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Spatial autocorrelation and the analysis of invasion processes from distribution data: a study with the crayfish *Procambarus clarkii*

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Abstract Complex spatial dynamics are frequent in invasive species; analyzing distribution patterns can help to understand the mechanisms driving invasions. We used different spatial regression techniques to evaluate processes determining the invasion of the red swamp crayfish *Procambarus clarkii*. We evaluated four a priori hypotheses on processes that may determine crayfish invasion: landscape alteration, connectivity, wetland suitability for abiotic and biotic features. We assessed the distribution of *P. clarkii* in 119 waterbodies in a recently invaded area. We used spatially explicit statistical techniques (spatial eigenvector mapping, generalized additive models, Bayesian intrinsic conditional autoregressive models) within an information-theoretic framework to assess the support of hypotheses; we also analyzed the pattern of spatial autocorrelation of data, model residuals, and eigenvectors. We found strong agreement between the results of spatial eigenvector mapping and Bayesian autoregressive models. *Procambarus clarkii* was significantly associated with the largest, permanent wetlands. Additive models suggested also association with human-dominated landscapes, but tended to overfit data. The results indicate that abiotic wetlands features and landscape alteration are major drivers of the species' distribution. Species distribution data, residuals of ordinary least squares regression, and spatial eigenvectors all showed positive and significant spatial autocorrelation at distances up to 2,500 m; this may be caused by the dispersal ability of the species. Our analyses help to understand the processes determining the invasion and to identify the areas most at risk where screening and early management efforts can be focused. The comparison of multiple spatial techniques allows a robust assessment of factors determining complex distribution patterns.

Keywords A priori inference · Habitat selection · Isolation · Landscape composition · Spatial autocorrelation

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Introduction

Understand the mechanisms determining the invasion dynamics can allow us to identify areas where the risk of establishment and invasion is highest, helping to tackle the invasion at the earliest stages and therefore increasing the effectiveness of management (Hulme 2006). However, invasion dynamics are determined by multiple processes embedded within a complex spatial context (McIntire and Fajardo

2009; Gallien et al. 2010); therefore, the identification of ongoing mechanisms can be difficult. Spatial autocorrelation (SAC) is pervasive in ecological data, and arises when nearby localities have similar values for a given parameter. The distribution of invasive species is often affected by strong, positive SAC, as presences in one locality are associated with presence at neighbouring locations. This may occur because areas close to introduction sites have a higher probability of being colonized, determining a clustered distribution (Albright et al. 2009), or because some areas act as "sources" of individuals spreading across the landscape. In these cases, a positive SAC is determined by the dispersal processes occurring during biological invasion (endogenous autocorrelation). SAC can also arise when species distribution is related to (exogenous) environmental features (e.g., climate, landscape) which are in turn spatially autocorrelated (exogenous autocorrelation) (Chapman et al. 2009). SAC has been considered for long as a 'noise' that need to be removed from the data (Legendre 1993). However, recent developments of spatial statistics allowed the incorporation of SAC into models, showing that the analysis of autocorrelation can provide important information on ongoing biological processes (McIntire and Fajardo 2009; Beale et al. 2010).

Inland waters are highly impacted by invasive species (Strayer 2010). Multiple mechanisms, involving both abiotic and biotic parameters, can determine

biological invasions: we considered four hypotheses formulated to explain biological invasions in inland waters (Table 1). (1) Connectivity hypothesis: large, permanent wetlands or rivers can act as sources of invasive populations, therefore invasion risk is highest close to these large waterbodies (Cruz and Rebelo 2007; Rahel 2007). (2) Landscape alteration hypothesis: increased environmental disturbance due to human activities favours synanthropic species including many invasive species; furthermore introductions can be more frequent in human dominated areas. Therefore, human alteration of landscape can increase the risk of introduction and invasion (Ficetola et al. 2007; King and Tschinkel 2008; Leprieur et al. 2008; Cutway and Ehrenfeld 2009). (3) Wetland abiotic features hypothesis: abiotic features (e.g., size, hydroperiod) can strongly affect aquatic species, therefore hydrological and morphological features of waterbodies can determine the likelihood of establishment and invasion (Cruz and Rebelo 2007). (4) Wetland biotic features/vegetation hypothesis: biotic features such as vegetation within and nearby wetlands is a key feature of waterbodies that can have strong effects on animal communities (Van Buskirk 2005; Stohlgren et al. 2006), and therefore can be important also for the establishment of invasive species. Despite not being an exhaustive list of processes that can determine biological invasions, the available data suggest that these a priori general hypotheses may be of primary importance for the

Table 1 A priori hypotheses on processes that may explain the distribution of *P. clarkii*, and environmental variables recorded to test these hypotheses

	Hypothesis	Environmental variables	PCA factors
1	Connectivity along hydrographic network/major waterbodies	Isolation (m)[a]	–
2	Landscape alteration	Urban cover (%)[b]	–
3	Wetland abiotic features	Maximum depth (cm)[a]	Wetland
		Surface area (m^2)[a]	
		Hydroperiod (see text)	
4	Wetland vegetation features	Canopy cover (%)	Vegetation_1, Vegetation_2
		Shoreline vegetation (%)	
		Sum of subemergent, emergent and floating vegetation (%)	
		Surrounding grass (%)	
		Surrounding shrub (%)	

[a] The variable was transformed using natural logarithms

[b] The variable was arcsine square root transformed prior to analysis

study species (see below). Climatic suitability is a further factor that can be important for successful invasions, but our analyses are performed at landscape scale, where climatic heterogeneity is limited; available data suggest that the whole study area is climatically suitable for the study species (Capinha et al. 2011). Teasing apart the processes actually driving invasions from distribution data can be complex. Information theory, and recent developments of spatial statistics constitute a robust framework to develop and test explicit hypotheses on the mechanisms determining spatial patterns of invasive species, and can therefore help to identify the mechanisms driving species invasion (McIntire and Fajardo 2009).

The red swamp crayfish *Procambarus clarkii* is native of Eastern North America, but has been introduced worldwide because of its economic and alimentary value. It is considered among the most important commercial species of crayfish, and is now invasive in five continents (Huner 1994; Barbaresi and Gherardi 2000). Multiple features determine the high invasiveness of *P. clarkii*: it has great ecological plasticity, tolerating a wide range of physical, chemical, and biological conditions. Furthermore, *P. clarkii* can produce, depending on female size, more than 700 eggs; complex mother-offspring relationships can enhance offspring survival increasing the demographic growth of invasive populations (Gherardi 2006; Aquiloni and Gherardi 2008). *Procambarus clarkii* can have multiple negative consequences on native species, ecosystems and human health. It is a polytrophic and opportunistic crayfish, feeding on vegetal detritus but also on molluscs, insects, amphibians, fish and macrophytes, and therefore causing complex changes in food webs and leading to the decline in the abundance and diversity of several native species (Gherardi 2006; Souty-Grosset et al. 2006; Cruz et al. 2008; Ficetola et al. 2011). Furthermore, *P. clarkii* can spread the crayfish plague *Aphanomyces astaci* and outcompete native European crayfishes, thereby causing their decline (Souty-Grosset et al. 2006; Gherardi and Panov 2009). *Procambarus clarkii* is also able to accumulate heavy metals, pesticides and toxins of cyanobacteria transferring them to its consumers, and can spread parasite helminths of the genus *Paragonimus*, potentially pathogenic for humans (Gherardi 2006; Gherardi and Panov 2009). Moreover, *P. clarkii* can damage

agricultural areas such as rice plantations, by feeding on young rice plants, and dams, canals, river and lakes where with its burrowing activity may destabilize banks (Barbaresi and Gherardi 2000; Souty-Grosset et al. 2006; Gherardi and Panov 2009). Its excavation activities also cause sediment resuspension and nutrient release from the sediment to the water. Submerged macrophytes are destroyed using chelipads in non-consumptive actions. Therefore, *P. clarkiis* acts as an ecosystem engineer which modifies the flow of nutrients and alters multiple features of invaded wetlands (Matsuzaki et al. 2009).

The eradication or control of large, invasive populations of *P. clarkii* is challenging (Aquiloni et al. 2009, 2010). The identification of major processes determining the invasion of this species can also help to identify strategies for its management. This study analyzed the spatial distribution of *P. clarkii* at the invasion front, to understand how biotic and abiotic environmental features are related to the spread of this species. We considered four a priori hypotheses representing different biological processes that can explain the invasion of *P. clarkii* (Table 1). We analysed an area of Northern Italy where *P. clarkii* has been introduced only recently; the study area is at the leading edge of the invasion range (Barbaresi and Gherardi 2000; Fea et al. 2006). In this area, the abundance of *P. clarkii* is currently limited, therefore our analysis would allow to identify the mechanisms most important at the early stages of the invasion, i.e., the stages at which management and control can be more effective (Hulme 2006).

Methods

Study area and surveys

We considered 119 waterbodies (ponds, slow stream ditches and small lakes) in Lombardy, Northern Italy, within the upper plain of the Po river at altitudes of 132–397 m a.s.l. (Fig. 1). The study sites were selected to cover the different waterbody typologies proportionally to their abundance; we considered five non-contiguous areas (Fig. 1) to avoid that our data represent only a local situation, and for a more comprehensive assessment of species distribution at regional scale. This region is rich in wetlands, with a complex network of lakes, ponds, rivers and canals of
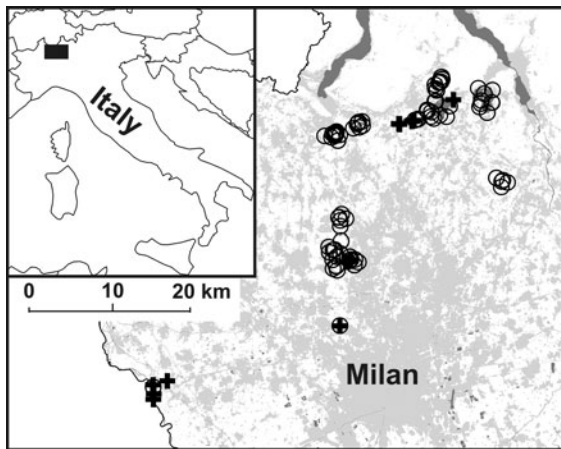
Fig. 1 Study area, and sampled wetlands. *Crosses*: *P. clarkii* detected; *circles*: *P. clarkii* not detected. Some points are superimposed due to geographic proximity

varying size. The study area is currently at the edge of the invasion range of *P. clarkii*; we surveyed areas with published and unpublished records of *P. clarkii* (Barbaresi and Gherardi 2000; Romanò and Riva 2002; Fea et al. 2006), as well as areas where *P. clarkii* has not been recorded, but the species might be present because of proximity to localities of presence and the existence of potentially suitable wetlands.

We surveyed each wetland seven times from March to August to assess the distribution of *P. clarkii*. We used multiple techniques to evaluate species presence, including nocturnal visual encounter surveys, repeated dip-netting of the wetland banks, bottom and vegetation, the identification of burrows and exuviae (Reynolds et al. 2006). Three surveys were held after sunset, using multiple light sources to perform night-viewing and four surveys were performed during daylight. At each survey, multiple researchers sampled each site for about 20 min. We recorded relative humidity and air temperature at each survey; data were recorded in the field using pre-printed tables and a personal digital assistant equipped with GPS and ArcPad GIS software.

Environmental variables

We measured 10 environmental variables describing features of wetlands and the surrounding landscape,

and representing the four a priori hypotheses on factors determining the diffusion of *P. clarkii* (Table 1). *Connectivity hypothesis*. We measured the overland distance to the nearest river, lake or large pond (surface ≥ 1 ha). We used overland distance because several wetlands were not connected to the main hydrographic network, and previous studies on *P. clarkii* showed that this measure may be more appropriate than distance along the hydrographic network, particularly in still water (Cruz and Rebelo 2007). *Landscape alteration hypothesis*. We measured urban cover % (i.e., the landscape percentage occupied by houses, buildings or human infrastructures) in a radius of 400 m from the wetland. We used a 400 m radius as previous studies showed that landscape features at this scale influence the distribution of other species living in similar wetlands (Ficetola et al. 2009); preliminary analyses performed at different scales (100 m; 1,000 m) yielded very similar results. We measured landscape features (connectivity, urban cover) on the basis of the regional Vector Map of Lombardy (2008 land use maps; www.cartografia.regione.lombardia.it). *Wetland features hypothesis*. For each wetland we recorded three abiotic features: Maximum depth, surface area, and hydroperiod (0: temporary, i.e. dry during at least one survey; 1: retained water during all the samplings) (Table 1). *Vegetation hypothesis*. In May, for each wetland we measured four features describing the vegetation of the wetland and of the nearby areas: percentage of canopy cover, percentage of shoreline and emergent vegetation of the wetland, cover of grass and shrubs within 30 m from the wetland. Variables were measured following standard assessment protocols (Ficetola and De Bernardi 2004; Van Buskirk 2005; D'Amore et al. 2010). Vegetation and canopy cover were visually estimated (10% intervals); shoreline vegetation was measured as the percentage of the wetland perimeter with presence of vegetation within 50 cm from the water.

Statistical analyses

A site is surely occupied by a given species if it is detected at that site, but non detecting a species during all sampling occasions does not necessarily indicate the species is absent. Occupancy modelling uses data on presence/absence collected at the same locality during multiple sampling occasions, and

estimates the detection rate of the species, and the probability of presences in sites where species was not detected. It is also possible include site and survey-specific parameters as covariates (MacKenzie et al. 2006; Sewell et al. 2010). We therefore used the software PRESENCE (Hines 2006; MacKenzie et al. 2006) to evaluate the probability of occupancy of sites where we did not detect it. For the analysis, we assumed that probability of detection can be affected by Julian date, hour of survey, air temperature, and relative humidity.

Some of our a priori hypotheses were represented by multiple environmental variables (Table 1). This can pose problems for the analyses, because variables representing the same process are inherently correlated, and intercorrelated variables can bias regression estimates (Berry and Feldman 1985). Furthermore, the number of variables included in an analysis affects its power and the Akaike's Information Criterion (see below). For this reason, we used principal component analysis (PCA) to reduce the variables representing the same hypothesis to a lower number of uncorrelated components. In our analyses, we used the variables extracted by PCA instead of the original variables.

Spatial regression models

Several methods have been proposed for regression analysis of spatial data. Particularly if the dependent variable is non-normal, performance can be quite different among the approaches proposed. Studies comparing the performance of spatial regression techniques have found mixed results, and some techniques showed good performance in some but not in all analyses (Dormann et al. 2007; Bini et al. 2009; Beale et al. 2010). On the other hand, non-normal data (e.g., counts, presence-absence) are extremely frequent in ecological studies. For these reasons, we built our models using three different techniques: spatial eigenvector mapping (SEVM), generalized additive models (GAM) and Bayesian intrinsic conditional autoregressive models (BCA). These methods have different strengths and peculiarities. The comparison among them can allow a more robust inference.

SEVM is relatively new approach, but is increasingly used for the analysis of ecological data. SEVM allows the translation of the spatial arrangement of data points into explanatory variables (eigenvectors)

capturing spatial effects (Dormann et al. 2007). There are multiple implementations of SEVM, depending on how the eigenvectors are generated, and how eigenvectors included into the models are selected (Bini et al. 2009; Peres-Neto and Legendre 2010). In our implementation, we generated eigenvector using Moran's Eigenvector Mapping (Dray et al. 2006; Peres-Neto and Legendre 2010), we selected the eigenvector(s) best reducing the spatial autocorrelation of residuals, and then included eigenvectors as spatial predictors into generalized linear models (Griffith and Peres-Neto 2006; Dormann et al. 2007). Comparisons among statistical methods showed that SEVM is flexible and efficient, also when analysing non-normal data (Dormann et al. 2007; Bini et al. 2009; Peres-Neto and Legendre 2010). Furthermore, the identity of eigenvectors included into models has been proposed to describe the scale at which autocorrelation takes effect (Diniz-Filho and Bini 2005). Our implementation was different from the one in Beale et al. (2010), which generated eigenvectors using principal coordinates of neighbour matrices, and selected eigenvectors correlated with the dependent variable. Simulation showed that the approach used here can be successfully applied for spatial regression of binomial data (Dormann et al. 2007; see also Peres-Neto and Legendre 2010).

GAM are semi-parametric extensions of generalized linear models, in which the response curves of independent variables may be data driven. Following Beale et al. (2010), we incorporated the coordinates of data in GAM as tensor product smooth terms, using thin plate regression splines (Beale et al. 2010); we assumed linear relationships between species distribution and the environmental predictors representing our hypotheses (Beale et al. 2010). Dormann et al. (2007) considered GAMs as non-spatial methods, because they merely account for trends in the data across geographical distances. Nevertheless, simulations showed that GAMs may be able to correctly estimate regression coefficients in spatially structured datasets, with relatively good performance in presence of violations of model assumptions, such as non-stationariety of autocorrelation (Beale et al. 2010).

BCA is a hierarchical Bayesian technique using Markov Chain Monte Carlo (MCMC) to estimate model parameters. BCA incorporates a spatial random effect, describing the neighbourhood of each site, into Bayesian regression models. BCA is therefore

extremely flexible and is able to incorporate the effect of space into the error of the model; simulations showed that BCA is among the spatial techniques with the best performance under a variety of conditions (Latimer et al. 2006; Beale et al. 2010). We built BCA assuming a Bernoulli error distribution following the approach of Latimer et al. (2006). To avoid numerical overflow, we used a stabilized logit function excluding extreme logit values (Kéry 2010, p. 281). For each analysis, we run three different MCMC chains, to ensure convergence. For each chain, we performed a burnin of 15,000 iterations, followed by 500,000 iterations sampled with a tinning interval of 10. For all models, examination of plots indicated convergence of chains in less than 15,000 iterations. We then calculated the estimates of regression coefficients beta, and their 90 and 95% highest posterior density Bayesian credible intervals (HPDI).

We used an information-theoretic approach, following the procedure detailed in Denoël et al. (2009), to evaluate the support of the hypotheses explaining the distribution of *P. clarkii* (Burnham and Anderson 2002; McIntire and Fajardo 2009). First, we built models relating to presence/absence of *P. clarkii* to the variables representing the four a priori hypotheses (Table 1). We built exploratory models considering only one hypothesis at each time; subsequently, we built complex models representing all combinations of hypotheses. We then calculated the Akaike's Information Criterion (AIC) for each model: AIC trades-off explanatory power versus number of predictors; parsimonious models explaining more variation have the lowest AIC values and are considered to be the "best models". AIC may select overly complex models (Raffalovich et al. 2008), therefore we considered a complex model as a candidate model only if it had AIC less than the AIC of all its simpler nested models (Burnham and Anderson 2002; Richards et al. 2011; but see also Symonds and Moussalli 2011 for comments on this approach). For each candidate model, we calculated the Akaike's weight w (AIC weight), representing the probability of the different models given the data (Lukacs et al. 2007). We estimated the amount of variation explained by models using Nagelkerke's R^2 (R_N^2), which is a generalized form of coefficient of determination that can be applied to maximum likelihood models (Nagelkerke 1991). This procedure was repeated

twice, with SEVMs and with GAMs; in these models, we assumed binomial error distribution.

Information criteria such as the Deviance Information Criterion can be used to compare Bayesian models, but are extremely problematic for complex hierarchical models such as BCA (Latimer et al. 2006; Kéry 2010). For this reason, we did not use the information-theoretic approach with BCA. Instead, having identified models with $w > 0.01$ in SEVM or GAM analyses, we built the corresponding BCA models, and evaluated the correspondence between the results of the three techniques.

We used variance partitioning to evaluate the amount of variation explained by the environmental variables and by "spatial variables", represented by extracted eigenvector(s) in SEVM, and by the coordinates included as covariates in GAMs (Cushman and McGarigal 2002; Beale et al. 2010).

Finally, we analysed the pattern of spatial autocorrelation, to evaluate whether it can provide information about the scale at which the invasion process occurs. We used Moran's I to assess at multiple spatial scales the spatial autocorrelation of (a) the distribution of *P. clarkii*; (b) the eigenvector(s) extracted by the best SEVM model to reduce spatial autocorrelation, because it has been suggested that eigenvectors may be indicative of the spatial scale at which autocorrelation takes effect (Diniz-Filho and Bini 2005; Dormann et al. 2007); and (c) the residuals of an ordinary least squares (OLS) logistic model relating *P. clarkii* distribution to wetland features and urban cover (the best model obtained in SEVM and GAM; see results). OLS is a non-spatial regression technique, and is clearly not appropriate for the analysis of our data. However, the variation not accounted for by environmental variables (i.e., the residuals) may be affected by intrinsic processes determining spatial distribution (Dormann 2009). We performed analyses using R 2.9 (www.r-project.org) and OpenBugs 3.1.1 (Thomas et al. 2006); we built correlograms using SAM 3.0 (Rangel et al. 2010).

Results

We detected *P. clarkii* in 16 out of the 119 wetlands (Fig. 1). In all wetlands where we detected its presence, we also detected the presence of juveniles,

indicating that these constitute reproductive populations.

The analysis of detectability showed that, for all sites where we did not observe *P. clarkii*, the probability of occupancy was always <0.01; for all wetlands, four surveys were always enough to detect *P. clarkii* with confidence > 95%. This indicates that our surveys estimated presence/absence with reliability.

For the variables describing wetland features, PCA extracted a single component representing 49% of variation of original variables; this variable (hereafter: WETLAND) was positively correlated to wetland area ($r = 0.56$, $P < 0.001$), depth ($r = 0.83$, $P < 0.001$) and permanent hydroperiod ($r = 0.68$, $P < 0.001$). For the variables describing vegetation features, PCA extracted two components. The first component (VEGETATION_1) explained 43% of variance, and was significantly correlated to riparian vegetation ($r = 0.88$, $P < 0.001$), surrounding grass ($r = 0.90$, $P < 0.001$) and shrubs ($r = 0.74$, $P < 0.001$); the second component (VEGETATION_2) explained 26% of variance, and was significantly correlated to canopy cover ($r = 0.81$, $P < 0.001$), riparian vegetation ($r = -0.21$, $P = 0.02$), emergent vegetation ($r = 0.74$, $P < 0.001$) and surrounding shrubs ($r = 0.24$, $P = 0.009$).

Exploratory models

Using both SEVM and GAMs, *P. clarkii* was significantly associated with less isolated wetlands, and to large, permanent wetlands (Table 2). Furthermore, in GAMs *P. clarkii* was associated with wetlands with low scores for the variable Vegetation_2, representing an association with limited canopy cover and abundant emergent vegetation. BCA supported the results of SEVM, indicating a strong association with the large, permanent wetlands, and a weaker association with the less isolated wetlands.

Spatial eigenvector mapping

In all SEVMs, one eigenvector was enough to reduce spatial autocorrelation to non-significant values and was included in the models. The eigenvector best reducing autocorrelation was the same in all models with high support (eigenvector #3).

The model with the highest AIC weight suggests that the distribution of *P. clarkii* is influenced by the joint effect of wetland abiotic features and landscape alteration (Table 3a). According to this model, *P. clarkii* was significantly associated to the largest, permanent wetlands ($\chi^2_1 = 12.4$, $P < 0.001$); although urban cover was included in this model, it did not show a significant effect ($\chi^2_1 = 2.7$, $P = 0.10$). This model explained a substantial proportion of variation ($R^2_L = 0.42$). In the best model, the SEVM eigenvector accounted for most of the explained variation (62%); wetland features were the environmental variable with the highest explanatory power, while the contribution of urbanization was limited (Table 4a). A simpler model, that did not consider urbanization, had a slightly lower support ($w = 0.41$), and explained a comparable amount of variation. A candidate model considering isolation only had a lower support ($w = 0.01$). Vegetation was not included in candidate model with high support.

Table 2 Exploratory models considering only one hypothesis

Variables	SEVM			GAM			BCA		
	B	χ^2_1	P	B	χ^2_1	P	Median	90% HPDI	95% HPDI
Isolation	−0.27	4.24	**0.039**	−7.74	15.82	**<0.001**	−0.35	**−0.69/−0.06**	−1.19/0.003
Urban cover	−2.16	1.94	0.163	−11.18	0.79	0.375	−0.27	−3.35/2.83	−3.97/3.44
Wetland[a]	1.61	11.65	**<0.001**	8.92	419.30	**<0.001**	1.02	**0.08/2.37**	**0.22/2.09**
Vegetation_1[a]	−0.27	0.39	0.531	−0.57	0.89	0.346	−0.06	−0.91/0.76	−1.14/0.95
Vegetation_2[a]	−0.19	0.81	0.367	−2.54	20.33	**<0.001**	−0.49	−1.42/0.45	−1.26/0.26

For SEVMs and GAMs, significance values are reported

For BCA, estimated beta values along with 90% and 95% highest posterior density intervals (HPDI) are reported; HPDI non overlapping zero are in bold

[a] PCA scores. See Table 1

Table 3 Candidate models explaining the distribution of *P. clarkii* in 119 wetlands, on the basis of environmental variables

Rank	Environmental variables	R_N^2	K	AIC	Δ-AIC	w
a:	*Spatial eigenvector mapping*					
a1	Wetland features[a] (+**); Urban cover (−), SEVM eigenvector	0.42	4	70.67	0.00	0.581
a2	Wetland features[a] (+**); SEVM eigenvector	0.39	3	71.38	0.71	0.406
a3	Isolation (−*), SEVM eigenvector	0.30	3	78.79	8.12	0.010
b:	*Generalized additive models*					
b1	Wetland features[a] (+**); Urban cover (+**)	0.99	7.4	15.36	0.00	0.691
b2	Wetland features[a] (+**); Isolation (−**)	0.99	8.7	17.59	2.23	0.227
b3	Wetland features[a] (+**)	0.99	9.7	19.75	4.39	0.077

a: Models built using spatial eigenvector mapping (SEVM); b: models built using generalized additive models (GAMs). Models are ranked according to their Δ-AIC; the model with the lowest Δ-AIC is the best AIC model. The sign after variable names represent the sign of regression coefficients. Only models with Δ-AIC < 10 are shown

R_N^2 Nagelkerke's R^2, *AIC* Akaike information criterion, *K* number of parameters in the model, Δ-AIC difference between the AIC of each model and the AIC of the best model, *w* AIC weight of the model

* $P < 0.05$; ** $P < 0.01$

[a] PCA scores, see Table 1. (+) indicate association with large, permanent wetlands

Generalized additive models

Also with GAMs, the model with the highest weight ($w = 0.69$) was the one considering the joint effect of wetland abiotic features and landscape alteration (Table 3b). According to this model, *P. clarkii* was significantly associated to the largest, permanent wetlands within the most human-dominated landscapes ($P < 0.001$ for both variables). A second model, considering the joint effect of wetland features and isolation, had a lower support ($w = 0.23$; Table 3b). This second model suggests that *P. clarkii* was associated to the large, permanent wetlands less isolated from the major waterbodies. A simpler model, considering wetland features only, had a limited support ($w = 0.08$). All models that excluded wetland features had very low support. Vegetation features were not included in models with high support (Table 3b). Also with GAMs, the spatial component explained most of variation; wetland features was the environmental variable with the highest contribution, while urban cover and isolation explained a minor proportion of variation (Table 4b, c). Finally, it should be remarked that when using GAMs, the best models explained nearly 99% of variation, suggesting that some form of overfitting may occur despite the limited number of parameters (Table 3).

Bayesian conditional autoregressive models

The results of BCA models were in strong agreement with those of SEVM. If wetland features and urban cover are included as independent variables in the same model (models a1 and b1 in Table 3), *P. clarkii* was strongly associated with the largest permanent

Table 4 Variance partitioning representing the amount of explained variation accounted for by the best models

Variable	%
a: Spatial eigenvector mapping	
Wetland features	26.4
Urban cover	6.9
Space (SEVM eigenvector)	62.1
Joint	4.6
b: Generalized additive models, Model 1	
Wetland features	22.3
Urban cover	7.1
Space (coordinates)	63.1
Joint	7.4
c: Generalized additive models, Model 2	
Wetland features	22.7
Isolation	12.8
Space (coordinates)	53.8
Joint	10.6

wetlands (beta = 1.05, 95% HPDI: 0.11/2.26) while for urban cover the credible intervals overlapped zero (beta = −1.07, 95% HPDI: −5.25/3.05, 90% HPDI: −4.54/2.14).

If wetland features and isolation are included as independent variables in the same model (model b2 in Table 3), *P. clarkii* was associated with the largest permanent wetlands, but 95% intervals slightly overlapped zero (beta = 0.89, 95% HPDI: −0.07/2.07; 90% HPDI: 0.08/1.86;). For isolation, the intervals overlapped zero more widely (beta = −0.20, 90% HPDI: −0.58/0.16).

Spatial autocorrelation

Autocorrelation of species distribution was positive and significant at distances up to 2,500 m (Fig. 2a). OLS residuals and the eigenvector extracted by SEVM showed similar autocorrelation pattern, with

generally positive and significant values at distance up to 2,500 m, and negative or nonsignificant values at distances > 5,000 m (Fig. 2a). Spatial autocorrelation was considerably lower for the residuals of SEVM and GAM (Fig. 2b).

Discussion

Comparison among statistical methods

The use of multiple statistical approaches, integrating spatial autocorrelation, allowed us to identify the processes that most likely explain the distribution of *P. clarkii* at the early stages of the invasion (discussed below). There was a strong agreement between the results of SEVM and those of BCA (e.g., Table 2). For instance, the regression coefficients estimated by SEVM were always within the
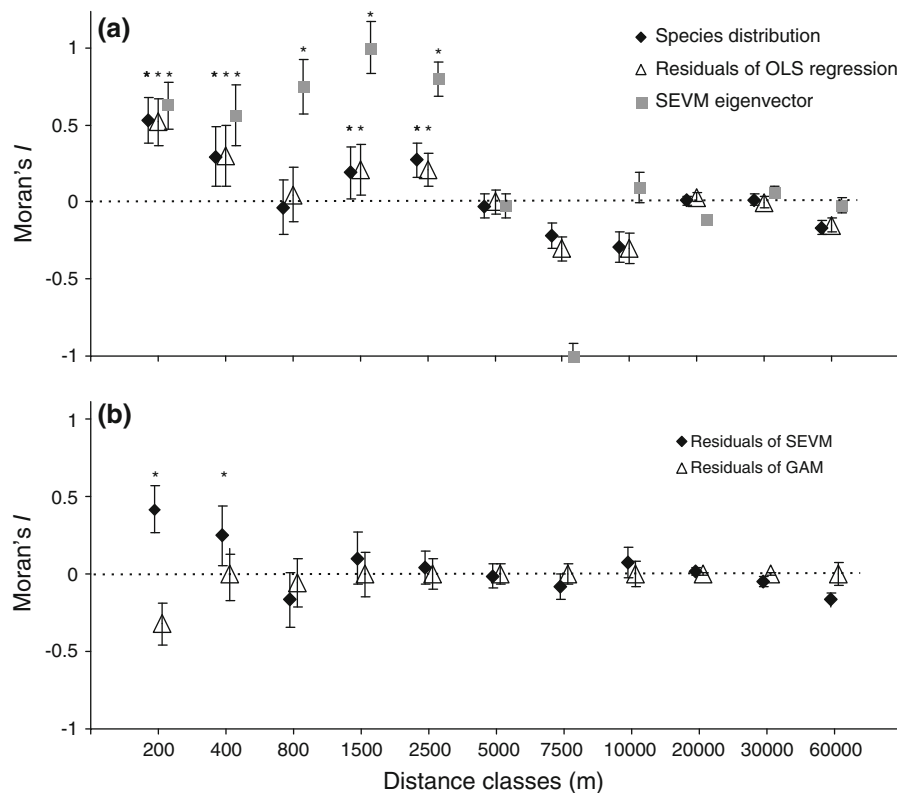

Fig. 2 Spatial autocorrelation (Moran's *I*), measured at multiple distance classes. **a** Distribution pattern of *P. clarkii* (*black diamonds*); residuals of OLS regression relating *P. clarkii* distribution to environmental variables (*empty triangles*); and eigenvector extracted by SEVM (*grey squares*).

b residuals of the highest AIC SEVM (*black diamonds*) and of the highest AIC GAM (*empty triangles*). *Error bars* represent twice the standard error of Moran's *I*; *asterisks* indicate that *I* was positive and significant

90% HPD intervals of BCA, and the signs of relationships were always in agreement (Table 2). BCA was slightly more conservative than SEVM. However, small differences between the methods are non unexpected, as Bayesian and inferential statistics have a completely different underlying approach (Kéry 2010). Furthermore, the two methods take into account autocorrelations in different ways (see methods section). The similarity of the results of these approaches suggests that the conclusions about the study system are robust. Nevertheless, the two approaches have different strengths. BCA is particularly flexible, because of the hierarchical Bayesian framework, and because it incorporates "space" in the error model (Latimer et al. 2006; Beale et al. 2010; Kéry 2010). However, the calculation of information criteria (such as AIC) may be problematic for hierarchical Bayesian models, limiting the possibility to use the information theoretic approach (Latimer et al. 2006; McIntire and Fajardo 2009; Kéry 2010). Strengths of SEVM include the possibility to analyze the extracted eigenvectors, which may provide information on the scale of ongoing spatial processes (Diniz-Filho and Bini 2005).

All three techniques identified abiotic wetland parameters as the most important features for crayfish invasions. However, results of GAM were somehow different, as they suggested also a possible strongly significant role for landscape alteration and isolation, and coefficient estimates were dissimilar from those of the other techniques (Table 2). Some debate is ongoing on the appropriateness of GAMs for spatial analyses (compare Dormann 2007; Beale et al. 2010). The situation may be particularly complex with binomial dependent variables; further simulation studies will have to assess their performance under these conditions. The spatially-explicit analysis of binary data is complex and still relatively uncommon in ecology, and to date there is not a "best technique" that can be applied under all conditions. Presence/absence data are among the most easily available data on species distribution, are invaluable to understand ecological processes, but often need to be analyzed within a spatially explicit framework. The use of multiple statistical approaches, and the comparison of results, can help a robust assessment of factors actually determining the spatial distribution of species.

Invasion processes

All models suggested that the suitability for abiotic features is the most likely driver of the distribution of *P. clarkii*. *Procambarus clarkii* is a generalist species that can occupy a wide range of wetlands, including small temporary waterbodies; it has been suggested that habitat characteristics can have only marginal significance (Gherardi 2006; Cruz and Rebelo 2007). Nevertheless, our analyses showed that, at the early stages of the invasion, wetland features can be extremely important for crayfish distribution: *P. clarkii* was strongly associated to large and permanent wetlands. Wetland hydroperiod is known to be a limiting factor for the presence of this species: *P. clarkii* can also be found in temporary wetlands, but in such habitats it needs shelter, like boulders, wood debris, crevices or a silt substrate to make burrows and retain the humidity, allowing their survival (Correia and Ferreira 1995; Ilhéu et al. 2003; Cruz and Rebelo 2007). Furthermore, wetlands should have a hydroperiod longer than 4 months for the persistence of *P. clarkii* (Gutiérrez Yurrita and Montes 1999). Large, permanent wetlands can therefore act as major sources of *P. clarkii*, and the proximity to such wetlands is a key factor determining crayfish presence in temporary biotopes (Cruz and Rebelo 2007). In our study, we have detected a significant effect of isolation in exploratory univariate models (Table 2), but the support of the isolation hypothesis was limited in multivariate models (Table 3). The difference between our results and the ones of Cruz and Rebelo (2007) may be related to differences in statistical modelling. In our analyses we included predictors describing the spatial arrangement of data. These "spatial predictors" were extremely important in explaining crayfish distribution and accounted for most of the variation explained by models (>50%; Table 4). Therefore, we do not argue that proximity to potentially source areas is unimportant. Instead, the analysis of spatial autocorrelation helps to explicitly assess the scale at which isolation may take effect, influencing wetland occupancy.

Spatial autocorrelation is pervasive in species distribution, and can be caused by exogenous and endogenous processes (Wagner and Fortin 2005; Beale et al. 2010). Discriminating between exogenous and endogenous autocorrelation is challenging; in principle, exogenous autocorrelation can be removed

from models if all relevant autocorrelated predictors are considered. Although it is always possible that some relevant, unidentified predictor is missing, the analysis of residual autocorrelation, or the analysis of "spatial predictors" removing autocorrelation (e.g., SEVM eigenvectors), can provide insight on endogenous processes determining species distribution (Diniz-Filho and Bini 2005; Dormann et al. 2007; Van Teeffelen and Ovaskainen 2007; Chapman et al. 2009; Dormann 2009). In our analysis, species distribution was positively autocorrelated at distances up to 2,500 m (Fig. 2); this indicates that wetlands that are less than 2,500 m apart tend to have similar occupancy. In other words, the presence of occupied wetlands within 2,500 m increases the likelihood of occurrence of *P. clarkii*. The pattern of autocorrelation was similar for raw species distribution data, for the residuals of OLS models and for the SEVM eigenvectors (Fig. 2); the similarity of results obtained through different approaches suggests that autocorrelation may be linked to some endogenous process. Dispersal is a major source of endogenous autocorrelation (Beale et al. 2010). *Procambarus clarkii* shows physiological and ethological adaptations allowing a remarkable dispersal ability (Barbaresi and Gherardi 2000; Payette and McGaw 2003; Gherardi 2006). It can disperse both in water and overland; the overall locomotory activity can even exceed 3 km per day (Barbaresi and Gherardi 2000; Gherardi et al. 2002). Therefore 2,500 m might correspond to the distance at which dispersal influences the distribution of populations; analyses performed in the Iberian peninsula using logistic regression yielded comparable results, and showed that the likelihood of presence of *P. clarkii* increases if there are occupied wetlands at distances ≤2,000 m (Cruz and Rebelo 2007). In this respect, the analysis of spatial autocorrelation may be more flexible and appropriate than logistic regression to identify such distance, because it is a spatially explicit approach, while logistic regression has constraints limiting its capability to detect threshold distances (Ficetola and Denoël 2009). Furthermore, dispersal is often context dependent, and individuals can cover different distances in diverse environments (Cruz and Rebelo 2007; Olden 2007). Lastly, natural dispersal is not the only possible explanation of the autocorrelation pattern. *Procambarus clarkii* is sometime captured by fishermen that may release it in nearby wetlands (i.e., human assisted dispersal). It is also possible that our analyses lack relevant autocorrelated predictors that influence species distribution.

Both global and landscape analyses showed that human impact and landscape alteration are key drivers of the distribution of invasive species (Ficetola et al. 2007; King and Tschinkel 2008; Leprieur et al. 2008; Cutway and Ehrenfeld 2009). The results of GAM were in agreement with this hypothesis (Table 3). Landscape alteration may facilitate the presence of alien species through multiple, nonexclusive mechanisms. First, proximity to urban areas increases the possibility that humans introduce alien species into new wetlands (Cruz and Rebelo 2007; Cutway and Ehrenfeld 2009; Hirsch 2009). Furthermore, wetlands in altered landscapes can have simplified communities with a reduced number of species and different predators (Pickett et al. 2001; Didham et al. 2007). Generalist invasive predators with high tolerance to human disturbance, such as *P. clarkii*, can take advantage of these environmental features, reaching high densities and potentially disperse to more natural environments (Didham et al. 2007; Cutway and Ehrenfeld 2009). Nevertheless, the other approaches (SEVM and BCA) did not clearly support this hypothesis, and in all models landscape alteration explained a limited amount of variation (Table 4), suggesting that the other processes may be more important.

It has been proposed that biotic factors are key parameters for the establishment of invasive species (Stohlgren et al. 2006). However, some studies performed in freshwaters showed that the distribution of alien species is most strongly related to abiotic features, suggesting a minor role for biotic features (Quinn et al. 2011). Our analyses are in agreement with these findings: vegetation was much less important than abiotic parameters for *P. clarkii*. Clearly, the importance of vegetation can be different for other invasive species.

Finally, it should remarked that our analysis considered only one time interval. Spatial analyses focusing on one snapshot can quickly provide useful information on dynamics (Chapman et al. 2009), helping to set up immediate conservation actions. Nevertheless, multi-year analyses are needed for a more accurate assessment of invasion processes, and allow to validate the findings of snapshot studies (Ficetola et al. 2010).

Conservation implications

Our analyses suggest that crayfish invasion can be favored by the colonization of large, permanent wetlands (e.g., small lakes, large ponds), where it can establish numerous and stable populations. These waterbodies can act as a source for the dispersal and colonization of nearby smaller, temporary or isolated wetlands (Gherardi et al. 2002; Cruz and Rebelo 2007; Keller et al. 2008). Prevention of new introductions would certainly be the optimal strategy to limit the spread of this species (Keller et al. 2008). Unfortunately, new introductions continue: the identification of major factors determining the early stages of invasion may help to set up protocols for early monitoring, and we feel that our analyses help to identify areas most at risk and where screening can be focused. Early detection when crayfishes are at low densities may allow for the establishment of control strategies that maintain low densities (Hein et al. 2007; Aquiloni et al. 2009; Aquiloni et al. 2010), and therefore limit the dispersal into nearby but isolated waterbodies.

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