

Combined modelling of distribution and niche in invasion biology: a case study of two invasive *Tetramorium* ant species

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ABSTRACT

Spatial modelling of species distributions has become an important tool in the study of biological invasions. Here, we examine the utility of combining distribution and ecological niche modelling for retrieving information on invasion processes, based on species occurrence data from native and introduced ranges. Specifically, we discuss questions, concerning (1) the global potential to spread to other ranges, (2) the potential to spread within established invasions, (3) the detectability of niche differences across ranges, and (4) the ability to infer invasion history through data from the introduced range. We apply this approach to two congeneric pavement ants, *Tetramorium* sp.E (formerly *T. caespitum* (Linnaeus 1758)) and *T. tsushimae* Emery 1925, both introduced to North America. We identify (1) the potential of both species to inhabit ranges worldwide, and (2) the potential of *T. sp.E* and *T. tsushimae*, to spread to 23 additional US states and to five provinces of Canada, and to 24 additional US states and to one province of Canada, respectively. We confirm that (3) niche modelling can be an effective tool to detect niche shifts, identifying an increased width of *T. sp.E* and a decreased width of *T. tsushimae* following introduction, with potential changes in niche position for both species. We make feasible that (4) combined modelling could become an auxiliary tool to reconstruct invasion history, hypothesizing admixture following multiple introductions in North America for *T. sp.E*, and a single introduction to North America from central Japan, for *T. tsushimae*. Combined modelling represents a rapid means to formulate testable explanatory hypotheses on invasion patterns and helps approach a standard in predictive invasion research.

Keywords

Biological invasions, distribution modelling, ecological niche modelling, invasion history, niche shift, spread of invasion.

INTRODUCTION

Predictive modelling based on the correlation of environmental data with occurrence data of a species has become a central tool in invasion research (Thuiller, 2007). To date, much of the work has focused on predicting species distributions (e.g. Loo *et al.*, 2007), with less attention being paid to the ecological niche itself (but see, e.g. Mau-Crimmins *et al.*, 2006; Roura-Pascual *et al.*, 2006). Recently, though, the importance of explicitly considering niches when predicting distributions was indicated by work showing that niches can considerably differ between different ranges of invasive species (Mau-Crimmins *et al.*, 2006; Broennemann *et al.*, 2007; Fitzpatrick *et al.*, 2007).

Here, we propose to combine modelling of both distribution and ecological niche to further understanding of overarching patterns of the invasion process, including future spreads, present niche characteristics, and dynamics of historical invasions. We base models on data from the native, the introduced, and combined ranges. We address the four following questions.

1 What is the potential for spread to other regions? Biotic exchange occurs on a global scale and identification of the regions where an invasive species will indeed be able to survive once it has arrived is paramount (Thuiller, 2007).

2 What is the potential for spread beyond current distribution limits within established invasions? Once an introduced species has established a population it becomes essential to identify the

areas in the introduced range that it will potentially inhabit (Mau-Crimmins *et al.*, 2006).

3 Can comparisons between native and introduced ranges of an invasive species provide evidence for present differences in ecological niches? Such differences would be meaningful for predictions as well as provide insight into evolutionary trajectories of niches. Exploring niche evolution empirically is comparatively new (e.g. Urban *et al.*, 2007) but relevant in the face of rapid global environmental change (Thuiller, 2007).

4 Can we determine the characteristics of the invasion history of introduced populations based on data from a species' introduced range? Determining the number and identity of source populations is essential to guide management strategies and also provides an appropriate reference for detecting adaptation to new environments; both of these goals are key to invasion research (e.g. Frankham, 2005). Neither niche nor distribution modelling have been used to explore historical invasion dynamics.

We explore the approach of combined modelling for answering these questions through a case study on two Palaearctic *Tetramorium* ants invasive in North America. This study system is relevant in that in-depth analysis of the invasion potential of the species is needed due to the increasing impact they threaten to impose on native North American ecosystems (Steiner *et al.*, 2006b), and possibly other regions. The recent clarification of taxonomic problems and establishment of identification routines (as outlined in Schlick-Steiner *et al.*, 2006; Steiner *et al.*, 2006a,b) minimize identification errors, and the species' biogeographies are well explored (Schlick-Steiner *et al.*, 2006; Steiner *et al.*, 2006b). Finally, opportunities of comparative analysis arise as the two species are subject to similar phylogenetic and ecological constraints (Sanada-Morimura *et al.*, 2006; Schlick-Steiner *et al.*, 2006; Steiner *et al.*, 2006b).

METHODS

The organisms

Tetramorium sp.E (formerly *T. caespitum* (Linnaeus 1758)) and *T. tsushimae* Emery 1925 have been introduced to North America from the Western and the Eastern Palaearctic, respectively. *Tetramorium* sp.E was introduced in the 19th century or earlier and has spread over the continent (Brown, 1957). *Tetramorium tsushimae* was probably introduced in the first half of the 20th century and is currently known from Missouri and Illinois, USA (Steiner *et al.*, 2006b). In North America the species are agricultural pests (*T. sp.E*: Merickel & Clark, 1994; *T. tsushimae*: J.C. Trager, pers. comm.), displacing native ants, and expanding into natural habitats (*T. sp.E*: G. Alpert, J.T. Longino, L. Rericha, P.S. Ward, A. Wild, pers. comm.; *T. tsushimae*: Steiner *et al.*, 2006b).

Samples

Samples were collected by the authors or obtained through a collector network coordinated by the first two authors (see Acknowledgements). We compiled 210 samples, stemming in roughly equal proportions from the native and introduced

Table 1 Sample sizes, 'balance' threshold values, and results of receiver operating characteristic (ROC) analysis expressed as area under the curve values, for *Tetramorium* sp.E and *T. tsushimae*, based on native, introduced, and combined data.

	Sample sizes		Threshold values		ROC	
	<i>T.</i> sp.E	<i>T.</i> <i>tsushimae</i>	<i>T.</i> sp.E	<i>T.</i> <i>tsushimae</i>	<i>T.</i> sp.E	<i>T.</i> <i>tsushimae</i>
Native	48	63	1.442	2.059	0.990	0.994
Introduced	54	45	1.797	0.213	0.983	1.000
Combined	102	108	2.383	2.435	0.985	0.996

ranges (Table 1). Of *T. sp.E*, we had samples from 15 Western Palaearctic countries, two provinces of Canada, and 26 states of the USA. Of *T. tsushimae*, we had samples from four Asian countries and two US states. For all ranges and species, the sampled habitats ranged from strongly human-modified to natural. Twenty-four percent of the samples were published in Schlick-Steiner *et al.* (2006), a further 15% in Steiner *et al.* (2006b), with the remaining 61% being novel occurrence information.

Both species were long regarded as *T. caespitum*; therefore, only identifications achieved after the taxonomic clarifications (Schlick-Steiner *et al.*, 2006; Steiner *et al.*, 2006b) were used in this study. We identified samples via mitochondrial DNA sequencing using cytochrome c oxidase subunit 1 (*cox1*), a gene of proven worth in identification of *Tetramorium* species (Steiner *et al.*, 2005), and classificatory discriminant analysis (SAS Institute, 2004) of morphometric data using Cyber Identification Engine, <http://homepage.boku.ac.at/h505t3/DiscTet/> (Steiner *et al.*, 2006a). Vouchers are deposited at the Institute of Forest Entomology, Forest Pathology and Forest Protection, Boku, Vienna.

Modelling

We used the program Maxent (Phillips *et al.*, 2006) for all distribution modelling. Maxent is based on a maximum entropy algorithm for the prediction of species' potential geographical distributions. Maxent has been shown to outperform other techniques traditionally used in distribution modelling (Elith *et al.*, 2006; Hernandez *et al.*, 2006) and was most capable of dealing with small sample sizes when compared with Bioclim, Domain, and GARP (Hernandez *et al.*, 2006). Advantages of Maxent include: the program uses presence only records; incorporates interaction effects of environmental variables; being a deterministic algorithm that always converges to a unique, optimal probability distribution (Phillips *et al.*, 2006); and most recently, when projecting onto a different set of environmental variables (different location or time), areas that fall outside the current conditions are identified (clamped areas) (S.J. Phillips, pers. comm.).

Suitability as part of the species' potential distribution is estimated as a function of the environmental variables for each

cell within a gridded domain (area of interest) and is represented as a continuous cumulative output value ranging from 0 to 100, with higher values indicating a higher probability of finding suitable habitat (Phillips *et al.*, 2006). Converting the cumulative output value Maxent estimates to a binary estimate of potential distribution/not distribution, we chose a threshold that balances false negative predictions in training, predicted area, and cumulative threshold values. For evaluation of model performances we used the threshold independent receiver operating characteristic (ROC) which addresses false negative predictions and false positive predictions. The ROC is quantified by the area under the curve (AUC), with values ranging from 0 to 1 and high values indicating good performance. For external evaluation of model performances, we assessed the number of introduced occurrences that were part of the distribution modelled using native data, and the number of native occurrences that were part of the distribution modelled using introduced data.

We used the geographical coordinates of sample records for all modelling. All relevant records were used for each model. We based models on data from the native range, the introduced range, and the combined ranges for each species separately. From the WorldClim data base (Hijmans *et al.*, 2005), the following 10 climatic variables, plausibly the most relevant to the species (e.g. Sanada-Morimura *et al.*, 2006; Schlick-Steiner *et al.*, 2006), were selected: mean annual temperature, annual temperature seasonality, mean temperature of warmest quarter, mean temperature of coldest quarter, mean annual precipitation, annual precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter. All climatic data layers had a spatial resolution of 1 km². In all models the global environmental space was used as background.

We used Ecological-Niche Factor Analysis (ENFA; Hirzel *et al.* 2002) for characterizing native and introduced niches, based on observed occurrences and modelled pixels (spatial resolution 1 km²) throughout the entire predicted range for each species. ENFA is a modified principal component analysis that compares climatic input data with the background climatic data – here, the species' native or introduced niches with that of the whole globe. ENFA returns values for 'marginality', a measure of niche position quantifying the difference of the input data mean from the background mean, and 'specialization', a measure of niche width quantifying input data variance relative to the background variance. Given identical background environmental space, the values of marginality and specialization for different species are directly comparable. Differing marginality values represent a shift in mean environmental niche used by species, whereas differing specialization represents a shift in the niche width. For ENFA, climatic data were Box–Cox transformed prior to analysis. We tested the significance of differences ($\alpha = 0.05$) in marginality and specialization across niches using Students' *t*-test and Bartlett's homogeneity of variance test, respectively. For visualization purposes, 1000 random numbers were drawn from a Gaussian distribution with a mean and standard deviation equal to that of the marginality and specialization for each of the native and introduced species occurrences and models.

RESULTS

Modelling performance was very good for all six Maxent models as shown by very high AUC values, ranging from 0.983 to 1.000 (Table 1). The cumulative output values corresponding to the balance threshold were low for all models (Table 1). The distribution modelled using native and introduced data combined included areas on six continents for both species (Fig. 1). The introduced distribution modelled using introduced data for both species included areas not covered by records, for *T. sp.E*, from 23 US states (Fig. 2; Alabama, Alaska, Arizona, Arkansas, Connecticut, Delaware, Georgia, Hawaii, Iowa, Kansas, Kentucky, Louisiana, Maine, Mississippi, Montana, New Hampshire, North Dakota, Oklahoma, Rhode Island, South Carolina, South Dakota, Texas, West Virginia) and five provinces of Canada (British Columbia, New Brunswick, Newfoundland and Labrador, Nova Scotia, Prince Edward Island), for *T. tsushimae*, from 24 US states (Arizona, Colorado, Connecticut, Delaware, Idaho, Indiana, Iowa, Kansas, Kentucky, Maryland, Massachusetts, Montana, Nebraska, Nevada, New Jersey, New Mexico, Ohio, Oregon, Pennsylvania, Rhode Island, Utah, Victoria, Washington, West Virginia) and one province of Canada (British Columbia). For *T. sp.E*, 51 of 54 introduced occurrences were inside the distribution modelled using native data, and all native occurrences were inside the distribution modelled using introduced data. For *T. tsushimae*, all introduced occurrences were inside the distribution modelled using native data, and 12 out of 63 native occurrences were inside the distribution modelled using introduced data. The native distribution modelled using introduced data included areas not covered by records, for *T. sp.E*, but was confined to a small area in central Japan, well covered by records, for *T. tsushimae* (Fig. 2).

The observed niches of both *T. sp.E* and *T. tsushimae* (Fig. 3) did not differ significantly in position (marginality) across ranges (*T. sp.E*: $t = 0.1485$, $P = 0.8822$; *T. tsushimae*: $t = 1.2431$, $P = 0.2166$), but the modelled niches did (*T. sp.E*: $t = 41.8203$, $P < 0.0001$; *T. tsushimae*: $t = 11.8786$, $P < 0.0001$). The width (specialization) significantly differed across ranges for the observed and the modelled niches (*T. sp.E*: $\chi^2 = 5.8618$, $P = 0.0150$, and $\chi^2 = 547.1076$, $P < 0.0001$, respectively; *T. tsushimae*: $\chi^2 = 115.9660$, $P < 0.0001$, and $\chi^2 = 1222.9777$, $P < 0.0001$, respectively). Both the observed and the modelled introduced niche of *T. tsushimae* significantly differed in position from those of *T. sp.E* ($t = 5.4079$, $P < 0.0001$ and $t = 31.1037$, $P < 0.0001$, respectively) and had a significantly smaller width ($\chi^2 = 167.7135$, $P < 0.0001$ and $\chi^2 = 765.5606$, $P < 0.0001$, respectively), the niche of *T. tsushimae* being a subset of that of *T. sp.E* (Fig. 3).

DISCUSSION

Our combined modelling approach yielded data on distribution and niche of the two pavement ants, based on records from the native range, the introduced range, and the ranges combined. Based on the modelling results we now seek explanatory hypotheses on patterns of the invasion process, and discuss pathways of

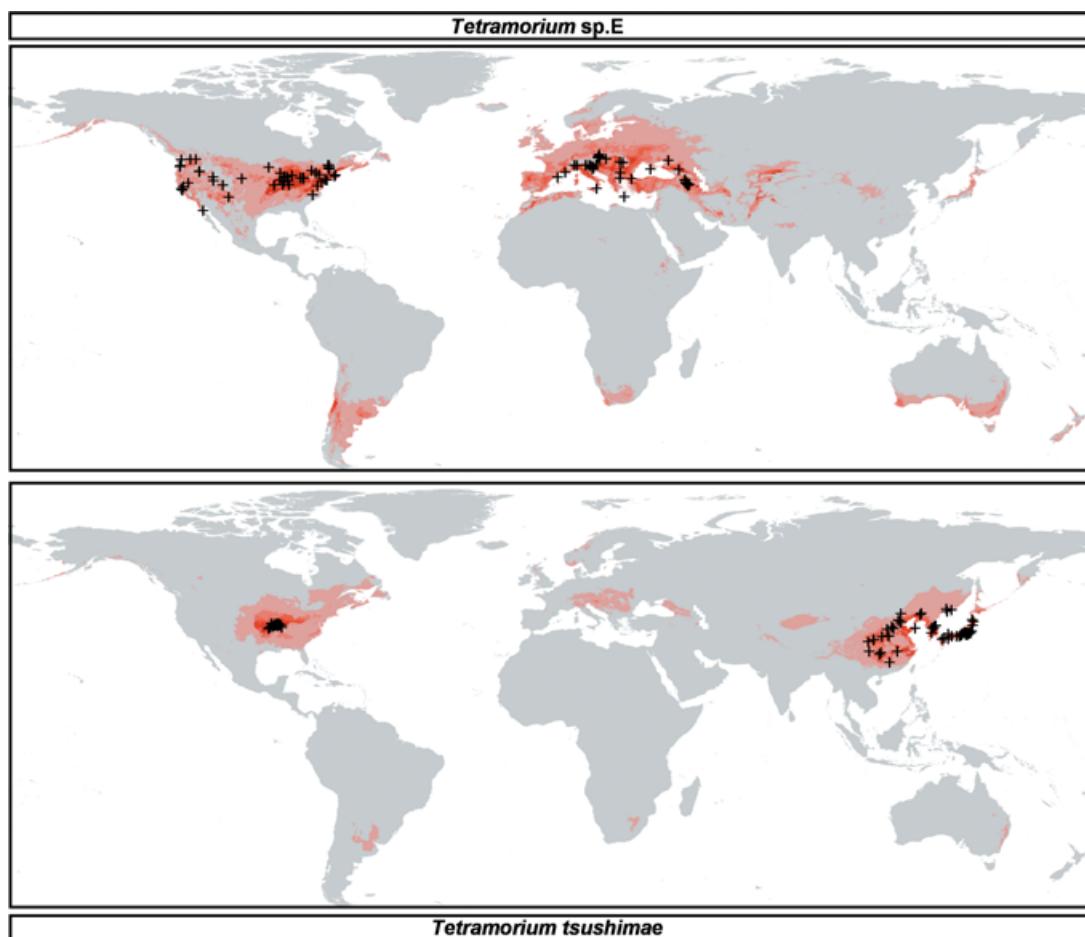


Figure 1 Modelled global distribution of *Tetramorium* sp.E and *T. tsushimae* based on native and introduced occurrences combined. Coloured areas represent the predicted distribution. Darker colours represent areas with better predicted conditions. Crosses indicate data used to build models.

future testing the hypotheses. A precondition for seeking answers to questions (1–4) is that our occurrence data are sufficiently informative on the respective niche: First, sample size needs to be sufficient to represent the niche, and second, for introduced populations, there must have been sufficient time for the population to spread so that the environmental space occupied in the new range indeed is representative of the niche. We are confident that our system fulfils both conditions, because significantly smaller samples have been successfully modelled through Maxent (Hernandez *et al.*, 2006), and because of the age of the introductions (see Methods).

What is the potential for spread to other regions?

To approach this question the distribution modelled by use of native and introduced data combined should be considered to include the maximum information available, which is especially meaningful if niche differences across ranges exist. Both *T. sp.E* and *T. tsushimae* have the potential to become a global threat (Fig. 1). Independent data will be needed for a thorough model validation. Currently we have only two additional records of *T. sp.E* from South America (Valparaiso, Chile, and Buenos Aires,

Argentine; F.M.S., unpubl. data), both sites being part of the modelled distribution.

What is the potential for spread beyond current distribution limits within established invasions?

For answering this question, the modelled distribution based on introduced data alone should be considered, as revealed by recent modelling efforts (Mau-Crimmins *et al.*, 2006; Broennimann *et al.*, 2007; Loo *et al.*, 2007) – in case of niche differences across ranges introduced data will be more informative. Our modelling suggests that *T. sp.E* and *T. tsushimae* have the potential to further spread in their introduced ranges (Fig. 2). On a finer geographical scale, the potential to spread could be affected by abiotic factors not included in our modelling such as urbanization. Also biotic factors could matter, including interspecific competition, and thus for fine-scale prediction, insight into the patterns of potential co-occurrence with competitors in the same habitat is needed. Because distributions modelled using large-scale data such as ours are not informative at that finer scale it could be useful to consider the niches of competing species. In terms of our species pair: the introduced niche of *T. tsushimae* is

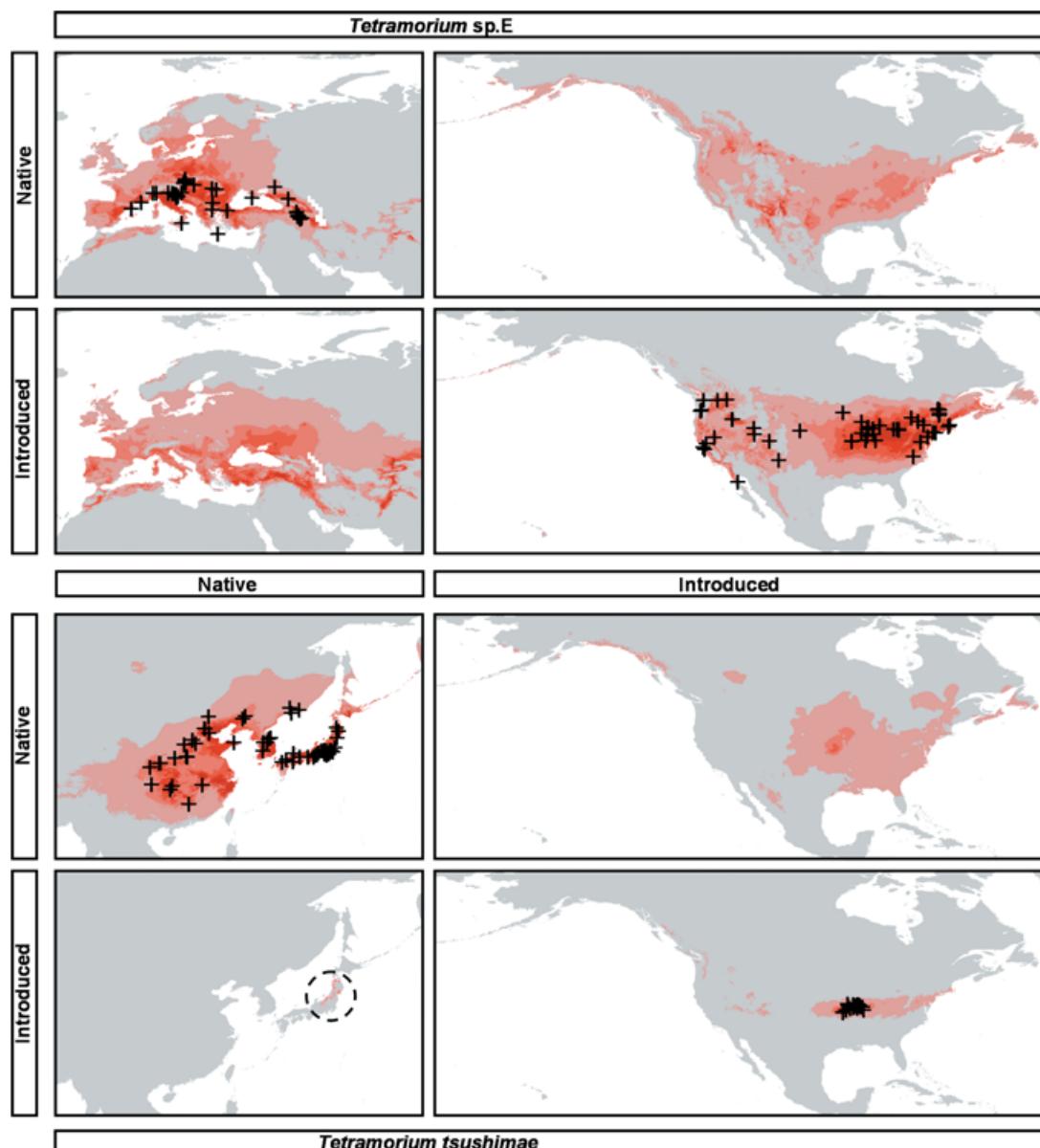


Figure 2 Modelled distributions of *Tetramorium* sp.E and *T. tsushimae* in their native and introduced ranges. Regions used to develop models are in each row, and columns indicate the region to which the model was projected. Coloured areas represent the predicted distributions. Darker colours represent areas with better predicted conditions. Crosses indicate data used to build models. A dashed circle is used to highlight small areas of modelled distribution.

a subset of that of *T. sp.E* (Fig. 3). As *T. tsushimae* is competitively superior to *T. sp.E* (Steiner *et al.*, 2006b), in such habitats only *T. tsushimae* may persist. However, *T. sp.E* may be able to inhabit habitats in the same area which are not part of *T. tsushimae*'s niche.

Can comparisons between native and introduced ranges of an invasive species provide evidence for present differences in ecological niches?

Recent work (Mau-Crimmins *et al.*, 2006; Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007) indicates that modelling may be useful as a rapid means to disclose niche changes, but additional

testing is needed. Modelling the native distribution through introduced data may allow for some insight, but as mentioned above, viewing distributions modelled through large-scale data may be less informative than viewing the niches themselves. Concerning niche width, our ENFA characterizations reveal that the introduced niches significantly differ from the native niches, by an increase in width of the *T. sp.E* niche, and a decrease in *T. tsushimae*. These results are retrieved through both observed and modelled data. Concerning niche position, the observed niches do not differ across ranges. For both species, however, the modelled niches significantly differ in position. It is conceivable that such pattern is, for example, the first sign of a niche shift.

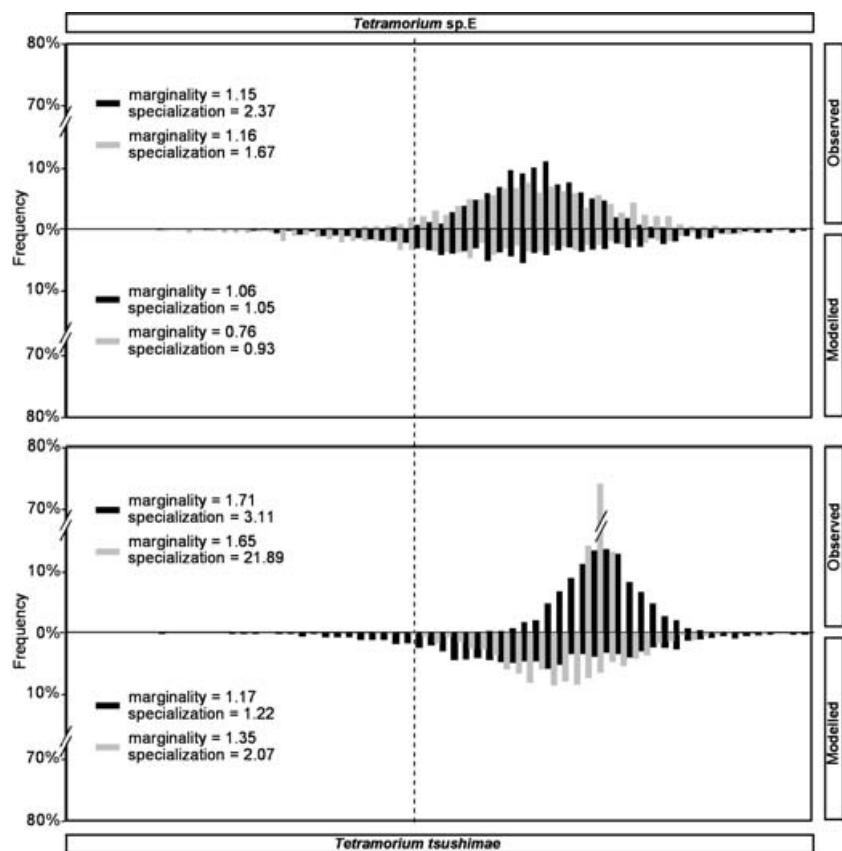


Figure 3 Characterization of the observed and modelled niches of *Tetramorium* sp.E and *T. tsushimae*, in their native (black) and introduced (grey) ranges, relative to the global environmental space. The x-axis spans the entire variance of the global space, from -2.9 to 3.5 standard deviation (SD), the dotted line depicts the mean of the global data. Niches are depicted through frequencies of data points in classes of 0.1 SD, relative to the total of data points per niche. For the native and introduced ranges, frequencies are depicted side by side within classes; frequencies of the global space are omitted. Data represent 1000 random numbers selected from a Gaussian distribution with a mean and SD representing the Ecological-Niche Factor Analysis marginality and specialization of a specific group of interest. Marginality and specialization values are given for all niches (notation following Hirzel *et al.*, 2002).

Clearly, future monitoring and independent cases are needed for validation.

Our results confirm that modelling may be generally applicable for disclosing niche differences across ranges, which could become important in the context of global climate change. But does a difference detected through modelling pertain to the fundamental niche, i.e. the sum of ecological conditions under which an organism can live, or the realized niche, i.e. the ecological conditions an organism actually lives in (Holt *et al.*, 2005)? We approach this challenging question separately for the case that the introduced niche is a subset of the native niche (*T. tsushimae*), and the case that the introduced niche covers parts of the environmental space not included in the native niche (*T. sp.E*). In the first case, the introduced environment could through, e.g. new enemies or new competitors hinder the invasive organism in realizing the complete fundamental niche. If this applies, the detected difference only pertains to the realized niche. Conversely, relevant genetic diversity may have been reduced through introduction, and thus the fundamental niche could be affected which we cannot refute for *T. tsushimae*.

The second case entails the question, how congruent the realized and the fundamental native niches are. One would generally expect them to be reasonably congruent, because evolution under selection is expected to reduce ‘unused’ parts of a fundamental niche – the ecological niche is a set of inherited traits, subject to selective pressure to reduce unused traits (Fong *et al.*, 1995), which notion is supported by theoretical (Holt & Gomulkiewicz, 1997)

and experimental (Cooper & Lenski, 2000; Kassen, 2002) research. If indeed the realized and fundamental native niches are congruent, this would mean that the detected differences across ranges concern the fundamental niche of *T. sp.E*. Possible explanations would include combination of genetic diversity not combined before (Frankham, 2005), and rapid evolutionary processes under the new selective regime in the introduced range (cf. Urban *et al.*, 2007). However, there is empirical evidence that the fundamental and the realized native niche may not always be congruent (Loo *et al.*, 2007). If the fundamental native niche of *T. sp.E* indeed is larger than we could discern through modelling, the observed difference across ranges could pertain to the realized niche exclusively. Such difference would be explicable through ecological release from native enemies and competitors (Holt *et al.*, 2005), or additional ecological heterogeneity in the introduced range (e.g. Loo *et al.*, 2007). We currently cannot distinguish whether we detected differences in the fundamental or the realized niche. Physiological laboratory experiments comparing ants from each range would be most informative to address this issue.

Can we determine characteristics of the invasion history of introduced populations based on data from a species' introduced range?

This question goes beyond established methods. However, modelling could potentially be useful, in that the environmental-space information of an occurrence in the introduced range

should be meaningful regarding the environmental space of the source population. This will only apply, though, if the information is not blurred by processes in the introduced range, like niche evolution. We postulate that, if the introduced niche does not cover environmental space other than that covered by the native niche, the native distribution modelled using introduced data might indicate the number and identity of geographical origin(s) of introduced populations. Such inferences will depend on the specialization of the source population relative to the fundamental niche of the species as a whole. Source populations specialized to a subset of the species' fundamental niche, such as hypothesized here with *T. tsushimae*, would be easier to detect using modelling techniques as utilized in this study; the applicability of such techniques may be reduced by processes such as admixture following multiple introductions or rapid evolution changing niche position (though within the environmental space of the native niche), and those problems could increasingly apply with increasing age of the introduction. Future testing is needed to evaluate how strongly precision can be affected by such problems.

The native distribution of *T. tsushimae* modelled using introduced data is confined to central Japan (Fig. 2). Hence, we hypothesize a single introduction from central Japan. This is in agreement with deductions from *cox1* data (Steiner *et al.*, 2006b): Two haplotypes were found in the USA, both otherwise known from central Japan only (Steiner *et al.*, 2006b). As *T. tsushimae* is multiple-queened, two *cox1* haplotypes do not conflict the introduction of a single colony, especially so as both haplotypes co-occur within the same Japanese habitat (Steiner *et al.*, 2006b).

In *T. sp.E*, the introduced niche covers environmental space not covered by the native niche (Fig. 3) which renders retrieving information on number and identity of source populations futile. Given that multiple introductions are indicated by independent evidence (two *cox1* haplotypes of the single-queened ant in the USA, not co-occurring natively, Schlick-Steiner *et al.*, 2006; populations of *T. sp.E*'s European obligate social parasite *Anergates atratulus* (Schenck 1852) in the USA, Brown, 1957, very rare in its native range) modelling still provides useful information into invasion history, despite the increase in niche width. Potentially, the native distribution modelled using introduced data which embraces the native distribution modelled using native data (Fig. 2) could indicate that admixture followed multiple introductions. Although speculative, admixture could account for the detected increase in niche width – it may have altered relevant genetic information through new allelic combinations (Frankham, 2005). The hypothesis of admixture will be tested through ongoing population genetic analysis.

We conclude that exploring invasion history through modelling using data from the introduced range may be a valuable auxiliary tool in invasion research in at least some cases. However, modelling-based hypotheses on invasion history need to be tested independently. In practical terms, our approach could be advantageous in that, whenever regions of origin are hypothesized, population genetic can start with sampling from just a part of the native range.

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