California - Davis Stable Isotope Lab for dual carbon and nitrogen analysis using a PDZ Europa 20–20 isotope ratio mass spectrometer. Stable isotope ratios are reported in δ notation as ¹³C/¹²C or ¹⁵N/¹⁴N ratios relative to a standard, with Pee Dee belemnite and atmospheric nitrogen as the carbon and nitrogen standards, respectively.

Statistical analyses.—We first compared trophic niche width of *P. leniusculus* between native and non-native range lakes using trophic position

range, $\delta^{13}\text{C}$ range, and total convex hull area of $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ biplots (Layman et al. 2007a, b, Olsson et al. 2009). We measured trophic position for these and subsequent analyses relative to mean $\delta^{15}\text{N}$ of primary consumers in the scraper trophic guild, following the recommendation of Anderson and Cabana (2007) for estimating trophic position when primary consumer taxa are not consistent between study sites. We also standardized $\delta^{13}\text{C}$ of each *P. leniusculus* population relative to the $\delta^{13}\text{C}$ mean and range of all consumers in its lake to place populations on an equivalent $\delta^{13}\text{C}$ axis (Olsson et al. 2009). We calculated convex hull areas of $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ biplots, and then evaluated whether the trophic niche of *P. leniusculus* was conserved between native and non-native range lakes with a multivariate analysis of variance (MANOVA) on trophic ranges, $\delta^{13}\text{C}$ ranges, and convex hull areas.

The influence of habitat size, spatial structure, and productivity on food webs and the functional niche of focal species have been extensively debated, particularly in aquatic systems where these habitat attributes can have strong effects on trophic position or reliance on allochthonous and autochthonous energy sources (e.g., Vander Zanden et al. 1999, Post et al. 2000, Layman et al. 2007b). We examined the influence of lake area on the trophic niche of *P. leniusculus*, predicting that smaller lakes would correspond with greater reliance on allochthonous terrestrial subsidies due to their greater relative proportion of adjacent riparian habitat (Doi 2009). This comparison was dependent on the general pattern of $\delta^{13}\text{C}$ enrichment in benthic autochthonous producers relative to C_3 terrestrial plants that has been documented in other lake systems (Hecky and Hesslein 1995). We also tested for an effect of lake area on *P. leniusculus* trophic position (Post et al. 2000). We did not evaluate productivity and the “productive space hypothesis,” which considers system size and productivity concurrently (Vander Zanden et al. 1999), because of our small sample size (Post 2007) and a confounding negative correlation between lake area and chlorophyll-a ($r = -0.73$, $P = 0.064$).

We used an analysis of covariance (ANCOVA) to test for differences in *P. leniusculus* trophic position and $\delta^{13}\text{C}$ between ranges with lake area ($\log \text{km}^2$) as continuous predictor. In the absence of significant differences between ranges and

confirmation of homogenous slopes, we combined lakes in linear regression modeling to increase statistical power. We did not use a stable isotope mixing model to estimate the contribution of allochthonous or autochthonous sources to crayfish $\delta^{13}\text{C}$ signatures (e.g., Phillips and Gregg 2003), because the diets of omnivores like *P. leniusculus* contain many potential prey items with widely differing C:N ratios that violate assumptions and efficacy of these models (Stenroth et al. 2006). Instead, we first confirmed significant differences in $\delta^{13}\text{C}$ values of allochthonous and autochthonous sources across lakes and ranges with a Mann-Whitney U-test and then used linear regression to test for shifts in resource reliance by *P. leniusculus* from one source to another in response to lake area. Potential contribution of pelagic energy sources (planktonic food chain) was not evaluated because this pathway has been found to contribute minimally to the diet of the study organism (Stenroth et al. 2006).

Lastly, we sought evidence for ontogenetic niche shifts in *P. leniusculus* in native and non-native range lakes. We first performed ANCOVA to test for an effect of sex on trophic position or $\delta^{13}\text{C}$, and in the absence of a significant effect used linear regression to model the relationship between crayfish size (mm total carapace length) and trophic position and $\delta^{13}\text{C}$. We then used Student *t*-tests on regression slopes of native and non-native range lakes to evaluate whether the direction of ontogenetic niche shifts in *P. leniusculus* was consistent between the two regions.

RESULTS

Grinnellian niche

A highly significant PCA (first two axes explained $\sim 70\%$ of variation, randomized broken-stick model $P < 0.001$ for each axis) demonstrated substantial differences in multivariate climate space between the native and non-native ranges of *P. leniusculus* (Fig. 1). The two regions ($F = 380.209$, $P < 0.001$) and the area of each region occupied by *P. leniusculus* ($F = 84.502$, $P < 0.001$) were significantly different by permutational linear models. An examination of this PCA and correlations between bioclimatic variables resulted in a reduction in the dataset to 11 variables for species distribution modeling

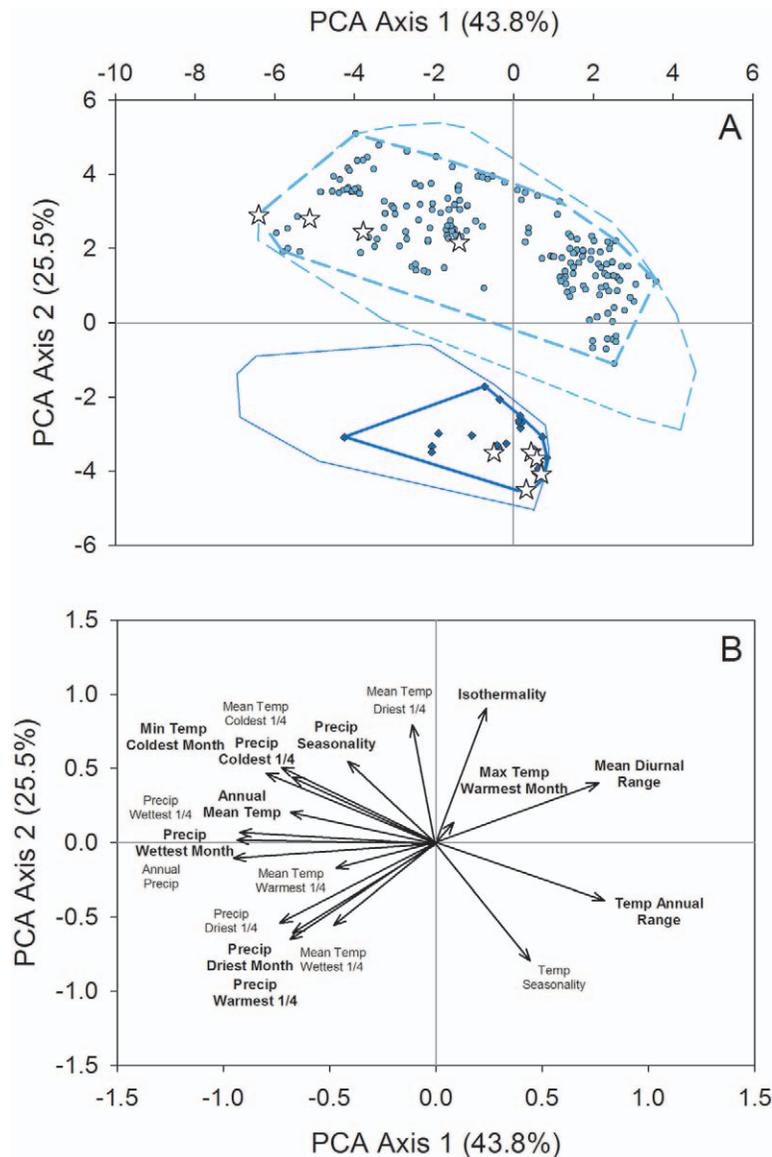


Fig. 1. Principal Components Analysis (A) on 19 bioclimatic variables (B) for the Pacific Northwest region of North America (convex hull as thin dashed line) and Japan (convex hull as thin solid line) with *Pacifastacus leniusculus* distributions in both native (occurrences as circles, convex hull as thick dashed line) and non-native ranges (occurrences as diamonds, convex hull as thick solid line). Stars represent study sites for tests of Eltonian niche conservatism (also in Fig. 2). Correlations of the 19 bioclimatic variables on PCA axes are provided (B) with variables selected for subsequent Maxent modeling in bold.

with Maxent: annual mean temperature, mean diurnal range, isothermality, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipita-

tion of warmest quarter, and precipitation of coldest quarter (Fig. 1).

The Maxent model trained in the native range performed well for predicting test occurrences in the Pacific Northwest region, with an AUC of 0.880 and an omission rate of only 4% ($P < 0.001$;

Fig. 2). Bioclimatic variables with high relative contributions to the native range model included minimum temperature of the coldest month (40.0%), annual mean temperature (17.1%), and temperature annual range (12.2%). This model performed poorly when projected to the non-native range, with a low AUC of 0.508 and a high omission rate of 96% ($P = 0.789$). Similarly, the Maxent model developed in the non-native range successfully predicted Japan test occurrences, with an AUC of 0.917 and an omission rate of only 7% ($P < 0.001$; Fig. 2). Bioclimatic variables describing precipitation seasonality (62.5%) and mean annual temperature (29.3%) exhibited the greatest relative contributions to this model. When projected to the Pacific Northwest, this model had a low AUC of 0.559 and a high omission rate of 75% ($P > 0.999$). Niche overlap was low between both the native model projected to the non-native range ($D = 0.172$) and the non-native model projected to the native range ($D = 0.277$). Niche equivalence was rejected for both comparisons ($P < 0.01$), supporting a Grinnellian niche shift. Overlap between the native range model projected to the non-native range was not more different or more similar than expected given the climatic conditions available in Japan, making niche shift or conservatism difficult to demonstrate owing to the

distribution of climatic conditions available in the non-native background (Warren et al. 2008; Fig. 1). By contrast, overlap between the non-native range model projected to the native range was more different than expected given the climatic conditions available in the Pacific Northwest of North America ($P < 0.01$).

Eltonian niche

Evaluation of stable isotope data supported conservatism of the Eltonian niche between the native and non-native ranges of *P. leniusculus*. There was no significant difference in trophic niche width of *P. leniusculus* between native and non-native range lakes (Wilk's lambda $F_{3,5} = 0.258$, $P = 0.853$; Fig. 3). We also found no difference in mean trophic position or $\delta^{13}\text{C}$, or their slopes by lake area, between native and non-native range lakes (all ANCOVAs $F \leq 0.227$, $P \geq 0.654$). Allochthonous and autochthonous energy sources had significantly different $\delta^{13}\text{C}$ values (Mann-Whitney $U = 126$, $P < 0.001$), with autochthonous energy sources enriched in $\delta^{13}\text{C}$ relative to allochthonous sources (Fig. 4). Crayfish $\delta^{13}\text{C}$ increased significantly with lake area ($r = 0.849$, $P = 0.003$), indicating a greater reliance on autochthonous energy sources in large lakes and a greater reliance on allochthonous energy sources in small lakes (Fig. 4). Trophic position of

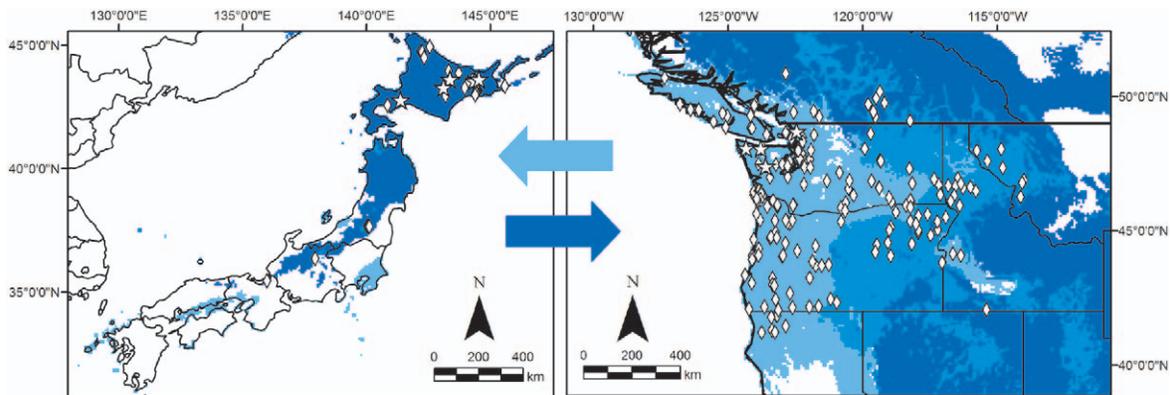


Fig. 2. Maxent model results supporting Grinnellian niche shift between the native (Pacific Northwest of North America) and non-native (Japan) ranges of the signal crayfish *Pacifastacus leniusculus*. Diamonds represent occurrences used to develop models, and stars represent locations of study lakes for tests of Eltonian niche conservatism (also in Fig. 1). Light shading in both ranges represents expected occupancy by minimum training presence threshold for the Maxent model developed using native occurrences and 11 bioclimatic variables (Fig. 1), while dark shading represents the same for the model developed using non-native occurrences. Intermediate shading represents overlap between the two models.

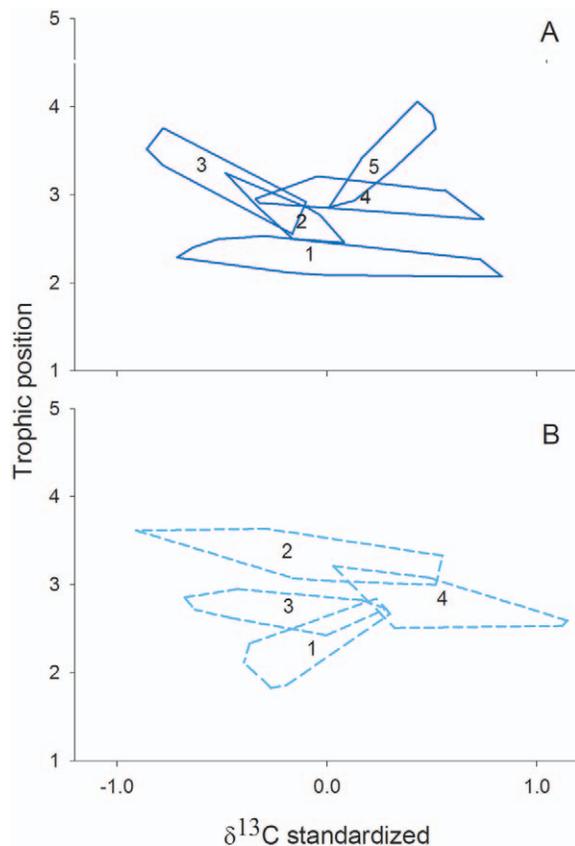


Fig. 3. The trophic niche of *Pacifastacus leniusculus* ($n = 14\text{--}16$ per lake) from five lakes in its (A) non-native range (Hokkaido, Japan) and four lakes in its (B) native range (Washington State, USA) represented as convex hull polygons on $\delta^{13}\text{C}$ (standardized to each lake community) and trophic position. Centroids of each polygon are labeled with numbers in ascending order of lake area (km^2) as follows: A1, Oketo (2.1); A2, Shikaribetsu (3.4); A3, Mashu (19.6); A4, Shikotsu (78.8); A5, Kussyaro (79.5); B1, Pleasant (2.0); B2, Wynoochee (4.6); B3, Whatcom (20.2); B4, Crescent (20.3).

P. leniusculus increased marginally with lake area ($r = 0.616$, $P = 0.078$; Fig. 3). Sex was not a significant determinant of trophic position or $\delta^{13}\text{C}$ (all ANCOVAs $F \leq 1.927$, $P \geq 0.188$), but consistent patterns of ontogenetic niche shifts were evident regardless of range (Fig. 5). Although not significant for all lakes, we found consistent evidence that increasing *P. leniusculus* body size corresponded with increasing trophic position and decreasing $\delta^{13}\text{C}$ (Fig. 5). There was

no significant difference in direction of these ontogenetic niche shifts between ranges based on t -tests of regression slopes (both $P \geq 0.430$).

DISCUSSION

We found strong empirical support for a Grinnellian niche shift but contrasting Eltonian niche conservatism in an arthropod generalist between its native and non-native ranges. Climatic conditions supporting populations of *P. leniusculus* in its non-native Japanese range differed dramatically from those in its North American native range, as demonstrated by multivariate statistical analyses and reciprocal species distribution models. *Pacifastacus leniusculus* shifted from warmer temperatures with strong precipitation seasonality in western North America to cooler temperatures with less precipitation seasonality in Japan. The reciprocal comparison of the non-native Grinnellian niche to the native range predicted that *P. leniusculus* should occur at higher elevations and more interior locations in North America than it is known to occupy. By contrast, the functional role of *P. leniusculus* was consistent regardless of geographic region. *Pacifastacus leniusculus* spanned multiple food chain positions and a wide range of carbon sources within individual lakes and between lakes in both non-native Hokkaido and native Washington State. As such, we conclude that the Grinnellian and Eltonian niches are decoupled in *P. leniusculus*, as this arthropod generalist has shifted into novel non-native range environmental conditions while simultaneously conserving its native range trophic function.

Our finding of a Grinnellian niche shift in *P. leniusculus* supports a rapidly growing literature on this subject. For example, Broennimann et al. (2007) found a shift in the climatic niche of an invasive plant between its European native range and North American non-native range, and Medley (2010) similarly identified climatic niche shifts across continents in the mosquito *Aedes albopictus*. Such niche shifts are the product of either expansion of the realized niche into a broader fundamental niche or alternatively a change in the boundary of the fundamental niche itself (reviewed in Pearman et al. 2008, Alexander and Edwards 2010). Shifts in the realized niche

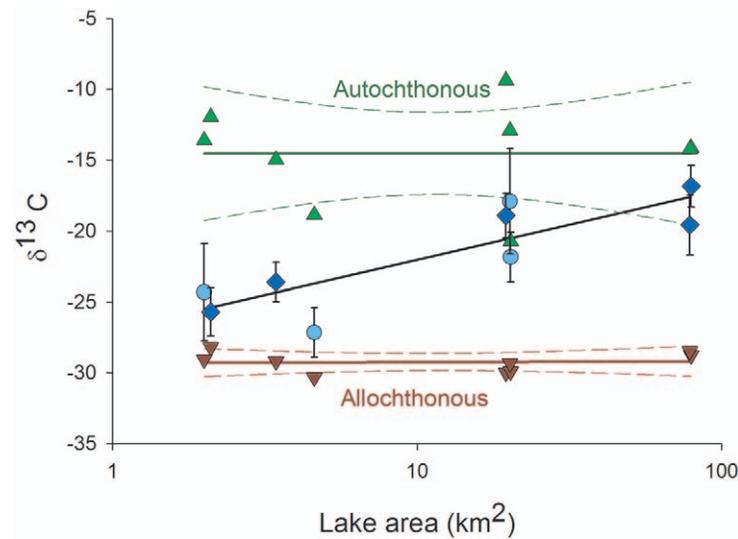


Fig. 4. *Pacifastacus leniusculus* mean $\delta^{13}\text{C}$ (SD) from native (circle) and non-native (diamond) lakes related to lake area (log km^2), with mean $\delta^{13}\text{C}$ for allochthonous (down triangle) and autochthonous (up triangle) basal resources from each lake. Regression lines (95% CI) on basal resources demonstrate consistency across range and lake size, and significant regression line ($r = 0.849$, $P = 0.003$) on *P. leniusculus* mean $\delta^{13}\text{C}$ from both ranges demonstrates shift from reliance on allochthonous to autochthonous energy sources with increasing lake size.

may be attributable to transport over historical dispersal barriers (e.g., oceans, mountain ranges, etc.) or ecological effects like release from native range competitors, parasites, or predators during the invasion process (e.g., Liu and Stiling 2006). Shifts in the fundamental niche may be attributable to evolutionary mechanisms such as founder effects, rapid adaptation, or novel genetic combinations in invasive populations (e.g., Lavergne and Molofsky 2007). Because Grinnellian and Eltonian niches are often treated as equivalent (Soberón 2007, Colwell and Rangel 2009), we predicted that the niche attributes of place and function would behave synchronously. For example, a Grinnellian niche shift into unfavorable new environmental conditions after invasion might correspond with contraction of the Eltonian niche owing to physiological stress or an altered life history strategy. Conversely, a Grinnellian niche that has expanded dramatically owing to ecological release from natural enemies might correspond with expansion of the Eltonian niche as the species capitalizes on fewer biotic constraints on resource use.

Contrary to these predictions, we failed to document any shift in the functional niche of *P. leniusculus*, whether expansion or contraction,

under climatic conditions unlike those encountered in its native range. Instead, a reciprocal comparison of the Eltonian niche of *P. leniusculus* supported the niche conservatism hypothesis. Whether in Japan or North America, *P. leniusculus* exhibited a broad reliance on allochthonous or autochthonous energy sources and differences in trophic position in response to both lake area and crayfish size (ontogenetic shifts). These findings demonstrate that the well-documented generalist Eltonian niche of *P. leniusculus* from its non-native range is not an artifact of the invasion process but rather an innate attribute of this species even in its native range. This finding supports the hypothesis that generalist species are well-equipped to be successful invaders (Jeschke and Strayer 2006, Snyder and Evans 2006), while simultaneously challenging the assumption of equivalence between the Grinnellian and Eltonian niche. We hypothesize that this latter contradiction can be explained by the realized and fundamental Eltonian niches of *P. leniusculus* being effectively congruent in the native range, while the realized Grinnellian niche of this species is instead restricted to a small fraction of the fundamental niche due to geographical dispersal barriers that become irrele-

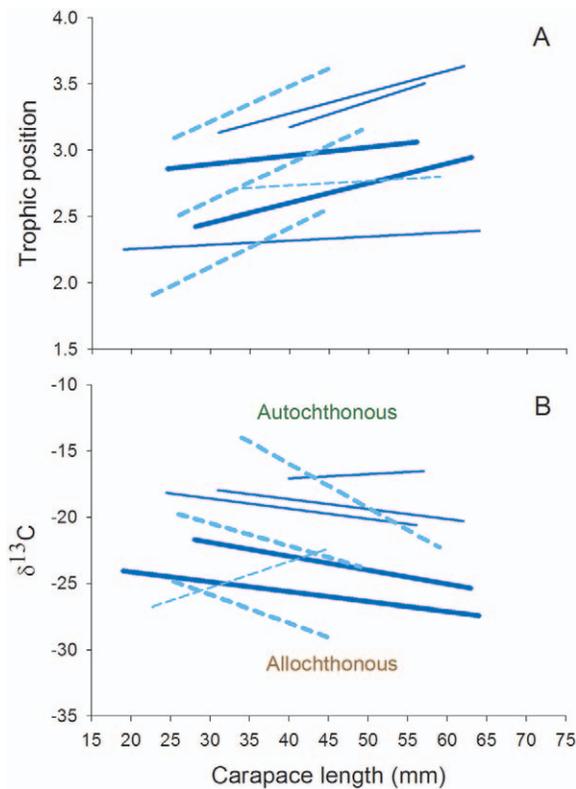


Fig. 5. Regression lines (bold lines significant at $\alpha = 0.05$) representing ontogenetic niche shifts in (A) trophic position and (B) $\delta^{13}\text{C}$ by size (mm carapace length) in *Pacifastacus leniusculus* from lakes in its non-native (solid line) and native (dashed line) ranges.

vant during the invasion process. As a result, we conclude that the ecological function of *P. leniusculus* is predictable across disparate geographic regions even though the geographic regions that can be occupied by *P. leniusculus* may not be predictable from knowledge of its native range only.

At present, our limited understanding of species functional roles between native and non-native ranges prohibits a generalization of whether the Grinnellian or Eltonian niche is more prone to conservatism or shifts (Soberón 2007). Resolving this question demands additional reciprocal studies of the Eltonian niche to keep pace with the near-exponential growth of such work on the Grinnellian niche (Hierro et al. 2005, Elith and Leathwick 2009). Emerging methodologies suitable for measuring the Eltonian niche offer a promising means to accomplish this

(Layman et al. 2007a, b), and likely bear no greater assumptions or limitations than those documented for the species distribution models applied to Grinnellian niche studies (Schmitz et al. 2003, Elith and Leathwick 2009). We expect that Grinnellian niches may be more prone to shifts than Eltonian niches because functional roles may be more rigidly defined by morphology, physiology, and phylogeny than species ranges, which can be strongly influenced by historical factors such as geographic barriers to dispersal. Accordingly, the dispersal ability of species could dictate the degree to which Grinnellian and Eltonian niches can be decoupled. Vagile species may exhibit more consistency between Grinnellian and Eltonian niche conservatism because of their greater capacity to overcome geographic barriers and subsequently increase similarity between the realized and fundamental Grinnellian niche. By contrast, dispersal-limited species, such as many freshwater organisms constrained by the hard boundaries of river drainages rather than soft gradients of climate (Olden et al. 2010), may have a greater disparity between the realized and fundamental Grinnellian niche even if they possess perfect congruence between the realized and fundamental Eltonian niche.

Researchers have only recently begun investigating the functional role of *P. leniusculus* in its native range, where they have failed to document or detect the negative impacts associated with *P. leniusculus* in its non-native range (Pintor et al. 2008, Bondar and Richardson 2009). Invasion biologists attribute this consistent disparity between native and non-native ranges to either intrinsic changes to invasive species during the introduction and establishment processes (rapid adaptation, ecological release) or lack of coevolution with the invader in the receiving community (Salo et al. 2007). Our results support the latter hypothesis as we demonstrated comparable trophic role of *P. leniusculus* in lakes of its native and non-native ranges. Receiving species, communities, and ecosystems that did not evolve with invasive arthropod generalists may simply be vulnerable to their introduction and novel function (Snyder and Evans 2006). However, even arthropod generalists can differ dramatically in niche width, as stable isotope analysis was used to demonstrate a substantially narrower

trophic niche in the native European crayfish *Astacus astacus* relative to populations of invasive *P. leniusculus* (Olsson et al. 2009). Taken together, the broad but conserved Eltonian niche and labile Grinnellian niche of *P. leniusculus* may explain the capacity of this species to have impacts as an invasive species even adjacent to its native range in North America. When introduced to California, *P. leniusculus* contributed to declines and even a possible extinction of other crayfish species (Hobbs et al. 1989, Light et al. 1995). Reciprocal models of the Grinnellian niche of *P. leniusculus* demonstrate that this species has capacity to expand its current range in both Japan and North America, where its broad Eltonian niche would likely lead to further impacts on native populations, communities, and ecosystems.

Tests of the niche conservatism hypothesis are complicated by the long history and rich diversity of ideas associated with the niche concept. For example, Hutchinson's (1957) model of the niche as an "n-dimensional hypervolume" makes falsification of niche shifts difficult, as no study is likely to simultaneously incorporate all niche dimensions where a shift may occur (Rosenfeld 2002). Furthermore, studies of the Grinnellian and Eltonian niche are no more immune to the scale issues of extent and grain than any other inquiry in ecology (Wiens 1989, Devictor et al. 2010). Our analysis was conducted at a broad geographic extent that necessitated coarse grains of climate attributes and general trophic patterns represented by stable isotopes. Studies conducted at a finer grain could produce different results. For the Grinnellian niche, this might mean evaluating habitat use and environmental tolerances of an organism at the scale of site (e.g., individual lakes) that can be difficult to generalize over large geographic extents due to the scarcity of suitable datasets. Similarly, some ecologists have criticized stable isotopes as a methodology for characterizing the Eltonian niche, arguing that the approximation of trophic function offered by our approach lacks adequate resolution (Hoeinghaus and Zeug 2008). By contrast, we believe that the repeated success of this methodology in distinguishing differences between functionally similar species and trophic shifts within the same species validates the ability of stable isotopes to characterize the

Eltonian niche (Layman et al. 2007b, Olsson et al. 2009).

To date, research on invasive species has prioritized applied management issues aimed at preventing or minimizing ecological and economic impacts. This represents something of a missed opportunity to use species invasions as experiments testing ecological and evolutionary theory, including the niche conservatism hypothesis (Wiens and Graham 2005, Sax et al. 2007, Pearman et al. 2008). This has primarily been accomplished via species distribution modeling evaluating only the Grinnellian niche (e.g., Broennimann et al. 2007, Medley 2010). Although the distinction between Eltonian and Grinnellian niches is often assumed to be semantic (Chase and Leibold 2003, Colwell and Rangel 2009), we believe that function is being neglected in favor of evaluating niche conservatism purely through place on the landscape. By contrast, we provide a persuasive example of decoupled conservatism of the Grinnellian and Eltonian niches of a major invasive arthropod, which we hope will serve as a template and inspiration to much-needed similar studies.

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