RESEARCH PAPER

Response of non-native European terrestrial gastropods to novel climates correlates with biogeographical and biological traits

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ABSTRACT

Aim Anticipating the propensity of species to persist outside the climatic conditions in which they are observed is important in assessing the uncertainty in climate-matching when applied to different locations or times. By using data from 27 European terrestrial gastropods (slugs and snails) established in new regions, we measured (1) the degree of climate match between native and non-native ranges and (2) the diversity of novel climatic conditions inhabited. We then tested for species traits as predictors of the patterns found.

Location Worldwide.

Methods We projected the occurrences of each species onto the climatic space defined by the two main axes of a principal components analysis. On the basis of the convex hull of native occurrences, we measured the proportion of non-native occurrences in novel climates and the diversity of the newly occupied climates. Generalized estimating equations were used to test for associations between climatic responses and species traits, while considering phylogenetic relatedness and introduction effort.

Results Approximately half of the species had a large proportion (> 25%) of non-native occurrences in novel climates. Climate mismatch was significantly higher for species with narrow native climatic niches, native ranges elongated in a north–south direction or native ranges with the southern limit at lower latitudes. Slugs occupied a higher diversity of novel climatic conditions than snails.

Main conclusions Climate matching showed varying levels of accuracy in predicting the non-native ranges of the studied species. Lower accuracy appeared to be mainly related to low levels of distributional equilibrium in native ranges. In addition, coarse-scale predictions for species that are able to take advantage of microclimatic variability – as appears to be the case with slugs – may be challenging. We conclude that species traits can contribute to understanding uncertainties in climate-matching exercises.

Keywords

Climate matching, climatic niche, global change, invasive species, niche conservatism, risk assessment, species traits, terrestrial gastropods.

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INTRODUCTION

Climatic requirements play a crucial role in shaping species' distributions (Gaston, 2003). Consequently, many researchers have attempted to predict the potential spread of invasive species or the response of biodiversity to climate change by matching the climatic conditions in which species are observed to the conditions in new areas or time periods. Several studies

have shown reliable results for this approach (e.g. Thuiller *et al.*, 2005; Hayes & Barry, 2008; Guo *et al.*, 2012), but recent analyses of large-scale biological invasions have shown that several species have become naturalized in novel climatic conditions (e.g. Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Capinha *et al.*, 2013). These idiosyncratic occurrences reduce the reliability of correlative approaches for predicting invasion risk or biodiversity change (Pearman *et al.*, 2008) and underscore the need for a better understanding of the circumstances and mechanisms that affect the ability of non-native species to persist in novel climates (Pearman *et al.*, 2008; Alexander & Edwards, 2010).

Underlying the climate-matching approach is the assumption that, in the absence of source–sink dynamics, the environmental conditions in which a species is observed (i.e. the realized niche, *sensu* Soberón & Nakamura, 2009) provide a reliable representation of the set of abiotic conditions in which it can maintain self-sustaining populations (i.e. the fundamental niche). Because of limited dispersal abilities or negative biotic interactions, however, the realized niche is often a subset of the fundamental niche (Araújo & Pearson, 2005). In addition, a species' fundamental niche may include conditions that do not exist in the landscape. Therefore, even if distributional equilibrium occurs (i.e. the full range of existing suitable conditions is occupied), the fundamental niche may still not be fully inhabited (Soberón & Nakamura, 2009; Barve *et al.*, 2011; Jiménez-Valverde *et al.*, 2011). Finally, evolutionary mechanisms – such as genetic drift or local adaptation – may modify the species' ecophysiology, allowing some populations to survive in otherwise unsuitable conditions (Alexander & Edwards, 2010; Hoffmann & Sgrò, 2011). Either independently or in combination, the above factors can cause correlative prediction methods to underestimate the ability of species to cope with novel climates.

Assuming that the processes that limit the distribution can be identified, the use of models based on ecophysiology (i.e. mechanistic models) may improve the robustness of predictions, particularly if used in combination with climate-matching (Kearney *et al.*, 2010). Because mechanistic models can be complex and time-consuming, however, their application for large-scale assessments remains impracticable. Alternatively, the identification of indicators of species' responses to novel climates can be examined (Pearman *et al.*, 2008). Species traits, either extrinsic or intrinsic, may indicate the tendency of species to conserve or shift their realized or fundamental climatic niches (Lavergne & Molofsky, 2007; Pyšek *et al.*, 2009; Alexander & Edwards, 2010). For instance, species with low competitive or dispersal abilities are often associated with low levels of distributional equilibrium (e.g. Svenning & Skov, 2007), whereas high phenotypic plasticity in traits related to climate adaptation may favour the ability of species to persist in novel climates (Hoffmann & Sgrò, 2011). If consistent associations are observed between variables representing the above or other important mechanisms and patterns of changes in climatic niches, then justifiable levels of confidence can be assigned to agreeing or disagreeing correlative predictions. Despite the potential value of such indicators, the relationship between the ability to survive in novel climates and species traits remains largely untested, particularly for invasive fauna (but see Strubbe *et al.*, 2013, for a recent example with birds).

In this study, we evaluate the propensity of 27 European terrestrial gastropods to become established in novel climates in non-native ranges. This group of species is particularly appropriate for our study because they were introduced to their non-native ranges by different routes (e.g. unintentional introduction through horticultural or agricultural import, intentional introduction as biological control agents, or intentional introduction and cultivation for human consumption) and have a long history of introduction into many climatically distinct regions of the world (Cowie, 2011). Moreover, terrestrial gastropods are desiccation-prone ectotherms and are expected to be particularly responsive to climatic conditions (Heller, 2001; Luchtel & Deyrup-Olsen, 2001). We initially determined whether the non-native populations were established in native-like or novel climates. We also classified the newly colonized climates into four types – colder and drier, colder and wetter, warmer and drier, or warmer and wetter than the climate in the species' native range. We tested a set of ecological and biological traits, considering phylogenetic relatedness and introduction effort, as predictors of (1) the proportion of non-native populations in novel climatic conditions, (2) the presence or absence of non-native populations in each of the novel climatic types, and (3) the total number of novel climate types inhabited. Our aim was to identify traits that may serve as indicators of species' responses to novel climatic conditions that, in turn, may be used to complement predictions of correlative species distribution models applied across space or time.

METHODS

Species selection and distribution data

To select suitable species for our study, we created a list of native European terrestrial gastropods with naturalized ranges (after the year 1500) based on two online databases (White-McLean, 2011; AnimalBase Project Group, 2012). We excluded species for which gene sequence data appropriate for phylogeny reconstruction was not publicly available (see 'Phylogenetic relatedness' section; see also flow-chart in Appendix S1 for the full list of species and a schematic representation of all selection criteria). Frequently misidentified species (cf. White-McLean, 2011) were excluded to reduce the number of taxonomic errors in the distribution data. For the remaining species, we collected native and non-native occurrence data from multiple sources, including monographs, research papers and online databases (Appendix S2). We restricted our searches to observations made after 1950 (the period for which climatic data were obtained; see below).

We collected three forms of data – geographical coordinates, mapped occurrences and names of locations where specimens were found. We assessed the positional accuracy of the coordinates by projecting them onto a global map in ArcGIS. Records

Table 1 Patterns of establishment under novel climatic conditions of 27 species of European terrestrial gastropods. 'Proportion' refers to the percentage of non-native populations falling outside the native climate space. The percentage of non-native populations outside the climate space realized in the native range but still within climatic conditions potentially available in the native region is given in parentheses. Columns from 'colder and drier' to 'warmer and wetter' indicate the presence of non-native populations in that novel climatic setting. The column 'any change' refers to the existence on non-native population in any of the previous conditions. The column 'diversity' corresponds to the sum of novel types of climatic conditions occupied.

Species	Proportion (%)	Colder and drier	Colder and wetter	Warmer and drier	Warmer and wetter	Any change	Diversity
Arianta arbustorum (Linnaeus, 1758)	0.0	no	no	no	no	no	0
Arion intermedius (Normand, 1852)	38.9 (9.9)	no	yes	yes	yes	yes	3
Cepaea hortensis (Müller, 1774)	0.0	no	no	no	no	no	0
Cepaea nemoralis (Linnaeus, 1758)	0.0	no	no	no	no	no	0
Cernuella virgata (Da Costa, 1778)	3.7 (3.7)	no	no	no	no	no	0
Chilostoma cingulatum (Studer, 1820)	0.0	no	no	no	no	no	0
Cochlicella acuta (Müller, 1774)	40.7 (3.7)	no	no	no	yes	yes	1
Cornu aspersum (Müller, 1774)	27.6 (9.5)	no	yes	yes	yes	yes	3
Deroceras reticulatum (Müller, 1774)	34.2 (10.9)	yes	yes	yes	yes	yes	4
Discus rotundatus (Müller, 1774)	0.0	no	no	no	no	no	0
Eobania vermiculata (Müller, 1774)	33.3 (6.6)	no	no	no	yes	yes	1
Helix lucorum Linnaeus, 1758	3.3 (3.3)	no	no	no	no	no	0
Helix pomatia Linnaeus, 1758	0.0	no	no	no	no	no	0
Hygromia cinctella (Draparnaud, 1801)	5.0 (3.8)	yes	no	no	no	yes	1
Lauria cylindracea (Da Costa, 1778)	3.7 (3.7)	no	no	no	no	no	0
Limacus flavus Linnaeus, 1758	52.1 (8.3)	no	yes	yes	yes	yes	3
Marmorana serpentina (Férussac, 1821)	60.0 (10.0)	no	no	no	yes	yes	1
Monacha cartusiana (Müller, 1774)	2.9 (2.9)	no	no	no	no	no	0
Otala lactea (Müller, 1774)	75.0 (12.5)	no	yes	no	yes	yes	2
Oxychilus alliarius (Miller, 1822)	66.2 (12.9)	no	no	yes	yes	yes	2
Oxychilus cellarius (Müller, 1774)	33.8 (4.4)	no	no	no	yes	yes	1
Rumina decollata (Linnaeus, 1758)	42.0 (2.9)	no	no	yes	yes	yes	2
Tandonia budapestensis (Hazay, 1881)	16.8 (7.9)	no	yes	no	yes	yes	2
Testacella haliotidea Draparnaud, 1801	33.3 (6.6)	no	no	no	yes	yes	1
Theba pisana (Müller, 1774)	40.7 (33.1)	yes	yes	yes	yes	yes	4
Vitrea crystallina (Müller, 1774)	36.8 (5.3)	no	no	no	yes	yes	1
Xerotricha conspurcata (Draparnaud, 1801)	0.0	no	no	no	no	no	0

showing incorrect placement (e.g. in the sea) were either deleted or corrected (if additional information was available). Maps of occurrences were imported and georeferenced in ArcGIS, and geographical coordinates were assigned to each occurrence point. For locality names, we extracted the coordinates of geographical centre-points using Google Earth (Google, Mountain View, CA, USA; available at: http://www.google.com/earth/). Localities that could not be unambiguously identified were ignored. In all cases, we evaluated common sources of positional uncertainty (e.g. map scale, extent of localities and arithmetical precision of the given coordinates) and records with a geographical uncertainty of more than 10 km were not considered. Finally, we converted the occurrence datasets of each species to one record per 20 km × 20 km grid cell. This level of spatial detail is expected to be compatible with the purposes of our study (e.g. Petitpierre *et al.*, 2012) and allowed most of the collected data to be used.

Before the data were treated any further, we confirmed whether the occurrence records we had collected could be used for assess-ing the climatic conditions occupied by each species in the native and non-native ranges. Using GIS, we drew an approximate representation of the native and non-native range boundaries of each species. Native range boundaries were drawn based mainly on information from Kerney & Cameron (2006), the AnimalBase Project Group (2012) and IUCN (2013). Non-native ranges were based mainly on Herbert (2010) and White-McLean (2011) and references cited therein. In both cases, we also used any other relevant information (see Appendix S2). We superimposed the corresponding set of species occurrences over each of the range maps. Species for which undersampling could be visually detected (e.g. noticeable coverage gaps or the absence of records in a non-native region) were excluded from our study. Our final dataset included 27 species (Table 1) spread across 13 families, with 16,814 occurrences in native ranges (mean 623; max. 3805; min. 13) and 2470 occurrences in naturalized ranges (mean 92; max. 506; min. 7). We have no reason to assume that these species are not representative of the pool of European terrestrial gastropods with non-native ranges.

Climatic variables

To shape species distributions, climatic factors must affect the organism's physiology (Rödder *et al.*, 2009); for terrestrial gastropods, this involves both temperature and humidity. The variability and interaction between these factors have a direct influence on several key aspects of the biology and phenology of these taxa, including growth rates, egg production and mortality, and the onset of dormancy/activity (Cook, 2001; Heller, 2001). Perhaps most important is the fact that terrestrial gastropods have a permeable integument that makes them particularly vulnerable to dehydration or hyperhydration (Luchtel & Deyrup-Olsen, 2001). Given this strong physiological influence, we collected six spatially explicit climatic variables from WorldClim (Hijmans *et al.*, 2005) representing means, extremes or seasonal variation in temperature and precipitation (1950–2000): annual mean temperature (*amt*); maximum temperature of the warmest month (*maxtwm*); minimum temperature of the coldest month (*mintcm*); annual precipitation (*anpre*); precipitation of the driest quarter (*predrq*); and precipitation of the wettest quarter (*prewetq*). To match the resolution of the species occurrence data, all variables were collected at $10' \times 10'$ resolution and projected onto a $20 \text{ km} \times 20 \text{ km}$ grid in ArcGIS.

Identification of establishment under novel climatic conditions

The purpose of this analysis was to compare the climatic conditions occupied by the naturalized and native populations of each species. For that purpose, we reduced the dimensionality of the climatic dataset using principal components analysis (PCA). This was performed in ArcGIS after standardizing all the variables to zero mean and unit variance, i.e. PCA on the correlation matrix. We retained the first two axes of the PCA, which accounted for more than 89% of the underlying climatic variation (PC1, 58.6%; PC2, 30.7%). Next, we projected the scores of these two axes onto the geographical space and the value of each was assigned to the overlaying species occurrences. We then used these scores to project the conditions occupied by the native and non-native occurrences of each species onto the two-dimensional climatic space. We defined native-like conditions as any climatic combination falling within the convex hull of the cloud of native occurrences.

We also captured the climatic space potentially available to each species in the native region. For this, we considered all contiguous climatic conditions in the geographical space within 100 km of each native occurrence to be available and delimited the convex hull of these conditions in the climatic space. We expect this buffer to represent available habitats, because most of the species in our study are synanthropic and are frequently dispersed passively by humans (Kerney & Cameron, 2006; Kappes & Schilthuizen, 2014). We also recognize, however, that this distance may not apply equally well to all species, and consequently, the delimited conditions were used only as general indicators of climatic availability and were not used in response-

trait calculations (see below). Naturalized populations falling outside the native convex hull were further assigned to one of four main types of novel climates: colder and drier; colder and wetter; warmer and drier; or warmer and wetter. We distinguished these conditions based on the intercorrelation of the variables defining the two-dimensional PCA space. On the basis of these relationships, we delimited the relative location of the each type of novel climate by intersecting the two semiplanes perpendicular to the loading vector of annual mean temperature (the central vector of temperature variables) with the two semiplanes perpendicular to the loading vector of annual precipitation (the central vector of precipitation variables). For each species, we then centred the origin of these planes in the centroid of the convex hull of native conditions. Finally, we classified the climatic position of non-native occurrences under the novel conditions based on the planes it overlaid (see Fig. 1 and Appendix S3 for a more detailed explanation, and Appendix S4 for plots for each species).

On the basis of the framework described above, we recorded eight distinct responses to novel climates: (1) the proportion of non-native occurrences falling outside the climate space realized in the native range; (2) the proportion of non-native occurrences falling outside the climate space realized in the native range but within the climatic space available in the native region; (3) the presence or absence of non-native populations under any novel climatic conditions; (4–7) the presence or absence of non-native populations in each of the four types of novel climates; and (8) the diversity of newly colonized climates – measured as the number of novel climate types occupied. For the latter six responses, we only classified a species as established outside the native climatic niche if there were three or more occurrence records, to reduce any bias caused by incorrect georeferencing or taxonomic misidentification.

Trait data

We collected data on egg volume, maximum shell length (snails only), presence or absence of a protective shell, presence or absence of polymorphism in shell colour or banding (snails only) and reproductive strategy (semelparous or iteroparous); data were collected from the literature (e.g. Falkner *et al.*, 2001; Heller, 2001; Kerney & Cameron, 2006; Cowie *et al.*, 2009). These traits were selected because life-history strategies and phenotypic plasticity may be related to the ability of terrestrial gastropods to occupy novel climatic settings (Heath, 1975; Heller, 2001). We also gathered trait data referring to the species' ecology and biogeography. These included habitat breadth, humidity preference, breadth of realized native climatic niche, ratio of latitudinal to longitudinal ranges, latitudes of the northern and southern range limits, and latitudinal range between the northern and southern range limits. Habitat breadth corresponded to the sum of first-level macrohabitat categories defined by Falkner *et al.* (2001). For a few species absent from this database, we verified the use of each of these macrohabitats from complementary literature (Appendix S5). Humidity preference, i.e. the relative occurrence of the species under wet,

Figure 1 Climatic conditions occupied by native and non-native populations of the brown garden snail (*Cornu aspersum*) along the first two axes of a principal components analysis (PCA). Names of locations are indicated for the most representative non-native ranges that are found outside the climatic conditions occupied in the native range, as defined by the convex hull of native conditions. The inset depicts the correlations between the climatic variables in the PCA and the four sectors that were defined on the basis of the collinearity of the variables in the subspace of the two main axes of the PCA. The climatic variables used were annual mean temperature (*amt*), maximum temperature of warmest month (*maxtwm*), minimum temperature of coldest month (*mintcm*), annual precipitation (*anpre*), precipitation of the driest quarter (*predrq*) and precipitation of the wettest quarter (*prewetq*).
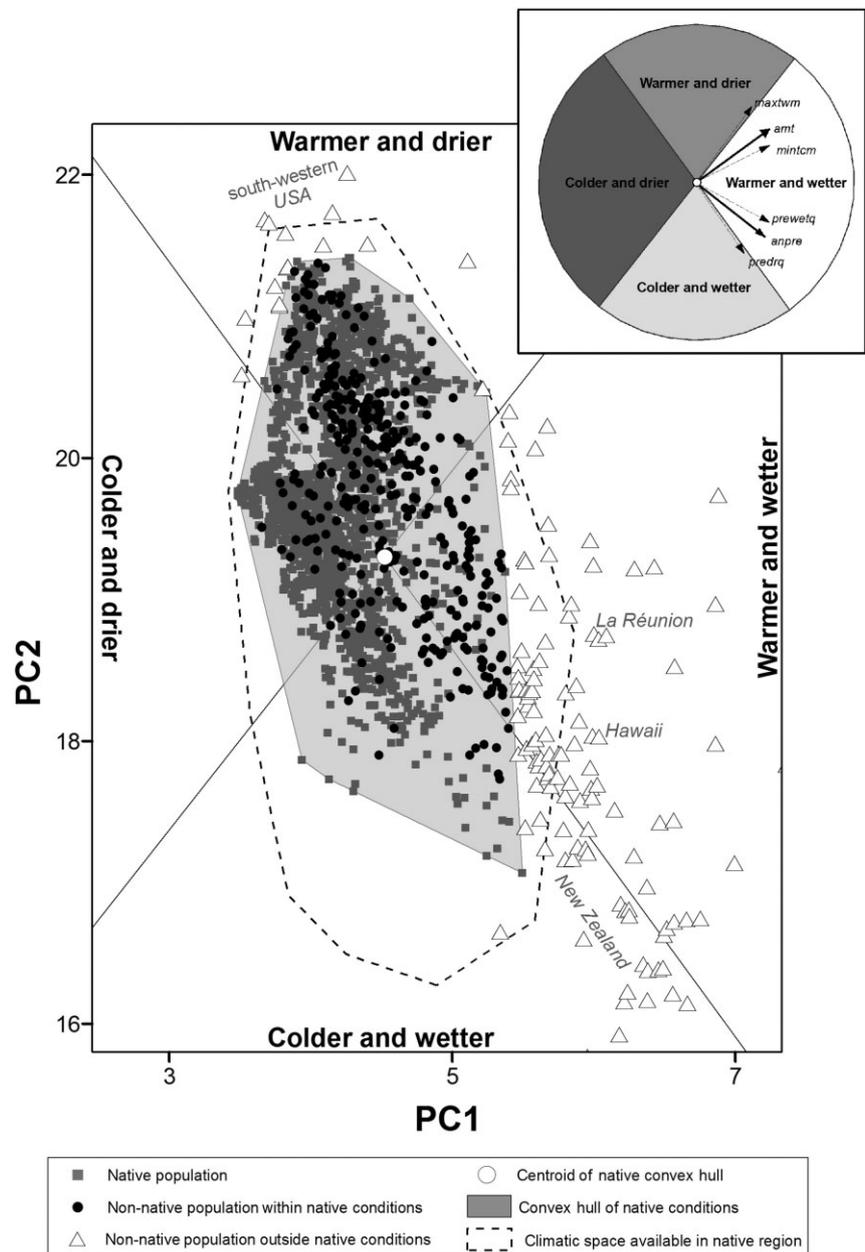
moist or dry conditions, was based on Falkner *et al.* (2001). We used the category with the highest relative occurrence to represent the condition preferred by the species. Information for species not found in the database was retrieved from the literature (Appendix S5). The breadth of the realized native climatic niche corresponded to the area of the convex hull enclosing the climatic conditions occupied by the species in its native range. The relationship between the latitudinal and longitudinal range extent was calculated in GIS and corresponded to the ratio of the Euclidean distance (measured in km) between the 5% most peripheral occurrences in each extreme of the *y*-axis to its equivalent on the *x*-axis. Finally, we measured the northernmost and southernmost latitude of the species' native ranges from the trimmed range limits.

We also aimed to quantify the extent to which the species were dispersed worldwide. Global introduction efforts are expected to bias patterns of climate matching because they can mediate the diversity of climatic conditions made accessible to each species. To represent this factor, we identified the non-native areas of the world (represented by each 20-km grid cell) having climates equivalent to those of the native range (i.e. falling inside the native-range convex hull) for each species. We then measured the proportion of these areas with the species present. By controlling for climatic compatibility, we expected this index to mainly reflect the influence of introduction effort, since these two factors are often considered to be the most important in determining the extent of non-native ranges (e.g. Thuiller *et al.*, 2005; Hayes & Barry, 2008; Pyšek *et al.*, 2009).

Phylogenetic relatedness

Species cannot be treated as independent samples in statistical analyses of comparative data because of phylogenetic autocorrelation. If species are used as independent samples, degrees of freedom may be inflated and statistical significance becomes equivocal (Paradis & Claude, 2002). We therefore built a phylogenetic tree for our 27 species, using nucleotide sequences available from GenBank. The majority of sequences came from Wade *et al.* (2001, 2006) (3′ end of the 5.8S gene, complete ITS-2 region, and the 5′ end of the 28S gene), but homologous sequences from other studies were also included (see Appendix S6 for GenBank accession numbers). For two species for which compatible data were unavailable – *Arion intermedius* and *Testacella haliotidea* – we used sequence data from their close relatives *Arion hortensis* Férussac, 1819 and *Testacella scutulum* Sowerby, 1821, respectively. The surrogate of *A. intermedius* was selected based on similarity levels of alternative sequences in blast (http://blast.ncbi.nlm.nih.gov/Blast.cgi); *T. scutulum* is sometimes considered a variety of *T. haliotidea* (Kerney, 1999). No congeners of these species occurred in our dataset. We used the opisthobranch *Aplysia punctata* (Cuvier, 1803) as an outgroup (cf. Wade *et al.*, 2006). Sequences were aligned using muscle (Edgar, 2004) and combined into a single matrix. Finally, we built maximum-likelihood phylogenies in mega (Tamura *et al.*, 2011). We used the general time-reversible model of nucleotide substitution with discrete gamma-distributed rates and a proportion of invariant sites (GTR+γ + I), which was the best fitting according to the Akaike information criterion in jModelTest 2 (Darriba *et al.*, 2012).

Data analyses

We analysed the association between the species' responses to novel climates and the collected traits using generalized estimating equations (GEEs). GEEs correspond to generalizations of standard generalized linear models that explicitly account for correlation among samples (Paradis & Claude, 2002). We applied GEE using the ape package (Paradis *et al.*, 2004) in R. This implementation translates the species phylogenetic tree into a species-to-species correlation matrix that is used as measure of strength of the dependence among samples (i.e. species) in GEE. Moreover, the degrees of freedom of GEE parameters calculated by ape are based on the procedure suggested by Paradis & Claude (2002), which considers both the number of species analysed and their phylogenetic relatedness.

Before running the GEE analyses, we tested for collinearity among trait variables using Kendall's rank correlation. No strong correlations were found (absolute tau > 0.8). Next, we used GEE to test for significant relationships between each response variable and each of the species traits. We included 'introduction effort' as a covariate in all models to account for the confounding effect of this factor. We fitted GEE binomial models for binary response variables (i.e. the presence or absence of non-native distributions outside the native climatic space and presence or absence of non-native distributions in each of the types of novel climates), Gaussian models for the dependent variable representing the proportion of non-native occurrences under novel climates (log-transformed), and Poisson models for the diversity of novel climates colonized (i.e. count data).

RESULTS

Establishment under novel climatic conditions

The proportion of non-native occurrences in novel climates differed markedly among species. Of the 27 species analysed, 14 had more than 25% of non-native occurrences outside their native climatic space and, of these, four exceeded 50% (Table 1). Conversely, 12 species had only marginal (i.e. < 5%) or no establishment in novel conditions. Most of the newly colonized climates were not available in the species' native regions (Table 1). In total, 16 species had three or more non-native occurrences in at least one novel climatic type (Table 1). Warmer and wetter climates were the most commonly occupied (15 species), followed by colder and wetter and warmer and drier climates (seven species each); colder and drier climates were the least occupied (three species). The total diversity of novel climates occupied also varied widely among species. Two species were found in all four types of climatic conditions (Table 1), three species were found in three types (see Fig. 1 for one example), four species in two types, and seven species in only one type of novel climate each.

Predictors of establishment under novel climatic conditions

GEE models showed that the proportion of non-native occurrences in novel climates is unrelated to the introduction effort ($P > 0.05$) (Appendix S7). However, the models suggested that species displaying wider climatic-niche breadths in their native range have a lower probability of becoming established outside the native climatic niche (d.f.$_{phylogenetic}$ = 8.06, coefficient estimate = -4.51×10^{-5}, $P = 0.040$) while the opposite was found for species with native ranges elongated north–south (d.f.$_{phylogenetic}$ = 8.06, coefficient estimate = 0.403, $P = 0.004$). The probability of climate mismatch was also higher for species having southern range limits at lower latitudes (d.f.$_{phylogenetic}$ = 8.06, coefficient estimate = -0.051, $P = 0.008$). None of the remaining traits was significantly associated with this response variable.

For several binomial GEE models, the phylogenetic correlation of the response variable was very high, which caused the effective sample size to be insufficient for model convergence (Appendix S7). When model convergence was achieved, we found no significant association with the tested traits.

The GEE models that analysed the diversity of novel climatic conditions occupied identified a significant positive association with introduction effort (d.f.$_{phylogenetic}$ = 8.06, coefficient estimate = 0.664, $P = 0.026$). In addition, diversity was significantly related to the presence or absence of a protective shell (d.f.$_{phylogenetic}$ = 8.06, coefficient estimate = -0.803, $P = 0.034$),

which suggests that species without a shell (i.e. slugs) are found in a more diverse range of novel climates than species with a shell (i.e. snails).

DISCUSSION

Our results show that climate-matching could predict non-native occurrences of about half of the studied species while, for the remaining half, a considerable proportion of these occurrences (> 25%) was unpredictable. These contrasting levels of accuracy mirror a pattern emerging in the literature that could address the effectiveness of climate-matching at predicting non-native ranges. In some cases (e.g. Thuiller *et al.*, 2005; Hayes & Barry, 2008; Guo *et al.*, 2012), most of the non-native range was predicted, whereas in others (e.g. Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Capinha *et al.*, 2013), the predictions failed. Consequently, identification of the circumstances under which species are likely to shift or conserve realized and fundamental niches is crucial for anticipating the reliability of these predictions (Pearman *et al.*, 2008). Although manipulative experiments are necessary for differentiating between shifts in realized or fundamental niches and to identify the processes that foster or hinder these shifts, our results suggest that the analysis of species traits may provide valuable information.

We found that species with narrower native climatic niches or with latitudinally elongated native ranges tended to be less predictable. Despite being distinct, these two traits appear to reflect the level of distributional equilibrium of species in their native regions. The breadth of native climatic niches is dictated by several factors, including the species' actual physiological tolerances. In the case of our species, however, the effect of geographical barriers to dispersal appears to be one of the most important factors. For example, the two species with narrowest climatic niches were *Marmorana serpentina* and *Otala lactea*. *Marmorana serpentina* is an insular species, whereas *O. lactea* is a Mediterranean species that occurs only in a small section of the Mediterranean basin (southern Iberian Peninsula, Balearic Islands and Morocco). These two species showed the third-highest (60%) and highest (75%) proportion of climate mismatch, respectively. The relationship between vertically elongated native ranges and distributional equilibrium is even more apparent. Variation in the direction of the elongation of species' ranges indicates the relative role of climate in shaping range boundaries (Brown *et al.*, 1996). Because of the latitudinal gradient of temperatures worldwide, a north–south elongation suggests a reduced role of climate, particularly of temperature, in shaping species' distributions. In other words, species with latitudinally elongated range boundaries are expected to be strongly conditioned by non-climatic constraints (e.g. biological enemies or natural barriers) and their distributions are likely to provide a poor indication of the environmental conditions they tolerate (i.e. their fundamental niche). Indeed, previous research has warned about the increased uncertainty of predictions made for species in these circumstances (Araújo & Pearson, 2005). Our results indicate that this uncertainty can, at least to some

extent, be assessed a priori by investigating the geographical attributes of the species' native ranges.

Our results also showed that species native to, but not necessarily restricted to, southern regions (i.e. southern Europe and North Africa) had a higher propensity for climate mismatch. The reason for this relationship is not clear. One possibility is that species restricted to high latitudes inhabit the warm edge of their thermal niche, while some of those occurring further south would not be able to do so because of the Mediterranean Sea (again a manifestation of distributional disequilibrium). Species reaching further south may also be better able to tolerate the climatic conditions at lower latitudes (e.g. in subtropical or tropical areas). For instance, most species native to the Mediterranean climate can tolerate high temperatures and drought and may therefore be pre-adapted to cooler and more humid conditions (i.e. the novel climates are within their fundamental niche; Alexander & Edwards, 2010). Our results show that most species native to southern Europe or North Africa have non-native populations in climates that are wetter and warmer (Table 1). However, because of data limitations (see Results), we could not test the statistical significance of the association.

We found that slugs colonized a wider diversity of novel climates than snails. There are many examples of range expansion of European slugs into novel climates (White-McLean, 2011) and our findings further support this pattern. Perhaps the best-known example is the European invasion of the slug *Arion lusitanicus* auct. non Mabille, 1868, a species that was originally confined to a limited area of Western Europe. Although one could expect snails to inhabit a wider diversity of climatic conditions, because having a shell provides protection from heat and dehydration, our findings suggest that the opposite is true. The reason for this may be the greater ability of slugs to take advantage of microclimates. Because slugs are shell-less, their bodies are more plastic, which may allow slugs to better search for and exploit suitable microenvironments (Luchtel & Deyrup-Olsen, 2001). Slugs also appear to be very selective in choosing these microenvironments and regularly exhibit homing behaviour (Cook, 2001), a strategy that ensures refuge from adverse macroclimates. Recently, Suggitt *et al.* (2011) showed that local thermal variability might compensate to some extent for thermal changes in extreme climate change. It seems likely that the ability to exploit microclimatic refuges in new areas may also enhance resistance to adverse macroclimates.

Our results also show clear differences between the types of novel climatic conditions inhabited by species in their non-native ranges, and show that warmer and wetter regions were the most commonly colonized. We did not, however, find any indication of these patterns being related to any of the analysed traits. We also found no significant association between any of the patterns of climatic niche change and traits related to the species' life history (i.e. egg volume, semelparity versus iteroparity, or shell size). Some studies have suggested that species that produce large numbers of offspring that grow and reproduce quickly but are small-sized and have a short life-span (i.e. *r*-strategists) will be better able to become successfully established outside their native regions (see examples in Sakai

et al., 2001). Our results suggest that, if these attributes do facilitate establishment, it is because they aid the species in overcoming challenges other than the change in climatic conditions (e.g. demographic stochasticity). The same conclusion appears to apply to habitat preferences or habitat generalism, because no relationship was found between the traits and any of the climatic responses measured. The albedo of shells determines the amount of solar radiation absorbed by snails and, consequently, their body temperature (Heath, 1975); plasticity in this trait may therefore favour survival in stressful climates through selection. We also found no distinct climatic responses between snails having variability in shell colour or banding and those that do not, however. Our results agree with other studies (e.g. Heller, 1981) in which this relationship was not observed.

There are several other methods for evaluating climate-matching predictions. Most distinctive from our approach are those that restrict predictions to climatic conditions shared between native and non-native regions (e.g. Petitpierre *et al.*, 2012) in an attempt to exclude climate mismatch due to pre-adaptation. As shown by our results, however, many of the climatic combinations occupied by species in non-native areas appear not to be available in native regions. Thus, disregarding species' responses to novel climatic conditions is likely to lead to an underestimation of their potential ranges (Webber *et al.*, 2012). Of course, physiologically based predictions are preferable in this context, but, because they may not be obtainable, recent studies have also investigated how the use of species distribution data can be optimized for new environments (e.g. Elith *et al.*, 2010; Owens *et al.*, 2013). For instance, Owens *et al.* (2013) introduced the mobility-orientated parity metric, a modification and extension of the multivariate environmental similarity surface (Elith *et al.*, 2010), which allows the locations in which extrapolation takes place to be mapped, and the degree of 'novelty' of the environmental conditions to be measured. Combining techniques such as this with an a priori knowledge of species attributes that consistently relate to niche conservatism or shift may be of great help in evaluating the uncertainty of climate-matching predictions made for new spatial or temporal domains.

CONCLUSIONS

We have identified variable levels of accuracy of native-range-based climate matching in predicting the worldwide non-native occurrences of European terrestrial gastropods. This variability was related to the level of climatic equilibrium of the species' native ranges: species with lower levels of distributional equilibrium had a greater propensity to becoming established in novel climates. We also found that slugs' ability to take advantage of microenvironments might increase their likelihood of survival in a wide diversity of macroclimates. Such aptitude may severely reduce the accuracy of coarse-scale climate-matching predictions. Although there is widespread agreement that ecophysiological experiments and genetic approaches are necessary to more precisely predict where a species could become established (Kearney *et al.*, 2010; Hoffmann & Sgrò, 2011), our findings

suggest that, in the absence of such approaches, analyses of species' traits may provide information about the uncertainty of correlative predictions. We therefore strongly encourage further studies that test the generality of relationships between species traits and accuracy of climate matching.

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SUPPORTING INFORMATION

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Figure S1 Schematics of the procedure used to classify the types of novel climatic conditions occupied by species in non-native ranges.

Appendix S1 Schematic representation of the criteria used for species selection.

Appendix S2 Sources of species occurrence data.

Appendix S3 Classification of novel climatic conditions colonized.

Appendix S4 Climatic conditions occupied by each species in native and non-native ranges.

Appendix S5 Alternative sources of data for macrohabitat usage and humidity preferences.

Appendix S6 GenBank accession numbers.

Appendix S7 Results of the generalized estimating equations.

BIOSKETCH

César Capinha is a postdoctoral researcher with research interests in invasion ecology and biogeography. He has focused mainly on assessing the relative role of the distinct factors that determine the distribution of non-native species, particularly climate.

Author contributions: C.C. led the project and the writing with contributions from the remaining authors. C.C and H.K. performed the data collection. All authors contributed in the interpretation of results.

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