

Assessing the consequences of biological invasions on species with complex life cycles: Impact of the alien crayfish *Procambarus clarkii* on Odonata



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ABSTRACT

The temporal dimension is a key parameter when analysing the impact of invasive alien species. Studies on early invasion stages allow a better understanding of how ongoing processes modify native communities, helping to plan effective management actions. *Procambarus clarkii* is an invasive crayfish influencing multiple features of invaded wetlands, but unravelling its impact on organisms with complex life cycles is difficult. We monitored 107 wetlands in Northern Italy, and evaluated the relationships between *P. clarkii* and the richness of three life history stages of odonates: adults, larvae and exuviae. We measured environmental features of each wetland and the natural vegetation in the surrounding landscape. We used an information-theoretic approach to relate species richness of the three life history stages of odonates to: wetland features, features of the surrounding landscape; crayfish presence. We used a spatially explicit technique (Moran Eigenvector Mapping) allowing the integration of spatial autocorrelation into analyses. Wetland and landscape features explained a significant amount of community richness. Wetland hydroperiod, canopy cover and stream velocity were the variables most strongly related to odonate richness. Furthermore, we observed significant relationships between *P. clarkii* and the richness of odonate communities, but the effect of the crayfish on the three odonate stages was different. Species richness measured using both larvae and exuviae was negatively related to the crayfish presence, while negative effects on adults were not evident. Furthermore, negative relationships were observed for Anisoptera (dragonflies) but not for Zygoptera (damselflies). A significant effect of eigenvectors representing spatial configuration suggests an important role of dispersal-related mechanisms in maintaining species richness in invaded wetlands, where fitness is likely lower. Larvae and exuviae may be more helpful for the assessment of the impact of invasive species at early stages of the invasions, while adults may better describe the long term consequences of the invasion at the landscape scale. Considering multiple life-history stages improves our understanding of the impact of biological invasions in freshwaters.

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1. Introduction

Many native ecosystems have been irretrievably modified by invasive alien species (IAS), which determined the decline and the

extinction of native species, and fresh waters may be particularly susceptible to the effects of invasions (Drake, 2009; Gherardi, 2007; Strayer, 2010). IAS can damage native species through multiple mechanisms, including competition, predation, spread of diseases and hybridization (Pimentel, 2002). Prevention of new introductions is the optimal strategy to avoid the negative consequences of IAS. However, if prevention fails, earlier management actions have, at the same cost, the greatest effectiveness (Allendorf and Lundquist, 2003; Leung et al., 2012), and management priority is given to species showing the strongest negative impact (Jeschke

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and Strayer, 2005; Vilà et al., 2010). Research is therefore required on the early assessment of the environmental impact of alien species, and to set up correct management actions (Leung et al., 2012; Vilà et al., 2010).

Biological invasions can be described as multi-step processes: first, the introduced species must arrive, survive, and establish itself in a new area; second, the alien species become invasive, spreads, and impacts on native environment and native species (Allendorf and Lundquist, 2003; Leung et al., 2012). During the different invasion stages, complex ecological processes occur in invaded habitats, including changes in the invaded biological community, in the features of invaders, in the abiotic environment, and in the interaction between the ecosystem components. The temporal dimension is a key parameter to be considered when analysing the effects of IAS (Strayer et al., 2006). Research on later phases of invasion often describes widely altered communities, in contrast, the study of early stages allow a better understanding how ongoing processes modify the invaded communities.

Procambarus clarkii is a crayfish native of Eastern North America, now invasive over five continents (Liu et al., 2011). It is considered one of the 100 worst IAS in Europe (Drake, 2009), it has high fecundity and great ecological plasticity that determine its invasiveness (Aquiloni and Gherardi, 2008; Gherardi, 2006; Hazlett et al., 2003; Siesa et al., 2011). *P. clarkii* is a polytrophic opportunistic crayfish that can modify habitats, altering the flow of nutrients, and determining multiple negative consequences on native species and ecosystems (Gherardi, 2006; Matsuzaki et al., 2009). *P. clarkii* feeds on detritus, macrophytes, molluscs, fishes, amphibians and insects, reducing the biodiversity of freshwater communities (Ficetola et al., 2012b, 2011b; Gherardi, 2006; Klose and Cooper, 2012; McCarthy et al., 2006; Nunes et al., 2013; Souty-Grosset et al., 2006).

Laboratory tests, gut contents and isotopic analyses showed that *P. clarkii* can feed on odonates, even preferring them to other food items like living fish and vegetal matter (Correia, 2003; Ilheu and Bernardo, 1993). However, information on the impact of *P. clarkii* on odonate communities in natural environments remains limited (Giugliano et al., 2012; Miyake and Miyashita, 2011; Ott and Samways, 2010). Odonates are frequently used bioindicators, and can help to evaluate freshwater biodiversity and to assess water-body health (Kutcher and Bried, 2014; Oertli, 2008; Sahlen and Ekstubbbe, 2001; Samways, 2008). However, odonates show a complex life cycle with aquatic larvae and adults living in sub-aerial conditions. *P. clarkii* is thus expected to have a strong direct impact on aquatic life stages only. Analysing relationships between *P. clarkii* and the different odonate life cycle stages can help to disentangle the mechanisms determining the impact of IAS on species with complex life cycles (McCauley et al., 2008), and to evaluate the optimal strategy which life history stages of odonates are most suitable for the monitoring of IAS on wetlands.

The aim of this study was to assess relationships between the richness of odonate communities and *P. clarkii* in a recently invaded area. In particular, we evaluated the relationships between *P. clarkii* and the community richness of (1) adult odonates; (2) larvae, and (3) exuviae. Performing analyses on these three different stages allows to assess their suitability as indicators of the overall impact of this IAS, and to identify processes determining impact. Adult odonates show a great dispersal ability, adults therefore represent the total distribution of dragonflies; larvae indicate that adults choose the wetland for reproduction and that the offspring grew in wetlands, and exuviae indicate the successful larval development and the complement of the life cycle (Corbet, 2004; Córdoba-Aguilar, 2008; Kutcher and Bried, 2014). In all our analyses we also considered spatial autocorrelation and environmental features, to take into account their potential effects on the investigated community.

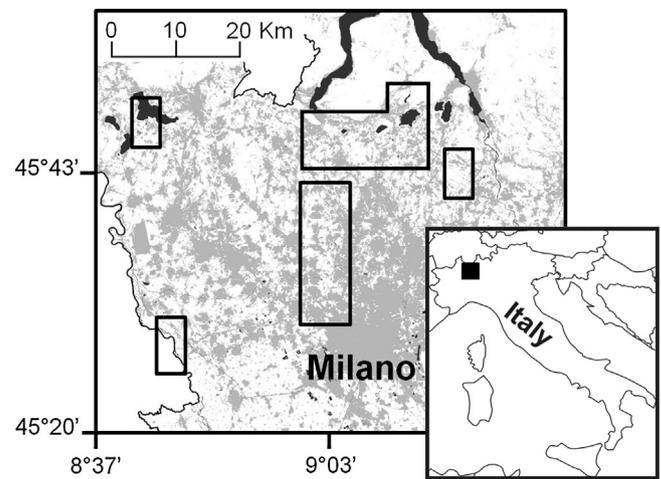


Fig. 1. Study area (Lombardy region, Northern Italy). Black lines enclose the areas where wetlands were located, dark shaded areas represent lakes and major rivers, light shaded areas represent urban areas.

2. Methods

2.1. Study area and methods outline

We considered 107 waterbodies [ponds ($N=66$), slow streams ($N=14$), ditches ($N=19$), and small lakes ($N=8$)] in the Lombardy region, northern Italy, in an area including the upper Po River plain and the Brianza foothills. The altitude ranges between 132 m and 397 m; the annual average temperature ranges between 10 °C and 14.4 °C, and the annual mean rainfall is 1400–1600 mm (Gerletti and Marchetti, 1977). The landscape is human dominated (Fig. 1), with large agricultural and urban areas, and is characterized by a complex network of lakes, ponds, rivers, and canals. In this region, several natural parks host important freshwater communities. The area was recently invaded by *P. clarkii*, approximately between 2004 and 2006 (Fea et al., 2006; Siesa et al., 2011), and *P. clarkii* currently has a highly fragmented distribution in the area (Siesa et al., 2011).

We performed six surveys for each wetland, to evaluate the presence/absence of *P. clarkii* and odonate adults, larvae and exuviae. In a subset of 34 wetlands, we performed additional sampling to obtain quantitative estimates of the abundance of odonate larvae and *P. clarkii*. Surveys including the three life cycle stages provide more detailed information than considering adults only; in particular, exuviae provide useful indications on all other life stages and represent the reproductive success at breeding sites (Córdoba-Aguilar, 2008; Ott, 2010).

2.2. Surveys: odonate communities and *P. clarkii*

From May to August 2009, we used a combination of multiple techniques to assess the presence of *P. clarkii*, adult odonates, larvae and exuviae. We performed at least 4 surveys in daytime and two surveys after dusk. For *P. clarkii*, we used nocturnal and diurnal visual census of individuals and exuviae helped by dip netting (Reynolds et al., 2006). Detectability analyses performed using PRESENCE (Hines, 2006; MacKenzie et al., 2006) showed that this sampling allows a reliable assessment of the presence of *P. clarkii* (after 4 surveys, probability of non-detecting present crayfish <0.05 ; Siesa et al., 2011). To assess the distribution of odonates, we explored wetlands during the central hours of the day, with sunny weather and little or no wind; during each survey we performed a visual census of adults and last instar exuviae by using aerial net, sweep net and binoculars. Captured adults

were identified in the field using magnifying lens (Oertli, 2008), while exuviae were collected and identified in the laboratory using standard keys (Carchini, 1983; Heidemann and Seidenbusch, 2002).

In late May–early June 2010 we performed an additional survey using pipe sampling to assess the abundance of odonate larvae and crayfish (McCauley et al., 2008; Werner et al., 2009). Pipe sampling was focused on a subsample of 34 wetlands, while keeping a balanced ratio (50%) between wetlands invaded and not invaded by the crayfish. We used a 0.25 m² circular pipe sampler (diameter: 0.6 m); samples were collected by quietly approaching an area and quickly sinking the pipe through the water column into the sediments, to seal the sample area. Special care was devoted to limit the escape of large individuals before sampling. Despite this approach may underestimate the presence of adult crayfishes, crayfish abundance obtained with pipe sampling correlates well with the density of multiple components of freshwater communities, suggesting that this technique provides a good index of their abundance and impact (Ficetola et al., 2012b). We used small nets (1 mm mesh size) to remove all animals from the water column and from the first centimetres of the sediment. Net sweeps were stopped after at least 10 consecutive sweeps without capturing any animal (Werner et al., 2009). To limit density bias caused by the aggregation of individuals, we collected multiple samples from different areas of the same wetland and from different microhabitats (average: four samples per wetland). Odonate larvae were stored in ethanol and identified in the laboratory following standard keys (Carchini, 1983; Heidemann and Seidenbusch, 2002). Because of the morphological overlapping, particularly during early larval stages, in our analysis we pooled larvae of the following species into one single species groups: (1) *Coenagrion puella* and *C. pulchellum* as *C. puella-pulchellum*; (2) *Sympetrum sanguineum* and *S. striolatum* as *S. sanguineum-striolatum* (see Supplementary Online Material, Appendix S1). During pipe sampling, individuals of *P. clarkii* were weighed to measure their mass (g/m²).

2.3. Environmental variables

In late May–June, we recorded five variables used as standard characterization of wetlands: surface area (m²), maximum depth (cm), water permanence [permanent: retained water during the whole study period (May–August 2009 + May 2010); temporary: found dry at least one time], average stream velocity (m/s), canopy cover percentage (visual estimate; rank scale). Variables were recorded using standard bio-assessment protocols; details on their measurement are reported elsewhere (Barbour et al., 1999; Ficetola et al., 2011a; Siesa et al., 2011; Van Buskirk, 2005). All wetlands where we performed pipe sampling had still water, therefore stream velocity was not included as environmental variable in the analyses of larval richness. Furthermore, as odonate communities are affected by landscape features (Hamasaki et al., 2009; Samways and Steytler, 1996), we used the ArcView GIS (© ESRI, 1999) to measure the percentage of natural vegetation in the landscape surrounding each wetland, on the basis of the 2008 vector map of the Lombardy region (www.cartografia.regione.lombardia.it). Landscape natural vegetation was measured in a radius of 400 m from each wetland, as this scale captures well the effect of landscape on the communities of semi-aquatic animals (Ficetola et al., 2009).

2.4. Statistical analyses

We used generalized linear models (GLMs) to evaluate the relationships between the richness of odonate communities, the presence of *P. clarkii*, and the environmental features. We repeated analyses three times (adults, larvae, and exuviae) and at three levels [whole community, Anisoptera only (dragonflies), and Zygoptera

only (damselflies)]. In each analysis, community richness (number of species) was the dependent variable, while we considered environmental variables and *P. clarkii* presence as independent variables. For the analysis of adults and exuviae, we considered 107 wetlands and the distribution of *P. clarkii* was described by presence–absence data. For the analysis of larvae, we considered 34 wetlands, and we included as independent variable the abundance of *P. clarkii* (g/m²) instead of crayfish presence/absence, because abundance probably provides a better estimate of crayfish impact (see e.g. Ficetola et al., 2012b).

We used an information-theoretic approach, based on Akaike's Information Criterion (AIC) to identify the variables best explaining the richness of odonate communities. First, we built GLMs (Poisson error distribution), relating community richness to all combinations of independent variables, and we calculated the 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 (Burnham and Anderson, 2002; Symonds and Moussalli, 2011). Models were ranked according to their AIC values. For each model *i*, we calculated the AIC weight w_i , which represents the probability that it is the best model, given a set of candidate models. We then used model averaging to identify the most supported relationships, while reducing model-based uncertainty. The magnitude and the direction of the effect size of independent variables was assessed on the basis of model-averaged parameter estimates, calculated by averaging the coefficients from all candidate models, weighted by w_i (Burnham and Anderson, 2002; Symonds and Moussalli, 2011). For each explanatory variable, we also calculated the summed AIC weight ($\sum w_i$) from all the model combinations where the variable occurred. $\sum w_i$ allows to assess the relative importance of independent variables: variables with largest $\sum w_i$ values are the most important, compared to the others (Burnham and Anderson, 2002; Symonds and Moussalli, 2011). Furthermore, to make the interpretation of relationships more clear, we also report the significance values of variables included in the best-AIC models (i.e., the model with the lowest AIC in each analysis) (Stephens et al., 2007), and the amount of deviance explained by best models (R^2_b) (Symonds and Moussalli, 2011). For all analyses, using AIC corrected for small sample size instead of AIC to rank models yield identical results. If GLMs showed overdispersion, we used a quasi-Poisson family instead of a Poisson family, and we used a Quasi-AIC instead of AIC to evaluate the support of models (Richards, 2008). We assessed significance using a likelihood ratio test for Poisson models, and a *F* test for over-dispersed models (Crawley, 2007). Our data have a strong spatial structure, and spatial autocorrelation may affect the analysis of spatially-structured data. Per each analysis, we used a permutation test to evaluate if spatial autocorrelation (Moran's *I*) of residuals of the best-AIC model was significantly higher than expected by chance (Lichstein et al., 2002). If autocorrelation was significant ($P < 0.05$), we used Moran's Eigenvector Maps (MEM) instead of standard GLMs. MEM allows the translation of the spatial arrangement of data points into explanatory variables capturing the spatial effects (Borcard et al., 2011; Dormann et al., 2007). We identified the eigenvector(s) best reducing spatial autocorrelation, and we included them into all the candidate models (Dormann et al., 2007). Simulations and comparative analyses showed that this implementation of MEM has a good performance, and produces results extremely similar to other well supported spatial regression tools (Dormann et al., 2007; Ficetola et al., 2013; Siesa et al., 2011). Unlike other spatial regression methods, MEM is extremely flexible, as it allows the analysis of non-normal and over-dispersed data, and the extraction of AIC parameters. In our analyses, the extracted eigenvector(s) successfully reduced residual autocorrelation of all best models to non-significant values (in all analyses $P > 0.05$).

We performed multiple analyses on the same community, and performing multiple tests may inflate the risk of incorrectly identifying significant relationships. We therefore repeated analyses using multivariate Poisson models (Wang et al., 2012). For multivariate analyses, a matrix including the richness of communities of adults and exuviae constituted the dependent, while environmental variables and eigenvectors extracted by MEM were considered as independent. Significance of variables within multivariate models was assessed through 999 bootstraps, by adjusting *P* values to account for multiple testing (Wang et al., 2012). Larvae were not included in the multivariate analysis, because data on larvae were only available for a subset of sites.

In all analyses, environmental variables were not strongly correlated among them (for all pairwise correlations, $|r| < 0.4$). If needed, environmental variables were transformed to reduce skewness and improve normality. Surface area, depth and stream velocity were log-transformed, while percentage data were transformed using square-root arcsine. We performed analyses in R (www.r-project.org) using packages SPDEP, MuMIn and mvabund (Barton, 2011; Bivand et al., 2010; Wang et al., 2012).

3. Results

3.1. Adult community richness

We detected *P. clarkii* in 28 wetlands (23%). During our surveys, we detected the presence of 42 odonate species, 17 Zygoptera and

25 Anisoptera (Appendix S1). The average richness was 6.6 species per wetland (SD = 4.1).

Stream velocity, canopy cover and water permanence were the most important variables to explain the overall richness of adult communities. The richest communities were associated with permanent wetlands with slow or no stream and low canopy cover (i.e., sunny wetlands). Furthermore, whole adult community richness tended to be highest in wetlands with *P. clarkii* (Table 1a). Relationships between adult community richness and environmental variables remained similar if only Anisoptera are considered (Table 1b). However, Anisoptera richness was not related to crayfish presence (Table 1b). The pattern was different for Zygoptera. Data from adults suggest that the richest Zygoptera communities are associated with permanent wetlands having slow or no stream, and with presence of *P. clarkii* (Table 1c). Residual autocorrelation was significant in the analysis of whole adult community and Zygoptera richness (Table 1), and was successfully removed by MEM ($P > 0.05$).

3.2. Larval community richness

P. clarkii was present in 50% of wetlands surveyed with pipe sampling; furthermore, we detected larvae of 14 odonate taxa (Appendix S1). In invaded wetlands we found seven odonate taxa only: *Chalcolestes viridis*, *Ischnura elegans*, *Coenagrion puella-pulchellum*, *Aeshna cyanea*, *Orthetrum albistylum*, *Orthetrum cancellatum*, and *S. sanguineum-striolatum*. For larvae, we detected

Table 1

Relationships between the richness of odonate adult communities, the presence of *P. clarkii*, and environmental features. Explanatory variables included in the best AIC model are in bold.

a. whole community ^{1,2}	Averaged model parameters		Best AIC model		
	RI	B	F	df	P
<i>P. clarkii</i>	0.73	+0.15	6.6	1, 101	0.038
Stream velocity	1.00	−2.98	24.0	1, 101	<0.001
Area	0.23	+0.00			
Depth	0.37	+0.06			
Canopy	1.00	−0.29	8.1	1, 101	0.005
Permanence	1.00	+1.23	42.7	1, 101	<0.001
Landscape veg.	0.50	+0.14			
MEM eigenvector	1.00		7.9	1, 101	0.006
					$R_D^2 = 0.46$
b. Anisoptera only ¹	Averaged model parameters		Best AIC model		
	RI	B	F	df	P
<i>P. clarkii</i>	0.22	+0.00			
Stream velocity	1.00	−3.55	10.4	1, 103	0.002
Area	0.23	+0.01			
Depth	0.37	+0.07			
Canopy	1.00	−0.37	12.4	1, 103	<0.001
Permanence	1.00	+0.93	26.9	1, 103	<0.001
Landscape veg.	0.26	+0.93			
					$R_D^2 = 0.30$
c. Zygoptera only ²	Averaged model parameters		Best AIC model		
	RI	B	χ^2	df	P
<i>P. clarkii</i>	1.00	+0.64	32.9	1	<0.001
Stream velocity	0.56	−0.90	4.1	1	0.049
Area	0.27	+0.01			
Depth	0.35	+0.09			
Canopy	0.47	−0.08			
Permanence	1.00	+2.21	43.0	1	<0.001
Landscape veg.	0.64	+0.28			
MEM eigenvector	1.00		11.8	1	<0.001
					$R_D^2 = 0.56$

RI: relative importance of the variable, calculated as the summed AIC weight ($\sum w_i$) from all the model combinations where the variable occurred.

B: model-averaged parameter estimates.

R_D^2 : proportion of deviance explained by the best AIC model.

¹ Model was affected by overdispersion, therefore we used QAIC instead of AIC and calculated significance using a *F* test.

² Residuals of OLS regression were spatially autocorrelated, therefore we used Moran Eigenvector Mapping (MEM).

Table 2

Relationships between the richness of odonate larval communities, the abundance of *P. clarkii*, and environmental features. Explanatory variables included in the best AIC model are in bold.

	Averaged model parameters		Best AIC models		
	RI	B	χ^2	df	P
a. Overall community					
<i>P. clarkii</i>	0.82	−0.28	3.1	1	0.079
Area	0.24	+0.01			
Depth	0.41	+0.25			
Canopy	0.71	−0.59	5.1	1	0.023
Permanence	0.29	+0.09			
Landscape veg.	0.58	+0.67			
					$R_D^2 = 0.29$
b. Anisoptera only					
<i>P. clarkii</i>	1.00	−0.34	12.8	1	<0.001
Area	0.26	+0.02			
Depth	0.46	+0.35	2.8	1	0.09
Canopy	0.27	−0.06			
Permanence	0.25	+0.04			
Landscape veg.	0.80	+1.36	5.2	1	0.023
					$R_D^2 = 0.30$
c. Zygoptera only					
<i>P. clarkii</i>	0.20	−0.01			
Area	0.20	+0.00			
Depth	0.21	+0.05			
Canopy	0.93	−1.25	5.1	1	0.025
Permanence	0.30	+0.20			
Landscape veg.	0.20	+0.07			
					$R_D^2 = 0.29$

RI: relative importance of the variable, calculated as the summed AIC weight ($\sum w_i$) from all the model combinations where the variable occurred.

B: model-averaged parameter estimates.

R_D^2 : proportion of deviance explained by the best AIC model.

less taxa than for adults and exuviae, but it should be considered that sampling of larvae was performed on a subset of wetlands (34/107).

The abundance of *P. clarkii* was the most important variable in explaining the overall richness of larval communities (Table 2a). Although this variable was marginally non-significant in the best-AIC model, the relationship between crayfish abundance and community richness was negative in all candidate models, and significant or nearly significant in most of them (not shown). Furthermore, we observed the richest larval communities in sunny wetlands (Table 2a).

If Anisoptera are analysed separately, crayfish abundance was the variable most important to explain community richness: the richest communities were found in wetlands with low crayfish abundance, within landscapes with high cover of natural vegetation (Table 2b). For Zygoptera, the richest larval communities were associated with sunny wetlands (Table 2c) while the abundance of *P. clarkii* was not included in models with high AIC weight.

3.3. Exuviae richness

We detected exuviae of 18 odonate taxa (Appendix S1); in invaded wetlands we found exuviae of eight species only: *Calopteryx virgo*, *Cal. splendens*, *C. viridis*, *Platycnemis pennipes*, *C. puella*, *Aeshna isosceles*, *O. cancellatum*, and *S. sanguineum*.

If exuviae are considered, presence of *P. clarkii* and wetland permanence was the variables most important to explain the overall richness of odonate communities. The highest richness was found in permanent wetlands without *P. clarkii* (Table 3a). The pattern was similar if Anisoptera are analysed separately: crayfish presence and water permanence were the variables most important for Anisoptera exuviae and the highest richness was associated with permanent wetlands without the crayfish (Table 3b). If Zygoptera

Table 3

Relationships between the richness of odonate exuviae, the presence of *P. clarkii*, and environmental features. Explanatory variables included in the best AIC model are in bold.

	Averaged model parameters		Best AIC models		
	RI	B	χ^2	df	P
a. Overall community ¹					
<i>P. clarkii</i>	0.94	−0.67	4.2	1	0.040
Stream velocity	0.51	−2.30	2.4	1	0.12
Area	0.28	+0.07			
Depth	0.29	+0.11			
Canopy	0.24	−0.04			
Permanence	1.00	+18.80	38.1	1	<0.001
Landscape veg.	0.21	+0.02			
MEM eigenvector	1.00		15.1	1	<0.001
					$R_D^2 = 0.29$
b. Anisoptera only ¹					
<i>P. clarkii</i>	1.00	−1.23	7.2	1	0.007
Stream velocity	0.32	−1.36			
Area	0.61	+0.36	3.9	1	0.048
Depth	0.26	+0.11			
Canopy	0.32	−0.13			
Permanence	1.00	+17.6	14.7	1	<0.001
Landscape veg.	0.24	+0.12			
MEM eigenvector	1.00			1	<0.001
					$R_D^2 = 0.32$
c. Zygoptera only ¹					
<i>P. clarkii</i>	0.20	−0.03			
Stream velocity	0.30	−1.40			
Area	0.19	+0.02			
Depth	0.20	+0.03			
Canopy	0.20	−0.03			
Permanence	1.00	+17.7	13.7	1	<0.001
Landscape veg.	0.19	+0.01			
MEM eigenvector	1.00		6.5	1	0.011
					$R_D^2 = 0.18$

RI: relative importance of the variable, calculated as the summed AIC weight ($\sum w_i$) from all the model combinations where the variable occurred.

B: model-averaged parameter estimates.

R_D^2 : proportion of deviance explained by the best AIC model.

¹ Residuals of OLS regression were spatially autocorrelated, therefore we used Moran Eigenvector Mapping (MEM).

were analysed separately, wetland permanence was the only variable important to explain the species richness of exuviae (Table 3c). For all these analyses, residual autocorrelation was significant. MEM eigenvectors were integrated into models and successfully removed spatial autocorrelation ($P > 0.05$) (Table 3).

3.4. Multivariate analyses

Multivariate tests confirmed the robustness of results of univariate models. The overall richness of the odonate community was related to the presence of *P. clarkii*, stream velocity, canopy cover and pond permanence. The pattern was similar if Anisoptera are analysed separately, while if Zygoptera are analysed separately community richness was related to the presence of *P. clarkii* and to pond permanence (Appendix S2).

4. Discussion

Our study shows that performing separate analyses on different odonate life history stages allows a more complete description of the actual impact of crayfish invasion. We observed a strong relationship between *P. clarkii* and the odonate communities, but the impact of the crayfish on native species was different when the distribution of odonate adults, larvae, and exuviae was considered separately.

In our analyses, features of wetlands and of the surrounding landscape where the main drivers of adult community richness (Table 1a). We found the highest adult richness in permanent, sunny, standing waters. The separate analysis of adult Anisoptera richness was in agreement with the analysis of the full adult community of odonates (Table 1b); conversely, if analysed separately, adult Zygoptera showed a positive relationship with water permanence and lower stream velocity only (Table 1c). Overall, environmental features showing the strongest relationships with species richness were similar to the ones identified in other regions (Mabry and Dettman, 2010; McCauley et al., 2008; Sahlen and Ekestubbe, 2001), confirming the importance of these variables for odonate communities. *P. clarkii* is an active predator of larval odonates, therefore we expected to detect a negative impact of this invasive crayfish on the whole community, with effects evident for all life history stages. Contrary to this expectation, the richness of the adult community was not negatively related to the presence of the invasive crayfish; our results would even suggest a positive relationship between adult Zygoptera and the invasive crayfish (Table 1). Limiting our analysis to adult distribution would therefore lead to the incorrect conclusion that the invasive crayfish did not negatively affect odonate communities, and that positive relationships might be present.

The pattern was very different if larvae or exuviae were analysed. If the whole communities or Anisoptera only are considered, the richest communities were found in wetlands without *P. clarkii* (Tables 2 and 3), while crayfish abundance was not an important predictor of the richness of Zygoptera larvae and exuviae (Tables 2 and 3), even if adult damselflies were often observed in wetlands with *P. clarkii* (Table 1). The strikingly different patterns among life history stages may be explained by the different processes that determine their abundance. Adult odonates actively select wetlands with environmental features suitable for oviposition and for the development of their larvae (Corbet, 2004), and they would benefit from the avoidance of wetlands where *P. clarkii* is present. In principle, crayfish presence might be detected by multiple cues. For instance, at high densities *P. clarkii* removes aquatic macrophytes, which are important factors for the selection of odonate breeding sites, and the crayfish could directly affect deposition of endophytic species, by attempting to prey on adults that, during eggs laying, spend time submerged in the water (Corbet, 2004; Córdoba-Aguilar, 2008). Nevertheless, the lack of negative relationships between *P. clarkii* and adult odonates suggests that they often attempt breeding in invaded wetlands. For the selection of reproductive sites, odonates use mainly visual and tactile cues based on habitat structure, while they have a limited ability to detect predators (Corbet, 2004; Córdoba-Aguilar, 2008). It is thus possible that the alien crayfish remains undetected. Actually, laboratory studies showed that other native preys (tadpoles) have a limited capability to detect invasive *P. clarkii* (Gomez-Mestre and Diaz-Paniagua, 2011). The positive relationship between adult damselflies and crayfish is particularly difficult to explain. After the metamorphosis, Odonata are very mobile and often move to safe sites until they get the sexual maturity. Only after sexual maturity is attained they return back to the emergence area to reproduce. Lack of direct interactions at this life stage, and similar environmental preferences between crayfish and damselflies might therefore cause the apparent positive relationship. Indirect effects are also possible, such as the reduction of native predators/competitors, or specific environmental features of invaded wetlands (e.g. higher connectivity) (Pierce et al., 1985; Blaustein et al., 2004; Siesa et al., 2011). Specific tests will be needed to evaluate these hypotheses.

Conversely, *P. clarkii* had a clear impact on juvenile aquatic stages of dragonflies; this negative effect is likely the result of direct interactions (i.e., predation) (Correia, 2003; Ilheu and Bernardo, 1993; McCarthy et al., 2006; Nyström et al., 1996).

Indirect interactions are also possible (Klose and Cooper, 2012; White et al., 2006): *P. clarkii* can reduce richness and abundance of invertebrates and amphibian larvae that constitute the main prey of larval odonates (Correia and Anastacio, 2008; Cruz et al., 2008; Ficetola et al., 2012b) and reduce richness and abundance of the hydrophytes (Gherardi and Acquistapace, 2007) that are used by odonate larvae for anchorage, concealment, defence, and as foraging sites (Córdoba-Aguilar, 2008). By consuming plant material, *P. clarkii* could also destroy eggs laid on this substrate. Aquatic predators can also induce defensive mechanisms reducing activity and metabolism of larval odonates (Córdoba-Aguilar, 2008; Heads, 1985) slowing the larval growth, and forcing larvae to remain longer in water. Under these conditions, larvae may metamorphose later and at smaller size, being exposed for longer to mortality sources like predation and wetland drying (Córdoba-Aguilar, 2008; McPeck, 1990). The lack of a significant negative relationship for the larvae and exuviae of Zygoptera may also be related to the very little size of some individuals. On the one hand, the small body size and the large number of individuals of some Zygoptera may help them to better withstand crayfish predation. On the other hand, small size may make them more difficult to detect during sampling, limiting the power of statistical analyses.

Our study was correlative, therefore we cannot exclude that other factors not considered here (e.g. other predators) can be the cause of the negative relationships between crayfish and odonates. Nevertheless, the overall abundance of freshwater predators is strongly determined by wetland depth and hydroperiod, with more predators in deep and permanent wetlands (Van Buskirk, 2003), and in our analyses the impact of *P. clarkii* was clearly visible when taking into account waterbody features. Furthermore, quantification of predator taxa in a subset of wetlands showed that *P. clarkii* is far more abundant and exerts a stronger impact than other aquatic predators (Ficetola et al., 2012b). It is thus unlikely that the negative relationships between crayfish and odonates are caused by overlooked predators.

Exuviae provide the best indication of the successful odonate reproduction within a wetland (Oertli, 2008; Ott, 2010). Analyses on exuviae were the ones best confirming the negative relationship between the invasive crayfish and the dragonfly community richness (Table 3), and indicate that the crayfish makes the aquatic environment unsuitable for the development of juvenile stages, strongly decreasing the overall reproductive success. Therefore, the analysis of exuviae may provide the best indicators of the impact of aquatic invaders. Nevertheless, exuviae can be sampled only during limited periods of the year, and species show differences for the emergence periods. These phenological differences should be taken into account when planning environmental monitoring.

For several models, residual autocorrelation was significant and MEM eigenvectors were important predictors of community richness (Tables 1 and 3). This probably arises because adult dispersal is extremely important to maintain odonate communities and for the creation of crayfish populations; sites neighbouring species-rich wetlands therefore host more species than expected on the basis of the sole environmental features (Hamasaki et al., 2009; McCauley et al., 2008; Yamanaka et al., 2009). The importance of dispersal is supported by the observation that the several taxa were detected as adults but not as larvae or exuviae. The introduction of *P. clarkii* in this area is recent (Fea et al., 2006; Siesa et al., 2011), and only a subset of wetlands are currently invaded, therefore non invaded sites could support populations that disperse into the surrounding landscape and attempt reproduction in invaded wetlands, determining the pattern of spatial autocorrelation (Ficetola et al., 2012a). Simulation and empirical studies showed that, if the proportion of suitable patches in a given landscape falls below a given threshold, dispersal cannot anymore maintain populations, and species can undergo abrupt extinction (Fahrig, 2002; Ficetola and Denoël,

2009). Dispersal may allow the persistence of the community of dragonflies only if the number of wetlands without *P. clarkii*, where odonates can attain positive fitness, remain high.

P. clarkii is a generalist crayfish that is well adapted to temporary wetlands, but its reproductive success is higher in wetlands with longer hydroperiod, that are more easily and stably invaded (Alcorlo et al., 2009; Gutiérrez Yurrita and Montes, 1999; Siesa et al., 2011). It has been suggested that freshwater taxa associated to ephemeral wetlands may better withstand the invasion of *P. clarkii* (Ficetola et al., 2012c). Unfortunately, deep and permanent wetlands are also the ones hosting the richest odonate communities (Tables 2 and 3), and many species cannot successfully complete their life cycle in the ephemeral ones (Heidemann and Seidenbusch, 2002; Schultz, 2009). The control of this invasive crayfish is extremely difficult (Aquiloni et al., 2010; Gherardi, 2006), challenging conservation of odonate biodiversity in the quickly expanding invaded areas. To date, avoiding the introduction of *P. clarkii* into new regions remains the most effective approach to prevent their negative impact.

Our analysis shows that different life history stages of species with complex life cycles provide complementary measures of the impact of the crayfish invasion. Odonates, and particularly Anisoptera, can be extremely sensitive to the impact of this IAS, even at early invasion stages. Juvenile stages are the most affected by the crayfish, and show the earliest crayfish impact at the wetland scale, while negative effects on adults are not evident at early stages of the invasion. Actually, the impact on adults might become apparent only when most of wetlands are invaded and the situation is compromised at broad scale. Odonates constitute an effective tool for environmental assessment and monitoring, and all life history stages are useful for this task. It should be kept in mind that different stages provide different information on the consequences of AIS on communities. Monitoring of adults is fast and is the typical approach to the monitoring of odonates, but may lead to inaccurate results when impacts like the crayfish are present, as adults are very mobile and can be present at wetlands where they do not reproduce. If possible, multiple life history stages should be considered to better assess the ongoing processes; furthermore, the presence of larvae and exuviae is more tightly linked to reproductive success, and provides a more prompt assessment on the impact on freshwater communities.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2014.05.036>.

References

Alcorlo, P., Geiger, W., Otero, M., 2009. Reproductive biology and life cycle of the invasive crayfish *Procambarus clarkii* (Crustacea: Decapoda) in diverse aquatic habitats of South-Western Spain: implications for population control. *Fund. Appl. Limnol.* 173, 197–212.

Allendorf, F.W., Lundquist, L.L., 2003. Introduction: population biology, evolution, and control of invasive species. *Conserv. Biol.* 17, 24–30.

Aquiloni, L., Gherardi, F., 2008. Extended mother–offspring relationships in crayfish: the return behaviour of juvenile *Procambarus clarkii*. *Ethology* 114, 946–954.

Aquiloni, L., Brusconi, S., Cecchinelli, E., Tricarico, E., Mazza, G., Paglianti, A., Gherardi, F., 2010. Biological control of invasive populations of crayfish: the European eel (*Anguilla anguilla*) as a predator of *Procambarus clarkii*. *Biol. Invasions* 12, 3817–3824.

Barbour, M.T., Gerritsen, J., Snyder, B.D., Stribling, J.B., 1999. *Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers*. Environmental Protection Agency, Washington.

Barton, K., 2011. MuMIn: Multi-model inference. R package version 1.0.0, <http://CRAN.R-project.org/package=MuMIn>

Bivand, R., Altman, M., Anselin, L., Assunção, R., Berke, O., Bernat, A., Blankmeyer, E., Carvalho, M., Chun, Y., Christensen, B., Dormann, C.F., Dray, S., Halbersma, R., Krainski, E., Lewin-Koh, N., Li, H.F., Ma, J.L., Millo, G., Mueller, W., Ono, H., Peres-Neto, P.R., Piras, G., Reeder, M., Tiefseldorf, N., Yu, D., 2010. spdep. Spatial dependence: weighting schemes, statistics and models. R package version 0., pp. 5–24, <http://CRAN.R-project.org/package=spdep>

Blaustein, L., Kiflawi, M., Eitam, A., Mangel, M., Cohen, J.E., 2004. Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. *Oecologia* 138, 300–305.

Borcard, D., Gillet, F., Legendre, P., 2011. *Numerical Ecology with R* Springer, New York.

Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Verlag, New York.

Carchini, G., 1983. Odonata: guide per il riconoscimento delle specie animali delle acque interne italiane. Valdona, Verona: CNR.

Corbet, P.S., 2004. *Dragonflies: Behaviour and Ecology of Odonata*. Harley Books, Colchester, UK.

Córdoba-Aguilar, A., 2008. *Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research*. Oxford University Press, USA.

Correia, A.M., 2003. Food choice by the introduced crayfish *Procambarus clarkii*. *Ann. Zool. Fenn.* 40, 517–528.

Correia, A.M., Anastacio, P.M., 2008. Shifts in aquatic macroinvertebrate biodiversity associated with the presence and size of an alien crayfish. *Ecol. Res.* 23, 729–734.

Crawley, M.J., 2007. *The R Book*. John Wiley & Sons, Chichester, UK.

Cruz, M.J., Segurado, P., Sousa, M., Rebelo, R., 2008. Collapse of the amphibian community of the Paul do Boquilobo Natural Reserve (central Portugal) after the arrival of the exotic American crayfish *Procambarus clarkii*. *Herp. J.* 18, 197–204.

Dormann, C.F., McPherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30, 609–628.

Drake, J.A., 2009. *Handbook of Alien Species in Europe*.

Fahrig, L., 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecol. Appl.* 12, 346–353.

Fea, G., Nardi, P.A., Ghia, D., Spairani, M., Manenti, R., Rossi, S., Moroni, M., Bernini, F., 2006. Dati preliminari sulla distribuzione in Lombardia dei gamberi d'acqua dolce autoctoni e alloctoni. *Atti della Società italiana di Scienze Naturali Museo Civico di Storia Naturale di Milano* 147, 201–210.

Ficetola, G.F., Denoël, M., 2009. Ecological thresholds: an assessment of methods to identify abrupt changes in species–habitat relationships. *Ecography* 32, 1075–1084.

Ficetola, G.F., Padoa-Schioppa, E., De Bernardi, F., 2009. Influence of landscape elements in riparian buffers on the conservation of semiaquatic amphibians. *Conserv. Biol.* 23, 114–123.

Ficetola, G.F., Marziali, L., Rossaro, B., De Bernardi, F., Padoa-Schioppa, E., 2011a. Landscape – stream interactions and habitat conservation for amphibians. *Ecol. Appl.* 21, 1272–1282.

Ficetola, G.F., Siesa, M.E., Manenti, R., Bottoni, L., De Bernardi, F., Padoa-Schioppa, E., 2011b. Early assessment of the impact of alien species: differential consequences of an invasive crayfish on adult and larval amphibians. *Divers. Distrib.* 17, 1141–1151.

Ficetola, G.F., Manenti, R., De Bernardi, F., Padoa-Schioppa, E., 2012a. Can patterns of spatial autocorrelation reveal population processes? An analysis with the fire salamander. *Ecography* 35, 693–703.

Ficetola, G.F., Siesa, M.E., De Bernardi, F., Padoa-Schioppa, E., 2012b. Complex impact of an invasive crayfish on freshwater food webs. *Biodivers. Conserv.* 21, 2641–2651.

Ficetola, G.F., Siesa, M.E., Padoa-Schioppa, E., De Bernardi, F., 2012c. Wetland features, amphibian communities and distribution of the alien crayfish, *Procambarus clarkii*. In: Andreone, F., Angulo, A. (Eds.), Bridging the gap between science and policy in amphibian conservation: Beyond 2010 Alytes. *Muséum National d'Histoire Naturelle*, Paris.

Ficetola, G.F., Bonardi, A., Sindaco, R., Padoa-Schioppa, E., 2013. Estimating patterns of reptile biodiversity in remote regions. *J. Biogeogr.* 40, 1202–1211.

Gerletti, M., Marchetti, R., 1977. Indagini sui laghi della Brianza. I.R.S.A.

Gherardi, F., 2006. Crayfish invading Europe: the case study of *Procambarus clarkii*. *Mar. Freshw. Behav. Phys.* 39, 175–191.

Gherardi, F., 2007. Biological invasions in inland waters: an overview. In: Gherardi, F. (Ed.), *Biological Invaders In Inland Waters: Profiles, Distribution, and Threats*. Springer, Dordrecht, pp. 3–25.

Gherardi, F., Acquistapace, P., 2007. Invasive crayfish in Europe: the impact of *Procambarus clarkii* on the littoral community of a Mediterranean lake. *Freshw. Biol.* 52, 1249–1259.

- Giugliano, L., Hardersen, S., Santini, G., 2012. Odonata communities in retrodunal ponds: a comparison of sampling methods. *Int. J. Odonatol.* 15, 13–23.
- Gomez-Mestre, I., Diaz-Paniagua, C., 2011. Invasive predatory crayfish do not trigger inducible defences in tadpoles. *Proc. Roy. Soc. B.* 278, 3364–3370.
- Gutiérrez Yurrita, P.J., Montes, C., 1999. Bioenergetics and phenology of reproduction of the introduced red swamp crayfish, *Procambarus clarkii*, in Donana National Park, Spain, and implications for species management. *Freshw. Biol.* 42, 561–574.
- Hamasaki, K., Yamanaka, T., Tanaka, K., Nakatani, Y., Iwasaki, N., Sprague, D.S., 2009. Relative importance of within-habitat environment, land use and spatial autocorrelations for determining odonate assemblages in rural reservoir ponds in Japan. *Ecol. Res.* 24, 597–605.
- Hazlett, B.A., Burba, A., Gherardi, F., Acquistapace, P., 2003. Invasive species of crayfish use a broader range of predation-risk cues than native species. *Biol. Invasions* 5, 223–228.
- Heads, P.A., 1985. The effect of invertebrate and vertebrate predators on the foraging movements of *Ischnura elegans* larvae (Odonata: Zygoptera). *Freshw. Biol.* 15, 559–571.
- Heidemann, H., Seidenbusch, R., 2002. Larves et exuvies des libellules de France et d'Allemagne (sauf de Corse). Société française d'odonatologie.
- Hines, J.E., 2006. PRESENCE2-Software to estimate patch occupancy and related parameters. USGS-PWRC, <http://www.mbr-pwrc.usgs.gov/software/presence.html>
- Ilheu, M., Bernardo, J.M., 1993. Experimental Evaluation of Food Preferences of Red Swamp Crayfish, *Procambarus clarkii*: Vegetal Versus Animal. University of Southwestern Louisiana, Lafayette, LA, USA, pp. 359–364.
- Jeschke, J.M., Strayer, D.L., 2005. Invasion success of vertebrates in Europe and North America. *Proc. Natl. Acad. Sci. USA* 102, 7198–7202.
- Klose, K., Cooper, S.D., 2012. Contrasting effects of an invasive crayfish (*Procambarus clarkii*) on two temperate stream communities. *Freshw. Biol.* 57, 526–540.
- Kutcher, T.E., Bried, J.T., 2014. Adult Odonata conservatism as an indicator of freshwater wetland condition. *Ecol. Indic.* 38, 31–39.
- Leung, B., Roura-Pascual, N., Bacher, S., Heikkilä, J., Brotons, L., Burgman, M.A., Dehnen-Schmutz, K., Essl, F., Hulme, P.E., Richardson, D.M., Sol, D., Vilà, M., 2012. TEASing apart alien species risk assessments: a framework for best practices. *Ecol. Lett.* 15, 1475–1493.
- Lichstein, J.W., Simons, T.R., Shriver, S.A., Franzreb, E., 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecol. Monogr.* 72, 445–463.
- Liu, X.A., Guo, Z.W., Ke, Z.W., Wang, S.P., Li, Y.M., 2011. Increasing potential risk of a global aquatic invader in Europe in contrast to other continents under future climate change. *PLoS ONE* 6, e18429.
- Mabry, C., Dettman, C., 2010. Odonata Richness and abundance in relation to vegetation structure in restored and native wetlands of the Prairie Pothole Region, USA. *Ecol. Restor.* 28, 475.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.A., Hines, J.E., 2006. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier, Amsterdam.
- Matsuzaki, S.S., Usio, N., Takamura, N., Washitani, I., 2009. Contrasting impacts of invasive engineers on freshwater ecosystems: an experiment and meta-analysis. *Oecologia* 158, 673–686.
- McCarthy, J.M., Hein, C.L., Olden, J.D., Vander Zanden, M.J., 2006. Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. *Freshw. Biol.* 51, 224–235.
- McCauley, S.J., Davis, C.J., Relyea, R.A., Yurewicz, K.L., Skelly, D.K., Werner, E.E., 2008. Metacommunity patterns in larval odonates. *Oecologia* 158, 329–342.
- McPeck, M.A., 1990. Behavioral differences between Enallagma species (Odonata) influencing differential vulnerability to predators. *Ecology* 71, 1714–1726.
- Miyake, M., Miyashita, T., 2011. Identification of alien predators that should not be removed for controlling invasive crayfish threatening endangered odonates. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 21, 292–298.
- Nunes, A.L., Richter-Boix, A., Laurila, A., Rebelo, R., 2013. Do anuran larvae respond behaviourally to chemical cues from an invasive crayfish predator? A community-wide study. *Oecologia* 171, 115–127.
- Nyström, P.E.R., Brönmark, C., Graneli, W., 1996. Patterns in benthic food webs: a role for omnivorous crayfish? *Freshw. Biol.* 36, 631–646.
- Oertli, B., 2008. The use of dragonflies in the assessment and monitoring of aquatic habitats. In: Córdoba-Aguilar, A. (Ed.), *Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research*. Oxford University Press, USA, pp. 79–95.
- Ott, J., 2010. Using dragonfly exuviae in ecological investigations and population assessment. In: Samways, M.J., McGeoch, M.A., New, T.R. (Eds.), *Insect Ecology and Conservation – A Handbook of Techniques*. Oxford University Press, New York, 441 pp, pp. 180–183.
- Ott, J., Samways, M.J., 2010. Effects of climatic changes on Odonata: are the impacts likely to be the same in the northern and southern hemispheres? In: Settele, J., Penev, L., Georgiev, T., Grabaum, R., Grobelnik, V., Hammen, V., Klotz, S., Kotarac, M., Kühn, I. (Eds.), *Atlas of Biodiversity Risk*. Pensoft Publishers, Sofia-Moscow, 280 pp, pp. 84–85.
- Pierce, C.L., Crowley, P.H., Johnson, D.M., 1985. Behavior and ecological interactions of larval Odonata. *Ecology* 66, 1504–1512.
- Pimentel, D., 2002. *Biological Invasions: Economic and Environmental Costs of Alien Plant, Animal, and Microbe Species*. CRC Press LLC, Florida.
- Reynolds, J.D., Demers, A., Peay, S., Puky, P., Sibley, P., Souty-Grosset, C., Taugbol, T., 2006. Crayfish conservation and management. In: Souty-Grosset, C., Holdich, D.M., Noel, P.Y., Reynolds, J.D., Haffner, P. (Eds.), *Atlas of Crayfish in Europe*. Publications Scientifiques du Muséum national d'Histoire naturelle, Paris, pp. 151–157.
- Richards, S.A., 2008. Dealing with overdispersed count data in applied ecology. *J. Appl. Ecol.* 45, 218–227.
- Sahlen, G., Ekestubbe, K., 2001. Identification of dragonflies (Odonata) as indicators of general species richness in boreal forest lakes. *Biodiv. Conserv.* 10, 673–690.
- Samways, M.J., 2008. Dragonflies as focal organisms in contemporary conservation biology. In: Córdoba-Aguilar, A. (Ed.), *Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research*. Oxford University Press, USA, pp. 97–108.
- Samways, M.J., Steytler, N.S., 1996. Dragonfly (Odonata) distribution patterns in urban and forest landscapes, and recommendations for riparian management. *Biol. Conserv.* 78, 279–288.
- Schultz, T.D., 2009. Diversity and habitats of a prairie assemblage of Odonata at Lostwood National Wildlife Refuge, North Dakota. *J. Kansas Entomol. Soc.* 82, 91–102.
- Siesa, M.E., Manenti, R., Padoa-Schioppa, E., De Bernardi, F., Ficetola, G.F., 2011. Spatial autocorrelation and the analysis of invasion processes from distribution data: a study with the crayfish *Procambarus clarkii*. *Biol. Invasions* 13, 2147–2160.
- Souty-Grosset, C., Holdich, D.M., Noel, P.Y., Reynolds, J.D., Haffner, P., 2006. *Atlas of Crayfish in Europe*. Publications Scientifiques du Muséum national d'Histoire naturelle, Paris, pp. 190.
- Stephens, P.A., Buskirk, S.W., Hayward, G.D., Del Rio, C.M., 2007. A call for statistical pluralism answered. *J. Appl. Ecol.* 44, 461–463.
- Strayer, D.L., 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshw. Biol.* 55, 152–174.
- Strayer, D.L., Eviner, V.T., Jeschke, J.M., Pace, M.L., 2006. Understanding the long-term effects of species invasions. *Trends Ecol. Evol.* 21, 645–651.
- Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* 65, 13–21.
- Van Buskirk, J., 2003. Habitat partitioning in European and North American pond-breeding frogs and toads. *Divers. Distrib.* 9, 399–410.
- Van Buskirk, J.V., 2005. Local and landscape influence on amphibian occurrence and abundance. *Ecology* 86, 1936–1947.
- Vilà, M., Basnou, C., Pysek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P.E., partners, D., 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Front. Ecol. Environ.* 8, 135–144.
- Wang, Y., Naumann, U., Wright, S.T., Warton, D.I., 2012. mvabund— an R package for model-based analysis of multivariate abundance data. *Methods Ecol. Evol.* 3, 471–474.
- Werner, E.E., Relyea, R.A., Yurewicz, K.L., Skelly, D.K., Davis, C.J., 2009. Comparative landscape dynamics of two anuran species: climate-driven interaction of local and regional processes. *Ecol. Monogr.* 79, 503–521.
- White, E.M., Wilson, J.C., Clarke, A.R., 2006. Biotic indirect effects: a neglected concept in invasion biology. *Divers. Distrib.* 12, 443–455.
- Yamanaka, T., Tanaka, K., Hamasaki, K., Nakatani, Y., Iwasaki, N., Sprague, D.S., Bjørnstad, O.N., 2009. Evaluating the relative importance of patch quality and connectivity in a damselfly metapopulation from a one season survey. *Oikos* 118, 67–76.