ORIGINAL ARTICLE

Geographical variability in propagule pressure and climatic suitability explain the European distribution of two highly invasive crayfish

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ABSTRACT

Aim We assess the relative contribution of human, biological and climatic factors in explaining the colonization success of two highly invasive freshwater decapods: the signal crayfish (*Pacifastacus leniusculus*) and the red swamp crayfish (*Procambarus clarkii*).

Location Europe.

Methods We used boosted regression trees to evaluate the relative influence of, and relationship between, the invader's current pattern of distribution and a set of spatially explicit variables considered important to their colonization success. These variables are related to four well-known invasion hypotheses, namely the role of propagule pressure, climate matching, biotic resistance from known competitors, and human disturbance.

Results Model predictions attained a high accuracy for the two invaders (mean AUC $\geq$ 0.91). Propagule pressure and climatic suitability were identified as the primary drivers of colonization, but the former had a much higher relative influence on the red swamp crayfish. Climate matching was shown to have limited predictive value and climatic suitability models based on occurrences from other invaded areas had consistently higher relative explanatory power than models based on native range data. Biotic resistance and human disturbance were also shown to be weak predictors of the distribution of the two invaders.

Main conclusions These results contribute to our general understanding of the factors that enable certain species to become notable invaders. Being primarily driven by propagule pressure and climatic suitability, we expect that, given their continued dispersal, the future distribution of these problematic decapods in Europe will increasingly represent their fundamental climatic niche.

Keywords
Biotic resistance, climate matching, freshwater invasions, human disturbance, *Pacifastacus leniusculus*, *Procambarus clarkii*, propagule pressure, red swamp crayfish, signal crayfish.

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INTRODUCTION

As a result of human activity, species are now being introduced to new areas at unprecedented rates (Ricciardi, 2007). These events have led to the establishment of many highly invasive species with often dramatic effects in the recipient regions (Clavero *et al.*, 2009; McGeoch *et al.*, 2010). Nonetheless, it is also well acknowledged that the large majority of introductions fail to produce viable populations and, from those that succeed, only a small portion becomes invasive (Williamson, 1996). Given this apparent idiosyncrasy, unravelling the factors that determine invasion success and the prediction of future impacts has long been a central issue of invasion ecology and conservation biology (Kolar & Lodge, 2001; van Kleunen *et al.*, 2010).

Understanding the causes behind the establishment success of invaders is a complex task and efforts towards that end have led to the development of many hypotheses. Among these, the propagule pressure hypothesis (Lockwood *et al.*, 2005) is one of the most widely supported. Higher propagule

pressure increases the population's ability to overcome Allee effects (Drake & Lodge, 2006), endure environmental and demographic stochasticity (Simberloff, 2009), and adapt to local conditions (due to a wider gene pool) (Ahlroth *et al.*, 2003). Thus, a positive relationship between propagule pressure and the likelihood of invader establishment is expected. Another common expectation is that invaders are more likely to establish in areas with climates similar to that of their native range. This assumption underlies the 'climate matching' hypothesis (Williamson, 1996), which has received strong support in recent years (Wiens & Graham, 2005; Peterson, 2011). Biotic interactions are also expected to play an important role in the invasion process. The biotic resistance hypothesis is a prime example of this expectation, predicting that areas with higher competitor diversity will have a lower probability of invasion (Stachowicz & Tilman, 2005). This is likely to be especially relevant in the case of taxonomically similar species (e.g. Rivera *et al.*, 2005). Ultimately, anthropogenic disturbances can change the abiotic and/or biotic factors of an area, leading to an increase in vulnerability to invasion (see Catford *et al.*, 2009 and references therein). This 'human disturbance' hypothesis is based on the potential role of facilitative mechanisms, such as the release of resources, the alteration of biotic interactions and the creation of vacant space (Lockwood *et al.*, 2007). Besides these four main hypotheses, several others – not necessarily mutually exclusive and encompassing a relatively vast array of biotic, abiotic or human factors – have also been proposed to explain the establishment success or failure of non-native species (see Catford *et al.*, 2009).

Although the value of individual invasion hypotheses is usually supported by a number of studies, increasing evidence is accumulating that their relative importance is highly context-dependent (Catford *et al.*, 2009; Gurevitch *et al.*, 2011). For example, recently, Nuñez *et al.* (2011) analysed an 80-year dataset of tree introductions in an Argentinian national park and found that detailed estimates of propagule pressure largely failed to predict the current patterns of invasion of the area. They suggest that other factors, such as biotic resistance, may be playing a more important role and thus reducing the invasibility of the area. This influence of 'external' factors has led to suggestions that future research should focus more on untangling the relative role of the distinct factors involved in the process instead of simply testing the validity of isolated hypotheses (e.g. Thuiller *et al.*, 2006; Pyšek *et al.*, 2010). However, despite this recognition, few studies have thus far provided insight into the interaction of multiple factors during an invasion process. Additionally, most existing studies have focused on finding generalities among a large number of invasions (e.g. Thuiller *et al.*, 2006; Pyšek *et al.*, 2010) and therefore an acute knowledge of the mechanisms driving many of the most notable individual invaders is still lacking.

In this study we focus on two of the most widespread and harmful invaders so far reported in European freshwaters, the signal crayfish (*Pacifastacus leniusculus* Dana) and the red swamp crayfish (*Procambarus clarkii* Girard). Previous studies referring to the establishment of these invaders have identified a number of mechanisms explicitly related to the propagule pressure, climate matching, biotic resistance and human disturbance hypotheses. For instance, they refer to the existence of distinct efforts of introduction among countries (Souty-Grosset *et al.*, 2006; Holdich *et al.*, 2009), high tolerance to environmental heterogeneity (Geiger *et al.*, 2005), competitive interactions with other co-occurring crayfish species (Gherardi & Cioni, 2004; Dunn *et al.*, 2009), and the positive impact of human activities on the environment (Lindqvist & Huner, 1999). However, and although commonly acknowledged (e.g. Souty-Grosset *et al.*, 2006; Holdich *et al.*, 2009), the way these mechanisms interact to determine their colonization success or failure remains unknown, particularly on a continental scale.

We examine how propagule pressure, climatic suitability, biotic resistance and human disturbance interact to shape the current distribution of the signal and the red swamp crayfish in Europe. Specifically, we relate the spatial variability of these factors to the pattern of distribution of the invaders using a statistical ensemble model that assesses the relative contribution of each factor and its relationship with the species' probability of occurrence. The results of this analysis are intended: (1) to provide the first quantitative evaluation of the relative role of distinct human, climatic and biological factors in explaining the pattern of distribution of these two notorious invaders; (2) to compare the relative roles and form of relationships between the tested factors and the species' occurrence to the postulations of the four hypotheses described above; and (3) to provide insight on how the distributions of these invaders are likely to expand on the European continent.

MATERIALS AND METHODS

Species and distribution data

The signal crayfish and the red swamp crayfish are both native to North America and were imported to Europe in the 1960s and the 1970s, respectively. Currently, the signal crayfish is the most widespread invasive crayfish on this continent, found in 27 countries, while the red swamp crayfish occurs in 10 (Holdich *et al.*, 2009). These species are also invasive in other parts of the world. Non-native populations of signal crayfish are found in Japan and the south-west United States, while the red swamp crayfish, which has a much broader invasive distribution, is established in several areas of Africa, Asia, North America and South America (Souty-Grosset *et al.*, 2006).

For the purpose of this study, we defined our study area as the countries represented in the *Atlas of Crayfish in Europe* (Souty-Grosset *et al.*, 2006), which provided the bulk of the distribution data for Europe. From these, we excluded those referred to as strongly under-sampled (Fig. 1). We then collected current native and invasive occurrences of the signal
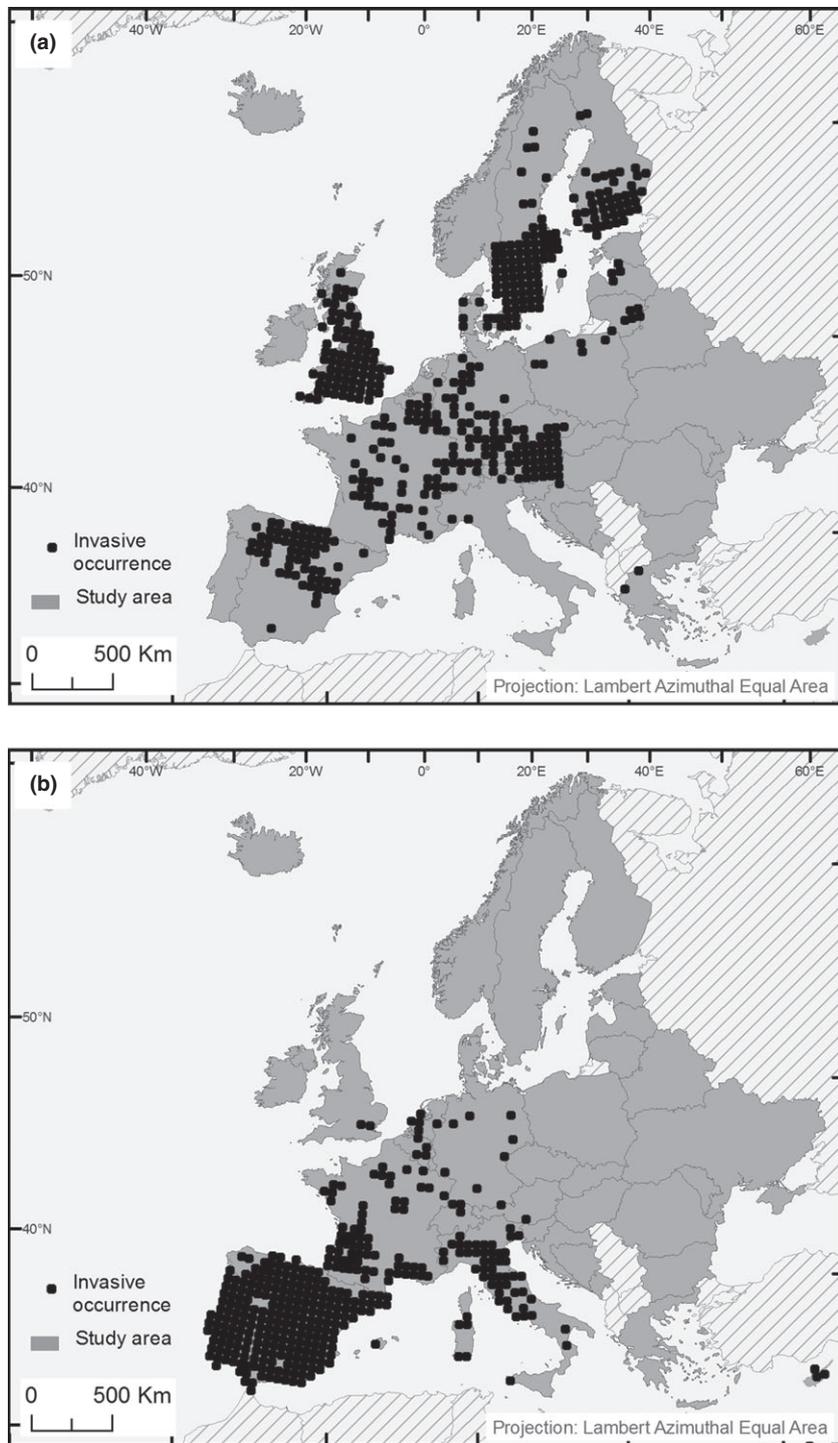
Figure 1 Current distribution of (a) the signal crayfish (*Pacifastacus leniusculus*) and (b) the red swamp crayfish (*Procambarus clarkii*) in the study area at a 50 km × 50 km cell resolution.

crayfish and the red swamp crayfish world-wide from the Atlas, natural history museum collections, the Global Biodiversity Information Facility (GBIF, http://data.gbif.org/; accessed 15 February 2011) and recent literature. From these sources, we also obtained current European occurrences of six other crayfish species known to establish competitive interactions with either of the two invaders (see list of species in Appendix S1 in Supporting Information). All distribution data was re-sampled to a 50 km × 50 km UTM grid, and allowing for only one record per grid square, we accumulated 597 records for the signal crayfish (454 in Europe, 52 in invaded areas outside Europe, and 91 in the native range; Fig. 1a, Fig. S1 in Appendix S2), 631 for the red swamp crayfish (377 in Europe, 80 in invaded areas outside

Europe, and 174 in the native range; Fig. 1b, Fig. S3 in Appendix S2) and 2587 for the crayfish species identified as competitors.

Explanatory variables

Both the signal crayfish and the red swamp crayfish were initially introduced into Europe for the purpose of being harvested in the wild or in aquaculture facilities. The success achieved by most harvesters soon motivated a large number of deliberate introductions into the wild in many new regions and countries. Currently, this is considered to be their major dispersal pathway through Europe (Hogger, 1986; Gutiérrez-Yurrita *et al.*, 1999; Gherardi, 2006; Souty-Grosset *et al.*, 2006). To obtain estimates of propagule pressure, we consulted a comprehensive collection of literature reporting on the history of introduction and human-mediated dispersal of the signal crayfish and the red swamp crayfish in Europe. Based on this information, using GIS, we categorized each country into one of three categories of introduction effort: (1) countries for which no attempt at introducing the species for harvesting into the wild is reported ('null' category); (2) countries where the introduction of the species into the wild was not supported by organized actions or was reported for only one region ('moderate' category); and (3) countries where the introduction of the species into the wild was promoted by governmental entities and/or commercial associations, and introductions were reported for more than one region ('strong' category).

Climatic suitability models (Guisan & Thuiller, 2005) were used as a measure of suitability of climatic conditions. To build these models, we collected five non-redundant (pairwise Pearson correlations $\leq \pm 0.8$) climatic variables from the WorldClim project (Hijmans *et al.*, 2005): mean diurnal temperature range, mean temperature of the warmest quarter, mean temperature of the coldest quarter, precipitation of the wettest quarter, and precipitation of the driest quarter. To be compatible with the spatial accuracy of our distribution data, these variables were re-sampled from their original resolution (10 km × 10 km) to a 50 km × 50 km cell resolution.

To quantify the potential effect of biotic resistance, we used the distribution data of competing crayfish species to calculate, for each invader, the richness of co-occurring competitors. This was done in a GIS and consisted simply of the sum of all competitors occurring in each UTM square comprising the study area.

To represent human disturbance, we used the human footprint index (Sanderson *et al.*, 2002). This index merges spatial data concerning population density, land transformation, accessibility and electrical power infrastructure to infer the degree of human influence on the land surface, and is available at the global scale using a 1 km × 1 km resolution. To include this variable in our analysis, we calculated the mean value within each of the UTM squares comprising the study area.

Three distinct climatic suitability models were built for each of the two invaders based on: (1) native range occurrences, (2) invasive occurrences outside the study area, and (3) these two ranges combined. To calibrate these models, we coupled the respective occurrences with pseudo-absences randomly generated world-wide, excluding areas with the species occurrence (cf. Capinha *et al.*, 2011). To maximize the pseudo-absences' representation of the available climatic conditions, we created 15 replicate datasets for each model. Each of these had the species occurrence records coupled with an equal number of independently drawn pseudo-absences.

Statistical analyses

Climatic suitability models can be built using a large variety of methods; however, there is still little agreement on which one delivers the 'best' results (e.g. Elith *et al.*, 2006). As an alternative, an ensemble of distinct but equally plausible models can be produced and their array of results analysed for agreement (Araújo & New, 2007; Capinha & Anastácio, 2011). Accordingly, we used three distinct statistical models to predict climatic suitability for the invaders: boosted regression trees (BRT), generalized additive models (GAM) and random forests (RF). These statistical models are amongst the most frequently used in niche modelling exercises where they have consistently revealed high predictive ability (e.g. Elith *et al.*, 2006; Capinha & Anastácio, 2011). Models were implemented in r-cran (R Development Core Team, 2011) using the biomod package (Thuiller *et al.*, 2009). Model parameters were kept at default values, with the exception of the number of trees in BRT which was set to 2000, and the degrees of freedom of the GAM smooth functions, which were set to four. The discrimination ability of each replicate model was evaluated in terms of the area under the receiver operating characteristic curve (AUC). The AUC was calculated by comparing predictions with 20% of the distribution data that was withheld from model development (Thuiller *et al.*, 2009). Final models of climatic suitability were obtained by averaging the 45 replicate predictions (15 replicates × 3 modelling algorithms) into a single prediction.

To prevent data redundancy in the explanatory variables, we measured the degree of correlation between all pairs of independent continuous variables collected, which revealed the absence of high correlation levels (|r| >0.8). Next, we created three distinct sets of explanatory variables for each of the two invaders. Each of these included one of the three climatic suitability models generated for each species, together with the remaining explanatory variables: country-level introduction effort, richness of co-occurring competitors, and human footprint (Appendix S2). To analyse the influence of these explanatory variables on the presence or absence of the invaders, we used boosted regression trees (BRT) (Friedman *et al.*, 2000; Friedman, 2001; Elith *et al.*, 2008). BRT consists of a machine-learning technique that

builds an ensemble prediction by iteratively fitting a chain of multiple decision trees. This method has performed well in several studies (e.g. Elith *et al.*, 2006; Guisan *et al.*, 2007), and is also particularly appropriate for exploring the combined influence of a set of predictors as a result of its ability to fit nonlinear responses and automatic detection of interaction effects between independent variables (Elith *et al.*, 2008). We used the GBM package version 1.6–3.1 (Ridgeway, 2010) for R-CRAN and the R functions, provided by Elith *et al.* (2008), to run all BRT models. Before analysing the datasets, we tested for the optimal parameters of the BRT models by running multiple models of varying complexity. For that purpose, five different learning rates (0.05, 0.025, 0.01, 0.005 and 0.0001) and six levels of tree complexity (1, 3, 6, 9, 12 and 15) were tested. Additionally, the optimal number of trees for each combination was automatically assessed using R code (Elith *et al.*, 2008). For each combination of parameters, we ran 100 replicate models as a way of dealing with the variability of BRT. The performance of each of these was tested using a 10-fold cross validation and measured using the AUC. The mean predictive performance across the 100 replicates was calculated and, from the replicates of the best performing combination, we extracted the mean relative influence of each explanatory variable. This relative influence is automatically calculated by the GBM package by relating the number of times a variable is used with the improvement it generates in the model (Friedman & Meulman, 2003).

We were also interested in assessing how the probability of occurrence of each invader changes along the gradient of each predictor. For that purpose, we extracted partial dependence plots, which show the marginal effect of each predictor on the species' probability of occurrence (Friedman, 2001; Friedman & Meulman, 2003). Partial dependencies were evaluated by calculating the mean response of a model to a single value of the predictor of interest while keeping the remaining predictors at their original values. This procedure was repeated with new values until a representation of how the mean response varies along the gradient of the predictor of interest was obtained. Partial dependence plots are sensitive to strong correlations and interactions among predictors. While the former were assessed prior to modelling (see above), the strength of interactions among pairs of predictors was evaluated using exploratory analyses in R and the nature of the relationships was visually assessed using joint partial dependence plots (cf. Elith *et al.*, 2008).

RESULTS

The mean AUC of all climatic suitability models achieved fair to good accuracy scores. For the signal crayfish, this accuracy ranged from 0.82 (± 0.04) for models based on invasive occurrences, to 0.84 for the models based on native occurrences (± 0.02) and on both occurrences (± 0.03). For the red swamp crayfish, the mean AUC of models based solely on invasive occurrences was 0.90 (± 0.02), for models

using only invasive occurrence, 0.93 (± 0.03) and, for models using both occurrences, 0.91 (± 0.03).

All boosted regression tree models had high predictive power (mean AUC ≥ 0.91) (Table 1) obtained through the combined effect of multiple factors (Fig. 2). All models showed strong (> 5%) pairwise interactions between introduction effort and climatic suitability, while the models for the signal crayfish also showed strong interactions between propagule pressure and richness of co-occurring competitors. However, visual analyses of joint partial dependence plots between these pairs of predictors revealed the absence of relevant contradictory effects on the responses shown by the partial dependence plots for single predictors.

The models for the signal crayfish identified climatic suitability as the most important predictor (≥ 35.6%), followed by introduction effort and richness of co-occurring competitors (≥ 32.4 and ≥ 17.9%, respectively) (Fig. 2a). Human footprint contributed least (≤ 11.9%). Also noticeable was the slightly higher relative influence of climatic suitability models using information from invasive ranges than models using native range data. A combined analysis of these results and the relationships shown by the partial dependent plots (Fig. 3a, Appendix S3) indicates that the invasive populations of the signal crayfish are found mainly in areas with suitable climate, predominantly within countries that had strong levels of introduction effort and, interestingly, where a large number of competing species occur. A (slight) tendency to avoid highly disturbed areas is also suggested.

The current pattern of distribution of the red swamp crayfish is shown to be largely explained by country-level introduction effort (≥ 63.5%), followed by climatic suitability (≥ 13.6%). Concerning this last predictor, a significant increase in its explanatory power was found when the invaded areas outside Europe were used to represent the species' climatic niche. Models based on the species' native range achieved a mean relative influence of 13.5% (± 0.5), whereas those based on the invasive range outside the study area achieved 19.6% (± 0.6) and, those based on both ranges, 20.5% (± 0.6). The combined analysis of the relative influence of the explanatory variables and their marginal effect on

Table 1 Accuracy of boosted regression tree models in predicting the current pattern of presence/absence of the red swamp crayfish (*Procambarus clarkii*) and the signal crayfish (*Pacifastacus leniusculus*) in Europe, measured by the area under the receiver operating characteristic curve (AUC). Three groups of models were evaluated using predictions of climatic suitability based on: (1) the species' native range (native); (2) the species' invasive range outside Europe (invasive); and (3) both ranges simultaneously (both). Mean values were calculated from a set of 100 replicate models. The standard deviation of mean AUC values was < 0.01 for all models.

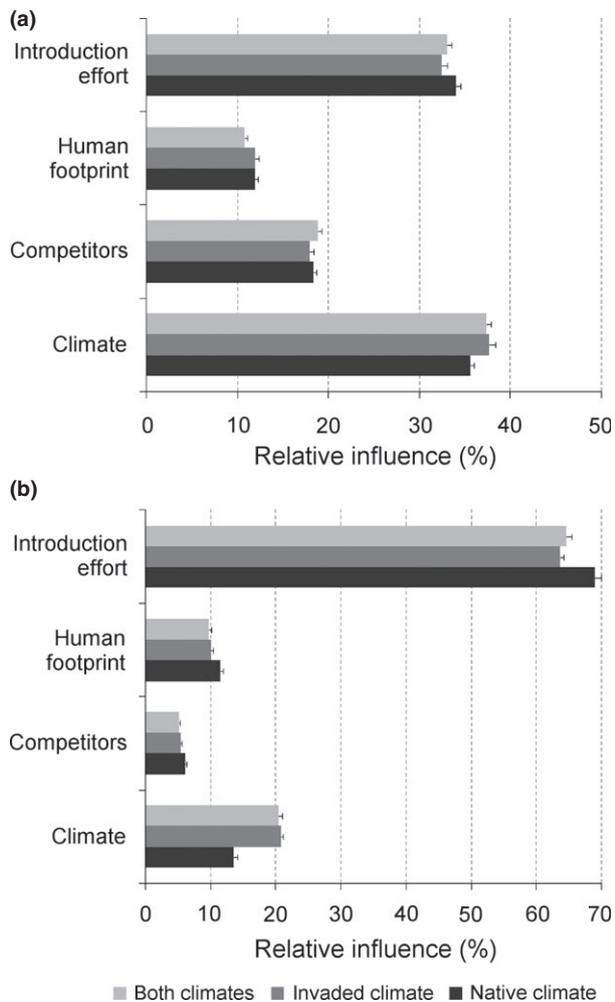| Range	Red swamp crayfish	Signal crayfish
native	0.95	0.92
invasive	0.97	0.91
both	0.97	0.93

Figure 2 Mean relative influence of explanatory variables for (a) the signal crayfish (*Pacifastacus leniusculus*) and (b) the red swamp crayfish (*Procambarus clarkii*) in Europe. Grey shades indicate the type of climatic suitability model used in model calibration based on: the species' native range (dark grey); the invaded areas outside the study area (mid grey); and these two ranges combined (light grey). Mean values and standard deviation were calculated from a set of 100 replicate models that were built with each dataset.

the species' probability of occurrence (Fig. 3b, Appendix S3) indicates that the red swamp crayfish is found mainly in the climatically suitable areas of countries with strong to moderate introduction effort. In addition, the occurrence of this invader also seems to be slightly favoured by high levels of human disturbance.

DISCUSSION

The results of our analyses demonstrate that the current distribution of the signal crayfish and the red swamp crayfish in Europe can be largely predicted by an interaction between country-level introduction effort, suitability of climatic conditions and co-occurrence with competitors (the latter only for the signal crayfish). In addition, they also highlight low

predictive power for human disturbance for both invaders and virtually no contribution from co-occurrence with competitors for the red swamp crayfish.

Drivers of colonization success

The high relative importance of country-level estimates of propagule pressure in determining current patterns of distribution is relatively unsurprising for these invaders. Being of commercial interest, these species were actively imported and intentionally introduced into the wild in several European countries while, in many others, they raised little commercial interest or their introduction into the wild was simply prohibited. For instance, the signal crayfish is widespread in Sweden, where vigorous introduction campaigns have taken place since the 1960s (Henttonen & Huner, 1999), but only one invasive population is known for Norway (Johnsen *et al.*, 2007), a bordering country which banned the importation of live specimens of this species before any wild population was known (Holdich & Pöckl, 2005). However, it is interesting to identify marked differences in the importance of this factor between the two invaders (which is noticeably higher for the red swamp crayfish). We believe that differences in residence time and the extent of areas receiving propagules are the most likely explanations for this result. These attributes largely mediate the degree of distributional equilibrium in invasive ranges and consequently the relative importance of other factors shaping the realized distribution (e.g. Wilson *et al.*, 2007). In the case of these two invaders, the signal crayfish had a longer and much wider dispersal in the study area (Gherardi, 2006; Souty-Grosset *et al.*, 2006; Holdich *et al.*, 2009) which also, considering the much lower relative importance of propagule pressure in its models, suggests that its current invasive distribution is closer to equilibrium than that of the red swamp crayfish.

Our results also highlight the strong influence of climate in shaping the current distribution of the two invaders. Climate, either directly or indirectly, affects the suitability of abiotic conditions and it is not surprising that it plays a large role in shaping invasive distributions (e.g. Roura-Pascual *et al.*, 2011). However, we found limited support for the 'climate matching' and related invasion hypotheses, which predict that invasions take place in environmental conditions for which the invaders are pre-adapted (e.g. the 'habitat filtering' hypothesis; Catford *et al.*, 2009). This is because the models calibrated with climatic data from other invaded areas were consistently more useful in predicting the species' European distribution than those based on data from native ranges – particularly for the red swamp crayfish. This agrees with previous findings that these invaders occupy new climatic conditions (i.e. shifted their climatic niche) in new ranges world-wide (Capinha *et al.*, 2011; Larson & Olden, 2012) and thus suggest that caution should be exercised when using native-based correlative models for predicting climatic suitability for invaders. Several non-mutually exclusive ecological or evolutionary mechanisms may be behind
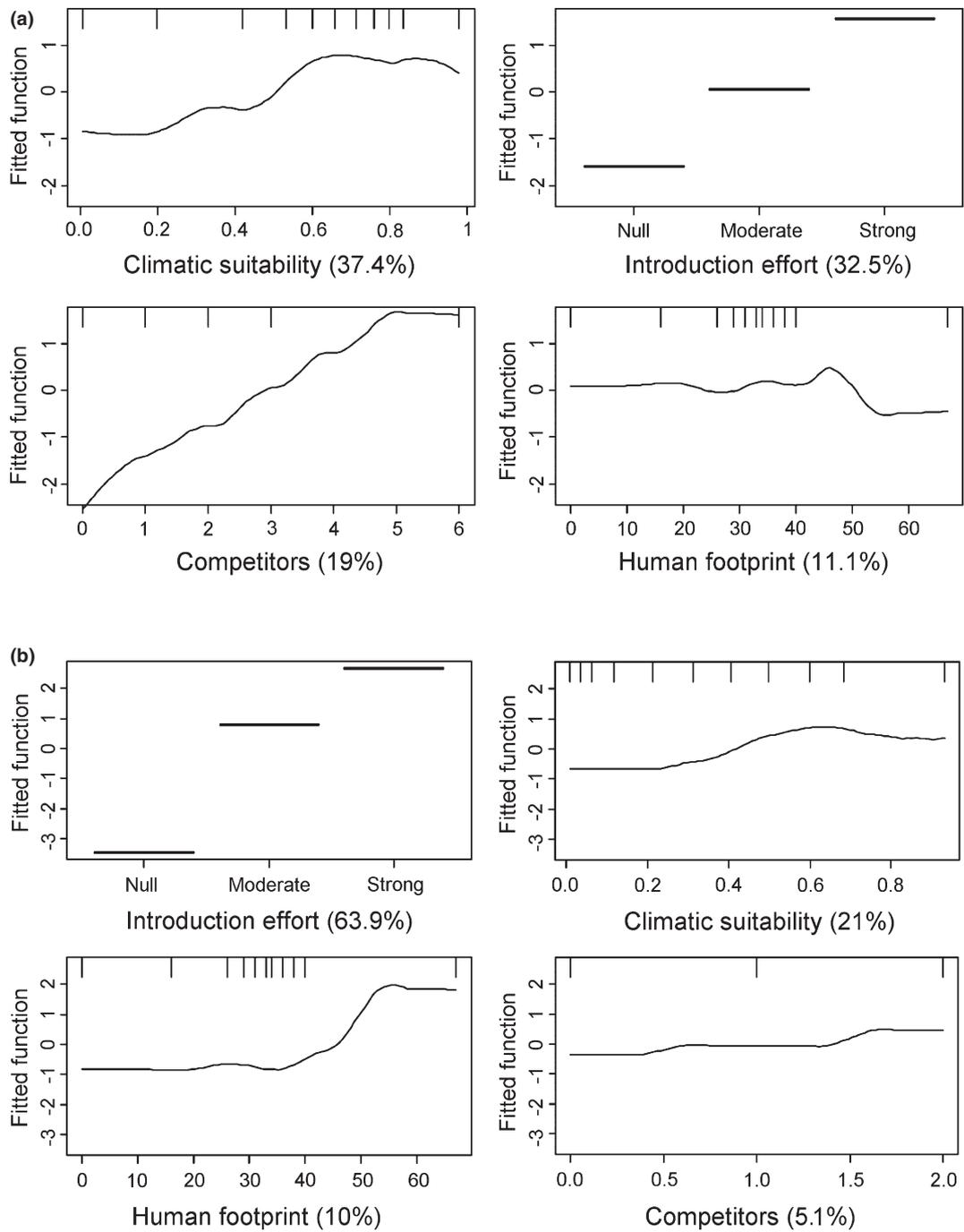
Figure 3 Smoothed partial dependence plots of one representative boosted regression tree model for (a) the signal crayfish (*Pacifastacus leniusculus*) and (b) the red swamp crayfish (*Procambarus clarkii*) in Europe. Climatic suitability models were calibrated with species occurrences from native ranges and invaded regions other than the study area. The relative contributions of each predictor in this specific model are shown in parentheses.

this capacity. Ecological mechanisms include the absence or reduction of natural enemies in the new range (i.e. the 'enemy release' and 'enemy reduction' hypotheses; Colautti *et al.*, 2004) or simply that these newly occupied conditions are not found in native regions. That said, more information about the ecological constraints on native populations would be necessary to test these possibilities. Rapid evolutionary

adaptation to the new conditions is another possible mechanism given that these invaders have relatively short generation times and the variability of the European genetic pool is favoured by the importation of large numbers of specimens from distinct origins (Gherardi, 2006; Souty-Grosset *et al.*, 2006). However, the instant success of non-European specimens of red swamp crayfish in colonizing separate European

regions with new climatic conditions (e.g. England, The Netherlands, Germany or Switzerland; Henttonen & Huner, 1999) seems to refute the necessity of this mechanism in the invasion of this species.

Despite the substantial evidence of strong biotic interactions taking place with other crayfish species occurring in Europe (e.g. reproductive interference or competition for food and shelter; Lindqvist & Huner, 1999; Westman *et al.*, 2002; Gherardi, 2006), we found no evidence of biotic resistance as an impediment to the establishment of these two invaders. Two possibly cooperating mechanisms may account for this result. First, these invaders are superior competitors (Lindqvist & Huner, 1999; Westman *et al.*, 2002; Gherardi, 2006), which could either be a consequence of innate traits, or have been promoted by their release from other biotic constraints (i.e. the 'evolution of increased competitive ability' hypothesis; Blossey & Notzold, 1995). Second, these invaders are also vectors and partially resistant to the 'crayfish plague' (*Aphanomyces astaci*), a disease that is deadly to European crayfish species (Lindqvist & Huner, 1999) – a mechanism clearly fitting within the 'enemy of my enemy' hypothesis (Colautti *et al.*, 2004). Somewhat surprisingly, we also found that the occurrence of the signal crayfish is strongly associated with the presence of known competitors. We hypothesize that this could be a geographical signal of propagule pressure since this invader was continuously introduced as a replacement for native species – with which it still co-occurs in many places (Gutiérrez-Yurrita *et al.*, 1999; Skurdal *et al.*, 1999) – and also because it shares some of the pathways of introduction of other exotic competitors (e.g. harvesting in the wild; Souty-Grosset *et al.*, 2006; Holdich *et al.*, 2009).

The occurrence of these two invaders was also found to be only marginally correlated with the human footprint index, suggesting that human disturbance has comparatively little effect on their distributions. Nonetheless, this influence becomes stronger in highly disturbed areas, which seem to affect the signal crayfish negatively and the red swamp crayfish positively. Despite 'human disturbance' sometimes being referred as a potentially important factor for these invaders (e.g. Lindqvist & Huner, 1999), there is little empirical evidence with which to compare our results. In addition, given the relatively low importance of this factor, it is also difficult to exclude the potential confounding effects of propagule pressure. This is because these two invaders have been highly stocked for harvesting in natural to semi-natural areas across Europe. However, the red swamp crayfish is also common as an aquarium pet or in garden ponds, which may explain why it has a higher probability of occurrence in highly urbanized (i.e. disturbed) areas (Henttonen & Huner, 1999). These pathways of introduction could be behind the associations found but more detailed data would be necessary to test this possibility.

Implications for management

The invasion of these two decapods in Europe is the subject of great conservation concern. They have had strong negative impacts on the already declining native crayfish populations (Holdich *et al.*, 2009) and are also associated with reductions in local biodiversity (e.g. Correia & Anastácio, 2008; Cruz *et al.*, 2008). It is thus worrying that our results point to a widening of their ranges in the future. Although also dependent on propagule pressure, the lack of restraining factors other than abiotic conditions, supported by our results, suggests that the distribution of these decapods may increasingly become a spatial representation of their climatic niche. Projections of climatic suitability using the entire range of these species have found that many suitable areas of Europe remain unoccupied (Capinha & Anastácio, 2011; Capinha *et al.*, 2011). In addition, conservationists should also be aware that these predictions may underestimate the actual potential distribution of these invaders due to their apparent ability to occupy climatic conditions not experienced in their native range. In this context, and since eradication has thus far proven difficult (Gherardi *et al.*, 2011), we suggest future efforts should focus primarily on impeding new introductions. Given the large country-related component found on the invasion pattern of these species, we believe that actions at country-level, such as effective legislation, can be of particular importance in this regard.

Future directions

Studies using geographical data to infer drivers of invasion can yield important and relevant information; however, they also suffer from a series of shortcomings and uncertainties. In our study, in particular, the relatively coarse resolution of the data used (50 km × 50 km and country-level) may overlook important aspects of the invasion process. This is even more relevant because identified relationships can be scale-dependent (Fridley *et al.*, 2007). Although our results clearly suggest that propagule pressure and climatic suitability are the most important drivers of the colonization success of these invaders, finer-grained data would be useful to analyse the consistency of these results at varying spatial scales. In addition, future analyses could also greatly benefit from using predictors more directly related to the tested factors. For instance, the human footprint index is focused on terrestrial ecosystems and, despite being unquestionably correlated, it does not provide a direct representation of human disturbance in the freshwater ecosystems which the studied species inhabit. The potential availability of better predictors in the future could be of special interest in further separating causal from co-varying factors, a difficulty often found in studies assessing drivers of invasion (Lockwood *et al.*, 2007) (e.g. here between propagule pressure and human disturbance).

There are also several untested but well-known invasion hypotheses that are not contradicted by our results (e.g. the 'enemy release' hypothesis or the 'evolution of increased competitive ability' hypothesis). It was not possible to test these in this study due to issues of either data availability or the requirement for completely different analytical approaches. However, we encourage future work on performing

such assessments. We further suggest that, when plausible, the implications of future findings should be discussed in terms of the invader's ability to establish under new environmental conditions – particularly in the case of the red swamp crayfish. Despite finding little support for the 'climate matching' hypothesis, this seems to be the exception rather than the rule in biological invasions (Wiens & Graham, 2005; Peterson, 2011). Thus, understanding the mechanisms that confer on certain invaders the ability to shift their climatic niches is of paramount importance in advancing predictions of future invasions (Pearman *et al.*, 2008).

Finally, it would be also of interest to evaluate the relative importance of the tested factors on future stages of invasion. Factors related to the species' introduction (e.g. propagule pressure) are important in emerging invasions, while distributions close to equilibrium mostly reflect the drivers of potential distributions (Wilson *et al.*, 2007). Thus, multistage analyses would help provide more robust estimates of the overall importance of distinct drivers of colonization success or failure.

CONCLUSIONS

We found evidence that, at a continental scale, the patterns of colonization of the signal crayfish and the red swamp crayfish in Europe are primarily determined by the combined influence of the level of introduction effort made in each country and the abiotic conditions of the receiving areas. Additionally, we found a reduced predictive power of the 'human disturbance', 'climate matching' and 'biotic resistance' hypotheses. These results are particularly useful for anticipating future range expansions in these species. Accordingly, and in the absence of measures impeding their dispersal, we predict that these species will increasingly occupy the many climatically suitable areas still available in Europe. This interplay between climatic suitability and propagule pressure also emphasizes the need to account for multi-causality when evaluating colonization success. Instead of testing the isolated role of particular factors, we have highlighted the need for future research in biological invasions to focus more on disentangling the relative roles of multiple, and often interacting, factors which determine invasion success or failure. The use of integrative approaches, such as the ones we used here, may prove particularly useful for this purpose.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of co-occurring crayfish competitors and key references.
Appendix S2 Maps of distribution data and independent variables.
Appendix S3 Supplementary partial dependence plots.

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