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The impact of the North American waterbug *Trichocorixa verticalis* (Fieber) on aquatic macroinvertebrate communities in southern Europe

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With 3 figures and 1 table

Abstract: The North American waterbug *Trichocorixa verticalis* (Heteroptera: Corixidae) has recently invaded brackish water systems on three continents. Despite its potential to be a keystone species in hypersaline waters in its home range, its effect on the communities it invades is yet unstudied. By doing a field survey in 29 ponds in Doñana, southern Europe some years after *T. verticalis* was first recorded there, we aimed to establish its prevalence and impact on the local invertebrate community, especially the local corixid community with which it is likely to compete. *T. verticalis* showed the highest prevalence among all seven Corixidae species found. It occasionally reached high local abundance, especially at high salinity. *T. verticalis* also appeared to be better than native Corixidae at coping with human disturbance. We could not identify significant effects of *T. verticalis* on the local corixid community nor on the invertebrate community at large. Further experimental research will be needed to confirm these results. Special attention should be paid to hypersaline systems where *T. verticalis* may act as a top predator.

Key words: exotic, ecological impact, Corixidae, non-native insect, anthropogenic disturbance.

Introduction

The increasing establishment of invasive species outside their native range is one of the most important threats to global biodiversity (IUCN 2008). Not all invasions have a large ecological impact, and relatively few invasive species are responsible for most of the current threats to biodiversity. Dramatic effects of invader species on host communities are mainly found in the case of ecosystem engineers where alterations of key aspects of the habitat may have ramifications throughout the community (Crooks 2002), as a result of strong trophic interactions such as herbivory (Joe & Daehler 2008), predation (Salo et al. 2007) and parasitism (Maloney et al. 2005) or through competition (Reitz & Trumble 2002). Increasing attention is now given to predicting the ecological impact of newly invading species (e.g. from life-history traits), since this helps prioritization of efforts to safeguard biodiversity. However, predicting ecological impact remains difficult, particularly with respect to trophic interactions where novel and sometimes unexpected interactions may emerge (Caroll & Fox 2007, Mondor & Addicott 2007). Experimental and field evaluations therefore remain vital.

Global diversity scenarios (Sala et al. 2000) predict that bio-invasions will rank fourth among the most important drivers of biodiversity loss in 2100, and will be the dominant cause of decline in particular regions, such as the Mediterranean biome. If we use the Iberian

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peninsula as an example, aquatic communities have already been affected by tens of exotic species including *Artemia fransiscana* Kellog (Amat et al. 2005), *Corbicula fluminea* Müller (Sousa et al. 2008), *Gambusia holbrooki* Girard (Cardona 2006), *Potamopyrgus antipodarum* Gray (Murria et al. 2008) and *Procambarus clarkii* Girard (Cruz et al. 2006) (for an overview, see Garcia-Berthou et al. 2007). A recent addition to this extensive list of invaders is *Trichocorixa verticalis* Fieber, a small aquatic waterbug (Heteroptera: Corixidae) originating from the northern Nearctic (Günther 2004). *T. verticalis* was first reported from Europe in 2004 from Sanlúcar de Barrameda in south Spain, but was later identified in samples from the Portuguese Algarve taken earlier in 1997 (Sala & Boix 2005). Recent records suggest that the species is now established and spreading along the Iberian Atlantic coast (Sala & Boix 2005, Rodríguez-Pérez et al. 2009). *T. verticalis* has a history of invading different parts of the world and is also newly present in New Caledonia (Jansson 1982) and Southern Africa (Jansson & Reavell 1999). Despite this, no studies yet have explicitly looked at the impact of *T. verticalis* on the ecosystems it invades (but see Rodríguez-Pérez et al. 2009).

Part of the invading success of *T. verticalis* has been attributed to its ability to survive in a hypersaline environment (Kelts 1979), this being the only corixid species that has ever been reported from the open sea (Gunter & Christmas 1959). In its native range, *T. verticalis* may reach extreme densities of several 10.000 individuals /m². Being a top predator in hypersaline species-poor communities (Williams 1998), it can exert strong effects on the whole community through cascading trophic effects (Wurtsbaugh 1992). Our study had the following objectives (1) to establish the distribution and reproductive status of *T. verticalis* in the area where it was first reported, (2) to identify the ecological niche of the species in the invaded area, paying special attention to salinity, and (3) to assess the relationships between the abundance of the invading species *T. verticalis* and that of native Corixidae and other members of the aquatic communities it inhabits, as a measure of the possible ecological impact of the invader.

Material and methods

Study area and sampling protocol

Between 25 November 2008 and 3 December 2008, we sampled 29 lentic water bodies in an area of approximately 50 × 50 km situated between the cities of Huelva, Sevilla and Cadiz in the Marismas del Guadalquivir, South Spain (Fig. 1). The majority of sampling sites are within the delta of the Guadalquivir river, which is largely protected within the Doñana National and Natural Parks (Rendón et al. 2008). The study area exhibits particularly strong gradients in salinity at a small geographical scale. To be able to fully understand salinity effects, we tried to balance the distribution of our sampling sites more or less evenly along the salinity gradient (conductivity range of 0.154–70.8 mS/cm, the latter corresponds to a salinity of 41.8 g/l). Two types of corixid samples were taken at each site: first we took five standard sweeps each at a different location in the pond to quantify local corixid densities ("quantitative sample"), to obtain a sample of the local invertebrate community ("invertebrate community" refers to aquatic macroinvertebrates excluding Corixidae) and to quantify densities of the alien fish *Gambusia holbrooki*. If the quantitative method yielded less than 100 adult corixids, we continued sampling until we reached this number and collected the additional individuals in a second sample ("proportional sample"). This sample allows us to compare the proportional presentation of corixid species between sites that have different corixid densities. We used a dip net with mesh 500 µm and a sampling surface of 520 cm². An average sweep had a length of 1.8 m. At each site, the following environmental variables were assessed upon sampling: pH, electrical conductivity (mS/cm) and dissolved oxygen (mg/l) were measured using a WTW multiline F meter (Geotech©, Denver, Colorado, USA). Water transparency was measured with a Snell tube (cm), average water depth at the sampling location was obtained from three measurements with a graduated stick to the nearest 5 cm, surface area (m²) of the sampled sites was measured in situ for small sites and from Google Earth (version 4.3.7284.3916, July 2008) for large sites. We estimated cover (%) by submerged vegetation, cover by tall (> 5 cm) submerged vegetation, and cover by emergent vegetation and substrate type (clay, sand-clay, sand, gravel). Fish other than *Gambusia* were rarely present and mainly occurred in the fish farm ponds and some large permanent waters and we simply noted their absence or presence. Due to the strong linear correlation between electrical conductivity and salinity in our study area ($r = 0.99$), from hereon we use the term salinity to describe this gradient as it is more appropriate in this context. Based on the current function of each site we classified it as either subject to low or high anthropogenic disturbance (0/1). Drainage and irrigation canals, rice fields, fish and shrimp breeding ponds and salterns were classified as subject to recurrent anthropogenic disturbance (regular input of high levels of nutrients, contaminants, abrupt changes in water level, etc). All ponds and pools not currently subject to anthropogenic disturbances were categorized as low impact sites, even if they were manmade.

Samples were sorted in situ on white trays and the retrieved animals preserved in 70 % alcohol. Corixidae were identified to species level with the key of Jansson (1986) and descriptions in Sailer (1976) for *T. verticalis*. Due to the difficulty of identifying juvenile *Sigara*, all juvenile Corixidae were identified to genus level. All other invertebrates were identified to genus except for Diptera which were only identified to family level.

Statistics

Relationships of *T. verticalis* occurrence and densities with the local environment, with corixid community structure, and with invertebrate community structure were studied both with univariate and multivariate statistics. We calculated Pearson rank

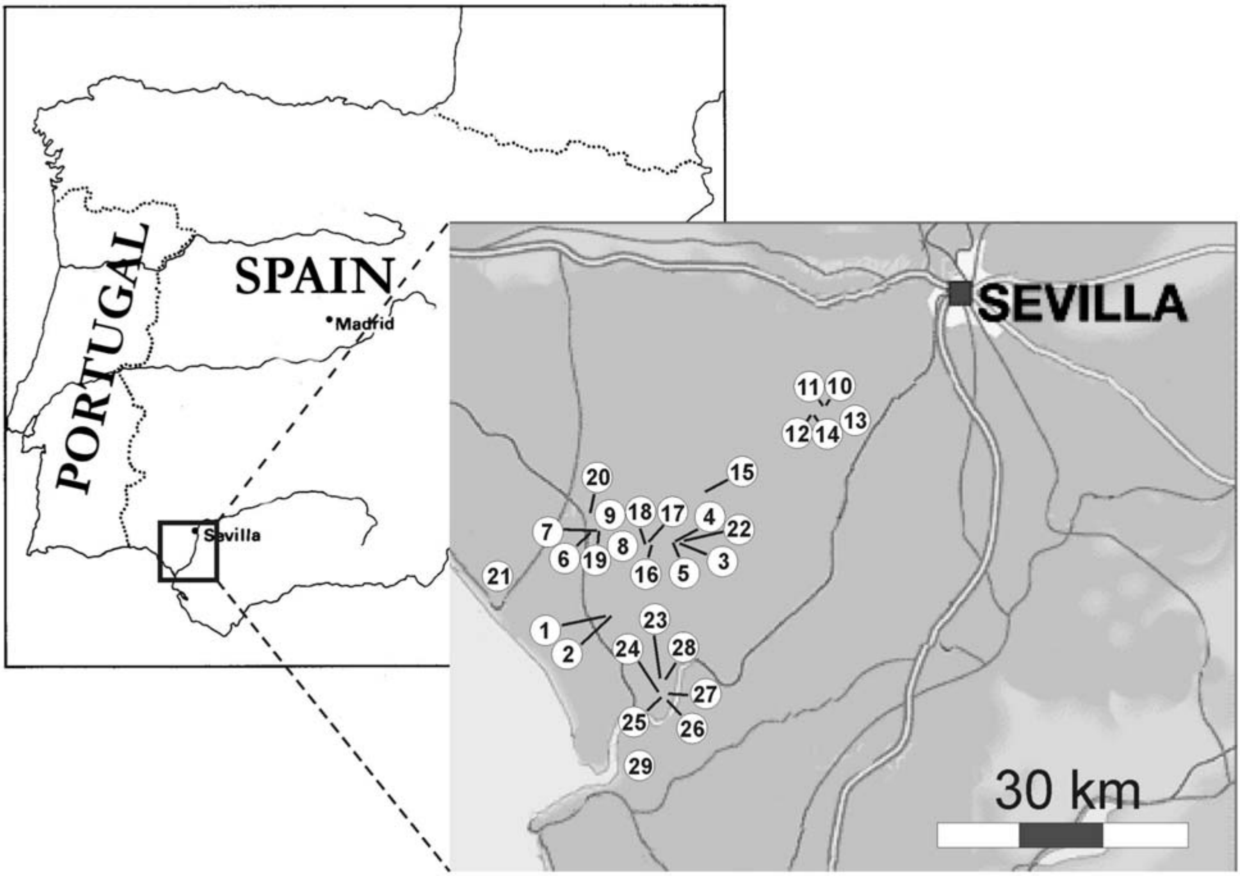

Fig. 1. Map of Spain with detailed inset of the study area. Sampling sites are given with their respective numbers cf. Table 1.

correlations between *T. verticalis* densities on the one hand and the corixid community abundance, corixid species richness, the abundance of the full invertebrate community and the species richness of the full invertebrate community on the other hand. A non-parametric analysis was chosen because our data did not meet assumptions of parametric methods. We used a stepwise multiple regression with forward selection of variables to identify the set of environmental variables that best explained *T. verticalis* densities.

General patterns in community structure were studied by Principal Component Analysis (PCA) for corixid communities and with Correspondence Analysis (CA) for invertebrate communities. The choice for PCA or CA was based on preceding Detrended Correspondence Analyses (DCA) that showed moderately long gradients in corixid communities (main gradient length 3.2), and high species turnover in the invertebrate communities (main gradient length 4.9). The contribution of environmental variables to explaining variation in community structure was studied with RDA (Redundancy Analysis) in corixid communities (separately for adults and juveniles), and with Canonical Correspondence Analysis (CCA) in invertebrate communities. Forward selection was used to identify important variables that contributed significantly to explaining variation in community structure. To study possible effects of *T. verticalis* on the corixid community and on the invertebrate community, *T. verticalis* densities were entered in the RDA and the CCA model as an explanatory variable. To look for possible partial effects of *T. verticalis* additional to patterns driven by environmental gradients, we included the environmental variables matrix as covariables to the latter models. All reported proportions of explained variation are full fractions, which may overlap with fractions of variance explained by other variables. All analyses on corixid community data were performed both on the quantitative and the proportional data (see above in Material and methods).

Since many taxa had very low prevalence (45 % of the taxa had < 3 occurrences), the data were analyzed at the family level for Dytiscidae, Hydrophillidae, Hydraenidae and Notonectidae. Taxa of other families found at more sites were analyzed at a lower taxonomic level (genus). Families which had only one or two occurrences were deleted from the data matrix prior to analysis, since they had a disproportional effect on the results. Taxon richness and community abundance (the total number of invertebrates in the sample, excluding Corixidae) were based on the full taxon list at the lowest available taxonomic level.

The quantitative corixid data and the data of other macroinvertebrates were logarithmically transformed, the proportional corixid data were square-root transformed, and all environmental variables were normalized prior to analysis. Univariate analyses were done with Statistica 8.0 (Statsoft 2007). Multivariate analyses were performed in Canoco 4.5 (ter Braak & Šmilauer 2002).

Table 1. Overview of the environmental variables recorded at the 29 sites within the study area. Legend and units: Substrate = bottom substrate type; Snell = Snell depth (cm); Subm = cover of submerged vegetation (%); SubmH = cover by submerged vegetation > 5 cm tall (%); Emers = cover by emergent vegetation (%); O_2 = dissolved oxygen level (mg/l); Conductivity = electrical conductivity (mSiemens/cm); Area = ponds area (m²); Depthmax = maximal depth along the transect (cm); Depthavg = average depth along the transect; disturbance = anthropogenic disturbance (0/1); Fish = fish presence (0/1); Latitude = degrees latitude; Longitude = degrees longitude.

Site No	Date	Substrate	Snell	Veg Subm	Veg SubmH	Veg Emers	O_2	Conductivity	Area	Depthmax	Depthavg	Disturbance	Fish	Latitude	Longitude
1	25/11/2008	clay	15	5	0	0	10.1	23.7	30	10	5	1	0	37.004916°	–6.333687°
2	25/11/2008	artificial	50	95	30	0	12.8	4.98	2.4	60	60	0	0	37.008177°	–6.328259°
3	25/11/2008	clay	22	0	0	0	15.5	22.9	250	20	10	0	1	37.071449°	–6.282073°
4	25/11/2008	clay	8	0	0	0	14.53	4.82	500	30	15	1	1	37.070582°	–6.286127°
5	25/11/2008	clay	33	75	2	15	20.2	14.05	255	18	10	1	0	37.071134°	–6.272415°
6	27/11/2008	clay	11	0	0	25	12.42	13.27	1000000	40	35	1	1	37.076737°	–6.386587°
7	27/11/2008	clay	34	95	20	75	20.2	3.94	200	25	15	1	0	37.076190°	–6.384441°
8	27/11/2008	clay	12	40	30	0	15.41	35.2	35000	65	60	0	1	37.071487°	–6.355004°
9	27/11/2008	clay	31	98	98	75	22.8	18	2000	60	60	0	1	37.088665°	–6.380065°
10	28/11/2008	sand	28	0	0	0	11.37	0.372	12000	75	35	1	0	37.228509°	–6.153545°
11	28/11/2008	sand	6	0	0	5	9.94	0.191	7500	140	140	1	1	37.222674°	–6.162855°
12	28/11/2008	sand	6	40	40	25	10.22	1.645	720000	100	50	1	1	37.200727°	–6.176092°
13	29/11/2008	clay	6	0	0	0	10.4	2.23	45000	30	10	0	1	37.178297°	–6.126242°
14	29/11/2008	sand	3	5	5	40	10.22	0.154	120	25	13	1	0	37.201984°	–6.172002°
15	29/11/2008	clay	15	60	0	0	10.8	6.11	300	15	10	1	0	37.103780°	–6.259297°
16	30/11/2008	clay	13	60	0	20	10.4	15.6	900	15	10	1	0	37.071118°	–6.314931°
17	30/11/2008	clay	19	30	0	0	10.2	4.56	200	30	15	1	0	37.071439°	–6.335424°
18	30/11/2008	clay	23	75	0	25	8.35	3.82	175	25	13	1	0	37.071454°	–6.338793°
19	30/11/2008	clay	25	90	90	0	8.77	15.4	150	50	40	1	0	37.076049°	–6.384000°
20	30/11/2008	clay	29	80	80	40	14.83	2.99	255	40	25	1	0	37.114583°	–6.415711°
21	30/11/2008	sand	48	85	85	25	11	0.184	292500	35	15	1	1	37.050465°	–6.569258°
22	1/12/2008	clay	14	80	80	25	12.09	4.75	16660	60	45	1	0	37.071399°	–6.271665°
23	2/12/2008	clay	12	0	0	0	17.03	6.7	1186100	20	20	0	1	37.005193°	–6.239634°
24	2/12/2008	clay	11	0	0	0	11.71	16.05	1533000	20	20	0	0	36.984277°	–6.258043°
25	2/12/2008	clay	11	0	0	0	5.13	17.46	357600	25	25	0	0	36.963270°	–6.225526°
26	2/12/2008	clay	15	0	0	0	16.95	37.6	155	60	45	0	0	36.965548°	–6.231134°
27	2/12/2008	clay	13	0	0	0	22.4	22.5	1950	30	15	0	0	36.982913°	–6.226445°
28	2/12/2008	clay	24	40	40	0	10.08	8.3	10920	150	150	0	0	36.989468°	–6.222672°
29	3/12/2008	clay	17	0	0	0	12.3	70.8	29700	25	25	0	0	36.833331°	–6.341841°

Results

Trichocorixa verticalis was the most widespread corixid species found along the salinity gradient. This species occurred as adults in 70 % of the samples (other species 26 %–52 %), and was present at nearly 80 % of all sites when including juveniles. It was absent only at sites with low salinity (< 1 g/l). Although the samples were taken in early winter, we found *T. verticalis* to reproduce (indicated by the presence of juveniles) in the majority of the sites where it was present (56 % of all sites).

Corixid community patterns

The sampled sites tended to have relatively species-poor corixid communities (mean number of species 2.70 ± 0.31 SE). Six species were regularly found (*Corixa affinis* Leach, *Sigara lateralis* Leach, *S. scripta* Rambur, *S. selecta* Fieber, *S. stagnalis* Leach, and *T. verticalis*) and one was present at one locality only (*Micronecta* sp., only juveniles). A PCA on the quantitative corixid data summarized 74.2 % of all corixid community variation in two dimensions, indicating the presence of few important community composition gradients. Leaving out two outlier sites (sites 8 and 16) barely changed this result (71.1 % of variation explained by two dimensions). *T. verticalis*, *S. selecta* and to a lesser extent *S. stagnalis* constitute one community gradient (all positively associated to the first axis, eigenvalue = 0.421), and largely perpendicular (independent) to this gradient are *C. affinis*, *S. lateralis*, and *S. scripta* (all positively associated to the second axis, eigenvalue = 0.321). The proportional community data were more multidimensional (59.4 % explained by two axes, 79 % by three axes). The main gradient (axis 1, eigenvalue 0.37) is composed of a turnover from *S. lateralis* dominated communities to *T. verticalis* dominated communities.

T. verticalis densities were not related to species richness nor abundance of the corixid community (excluding *T. verticalis*; species richness: R = 0.20, $t_{(27)} = 1.08$, p = 0.29; abundance R = 0.22, $t_{(27)} = 1.16$, p = 0.25). When using *T. verticalis* abundances as the explanatory variable to explain variation in corixid community composition (excluding *T. verticalis*), the model explains a significant 21.5 % of all variation (p = 0.003). Concordant with the above model, high numbers of *T. verticalis* coincided with high numbers of *S. selecta* and *S. stagnalis*. When using the environmental variables matrix as a covariable, the fraction of corixid community variation explained by *T. verticalis* becomes insignificant (6 %, p = 0.15).

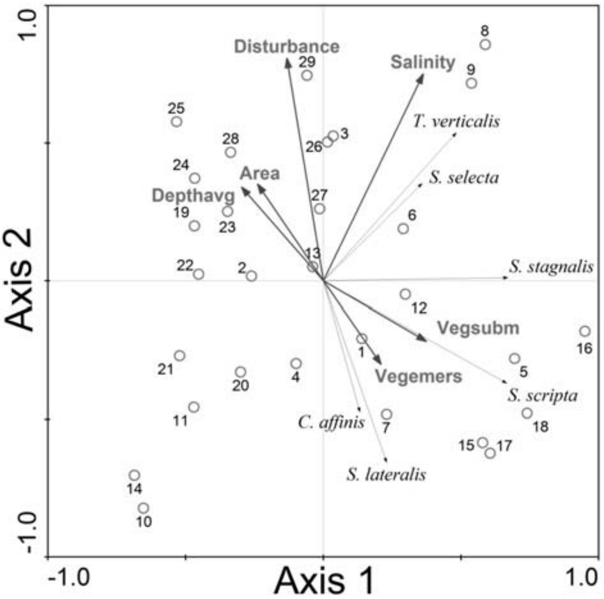

Fig. 2. Triplot showing the results of the RDA on quantitative corixid data and environmental variables. Shown are the sampled sites (circles), corixid species (small arrows) and environmental variables (bold arrows). To increase readability of the graph, only environmental variables with a correlation in the biplot of |r| > 0.25 are plotted. Codes of the environmental variables are as in Table 1.

Corixidae and environmental factors

The final multiple regression model explained almost half of the variation in *T. verticalis* densities ($R^2 = 0.45$, $F_{(3,25)} = 6.78$, p = 0.002). The selected variables were salinity (positive correlation), the presence of fish (positive correlation, fish was mainly *Gambusia*) and cover by emergent vegetation (negative correlation). However, salinity was the only variable significantly correlated with *T. verticalis* densities ($p < 0.0001$) and it accounted for 80 % of all explained variation (fish: 16 %, emergent vegetation: 4 %, both $p > 0.09$). The variable anthropogenic disturbance also explained a high fraction of variation, but this variation largely coincided with salinity, and the fraction of variation it could explain was much less than that explained by salinity (30 % less).

The RDA indicated a moderate fit of the measured environmental variables with variation in the quantitative corixid community structure (eigenvalues; axis1 = 0.240, axis2 = 0.215, p-values > 0.23; Fig. 2). Approximately half of the community variation could be explained by all environmental variables (sum of canonical eigenvalues = 0.567, p = 0.018). Forward selection revealed salinity (measured as conductivity) as the most important environmental variable, explaining 15.5 % of variation in the corixid communities

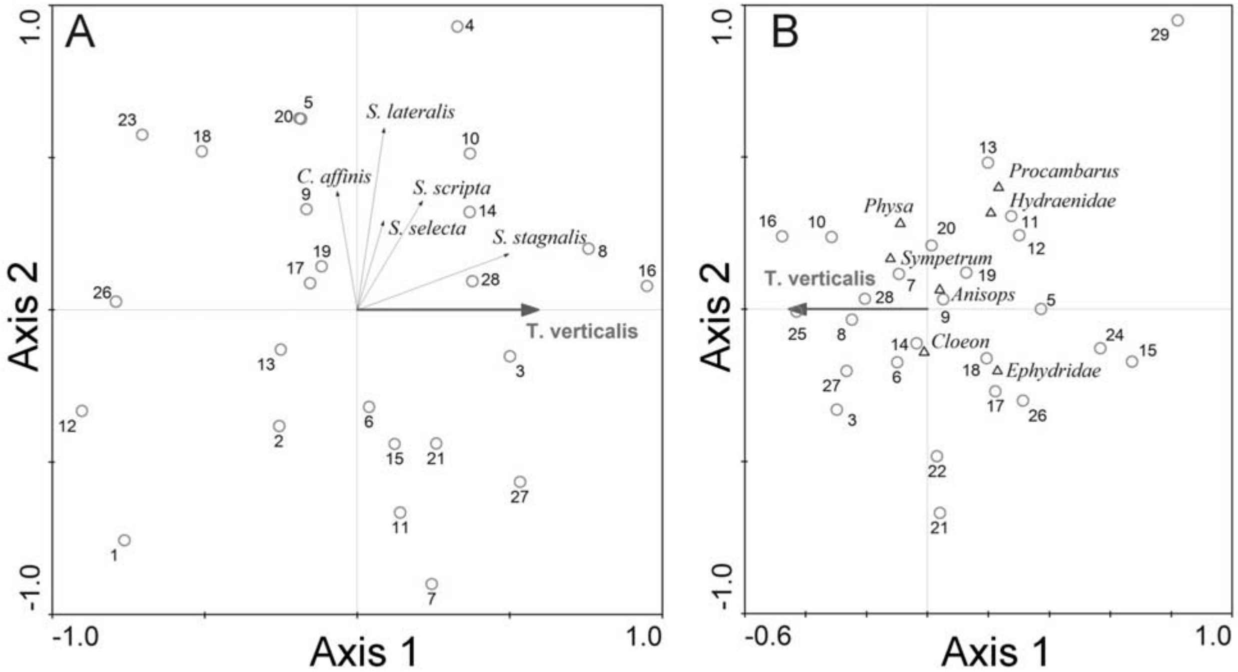

Fig. 3. **(A)** Triplot of the RDA on the quantitative corixid data testing for the effect of *T. verticalis* while correcting for environmental variation. **(B)** Biplot of the CCA on the invertebrate community corixid data testing for the effect of *T. verticalis* while correcting for environmental variation. Sampled sites are shown as circles, corixid species as small arrows, and invertebrate species as triangles. To increase readability of the CCA biplot, only invertebrate species with a correlation in the biplot of $|r| > 0.12$ are plotted.

(p = 0.001). However, salinity was highly positively correlated with anthropogenic disturbance (14.9 % of variation explained, p = 0.001). When we repeated the first RDA for the corixid community excluding *T. verticalis*, anthropogenic disturbance became a more important variable than salinity (disturbance 12.8 %, p = 0.017; salinity 11.7 %, p = 0.021).

Because collinearity between anthropogenic disturbance and salinity is mainly due to the lack of disturbed ponds at low salinities in our dataset (at higher salinities, disturbed and undisturbed sites are more evenly distributed) we can partially uncouple salinity from disturbance by leaving out these low salinity sites, and thus attain a better view of their respective effects. Since our interest is mainly in *T. verticalis*, we removed the five freshwater sites (< 1 g/L), from which *T. verticalis* was absent and did a restricted analysis. Anthropogenic disturbance now became the single most important variable explaining corixid community structure in the RDA on the quantitative corixid data (15.5 %, p = 0.006) and it correlated negatively with abundances of most Corixidae, whereas *T. verticalis* and *S. selecta* were not negatively affected. Salinity itself had only a marginally significant effect (10.7 % explained variation, p = 0.051). When we excluded *T. verticalis* from this restricted analysis, anthropogenic disturbance explained 18 % (p = 0.017), while all other variables explained a non-significant fraction (< 12 %, p > 0.20). Using *T. verticalis* densities to explain variation in densities of other Corixidae in this restricted analysis we found a fairly large effect (15.9 % explained, p = 0.001), but when controlling for environmental variables, this explanatory contribution was no longer significant 6.8 % (p = 0.13). Most Corixidae species were indifferent to the presence of *T. verticalis*, whereas *S. stagnalis* positively covaried with *T. verticalis* (Fig. 3A). We found no negative associations between *T. verticalis* and native Corixidae.

In the RDA on the proportional corixid community data, environmental variables explained a similar amount of community variation as for the quantitative data (eigenvalues: axis 1 = 0.316 p = 0.007, axis 2 = 0.110, p = 0.26; sum of all canonical eigenvalues = 0.584, p = 0.016). Three of the measured environmental variables contributed significantly to the model: salinity (21.6 %, p = 0.001), anthropogenic disturbance (19.5 %, p = 0.001) and cover by submergent vegetation (9.7 %, p = 0.026), but they shared large fractions of variance. When leaving out the five sites with lowest salinity as for the quantitative data, little changed and salinity and disturbance explained an equal amount of variation (19.7 %, p = 0.003). The coinciding salinity/disturbance gradient differentiated communities that are dominated by *T. verticalis* (at high salinity/disturbance) from communities in more ion-poor/less disturbed waters that are dominated by *C. affinis* and *S. lateralis*. Submergent vegetation and water depth had a negative effect on the proportional presence of S. *scripta* and *S. stagnalis*, and a positive effect on *C. affinis* and *S. selecta*. When we use *T. verticalis* abundances to explain proportional presences of other Corixidae (note that proportions were derived from samples including *T. verticalis*), we found only weak negative correlations for *C. affinis* and *S. lateralis* and even weak positive correlations for *S. selecta* and *S. stagnalis* (model results: 9.2 % explained variation, $p = 0.047$). After correction for environmentally related patterns, only 3.5 % of variation in the proportional presence of Corixidae other than *T. verticalis* was explained ($p = 0.61$, Fig. 3A).

Corixidae juvenile densities were significantly explained by a model (sum of all canonical eigenvalues 0.696, $p = 0.002$) in which cover of submergent vegetation (25.4 %, $p = 0.001$), anthropogenic disturbance (12.8 %, $p = 0.025$) and salinity (12.2 %, $p = 0.048$) were the main explanatory factors. Densities of *T. verticalis* juveniles were positively related to disturbance and negatively to cover of submergent vegetation; densities of *Corixa* and *Sigara* juveniles were negatively related to disturbance and positively to cover of submergent vegetation.

Community patterns

Forty-one invertebrate taxa (excluding Corixidae) were found. They were mainly aquatic Coleoptera (15 genera), macrocrustaceans (6 genera) and Diptera (4 families). The density of *T. verticalis* was not significantly correlated with invertebrate community taxon richness ($R = 0.17$, $t_{(27)} = 0.87$, $p = 0.39$) or with community abundance ($R = 0.18$, $t_{(27)} = 0.92$, $p = 0.36$). Macroinvertebrate communities showed a distinct species turnover, as indicated by the long gradients in the DCA. Total community variation was highly multidimensional, and only 37.2 % could be captured by a two-dimensional model in the CA. Taxa showing a high prevalence at the positive side of axis 1 were Ephydridae (Diptera), Hydraenidae (Coleoptera), the crustaceans Isopoda and *Palaemonetes*, and the gastropod family Hydrobiidae, which all have species indicative of high salinity. A model constructed of the environmental variables as explanatory variables and the invertebrate species that occurred in at least two ponds significantly explained variation in the invertebrate communities (CCA 56.8 % explained variance, $p = 0.009$). In concordance with the results of the CA, species variation was explained by multiple gradients (salinity 11.8 %, $p = 0.001$; disturbance 11.0 %, $p = 0.003$; submergent vegetation 10.3 %, $p = 0.003$; area 9.6 %, $p = 0.006$; cover by emergent vegetation 9.0 %, $p = 0.007$). *T. verticalis* densities explained 9.6 % ($p = 0.004$) of invertebrate community variation, which dropped to 3.8 % ($p = 0.32$) after accounting for environmental gradients (Fig. 3B).

Discussion

Our results confirm the findings of Rodríguez-Pérez et al. (2009) that *T. verticalis* has currently spread over the whole Doñana area around its initial discovery there in 2001, and currently is present in most of the habitats where it is able to survive. Furthermore, in contrast to Rodríguez-Pérez et al. (2009), we found *T. verticalis* to be reproducing in most of the sites where it was present, indicating that it may be well established. These findings are also surprising since *T. verticalis* is exceptional among Corixidae in that it is reported to overwinter solely in the egg stage (Tones 1977, Aiken & Malatestinic 1995), while this study was done at the onset of winter. Possibly, *T. verticalis* is able to reproduce throughout the annual cycle in the Mediterranean climate as long as water is present, as earlier suggested by Rodríguez-Pérez et al. (2009). Altogether, our data suggest that the invasion of southern Europe by *T. verticalis* is successful and ongoing. Given the extended latitudinal distribution of *T. verticalis* in North America, the species may have the potential to spread much further across Europe. There is relatively little ongoing monitoring of Corixidae in the Iberian Peninsula, and the current limits of *T. verticalis* distribution are unclear, although it occurs at least as far east as the Laguna Medina at Jerez de la Frontera (authors, unpublished data).

Abundances of *T. verticalis* were best explained by salinity: the species was absent from ponds with a salinity below 1 g/l and juveniles were not found below 3.4 g/l. With respect to salinity, *T. verticalis* occupies a similar part of the gradient as the autochthonous species *S. selecta* and *S. stagnalis*. In addition, *T. verticalis* was the only Corixidae found at a very high salinity (42 g/l), but highest densities were reached at intermediate salinity levels. In its native range, *T. verticalis* has been found in high abundances at hypersalinity, where it is the only aquatic predator in the simple food web (Wurtsbaugh 1992). The presence of fish also tended to explain part of *T. verticalis*' distribution. Surprisingly, fish correlated positively with *T. verticalis* abundance, even though they are likely to prey on them (Kelts 1979). In our study, the only fish in more than 75 % of the sites was *Gambusia*, which preferentially preys on small zooplankton (Cardona 2006) and predation impact on *T. verticalis* may thus have been low. Most likely, some unidentified underlying factor causes *Gambusia* and *T. verticalis* abundances to positively covary. Finally, the abundance of juvenile *T. verticalis* not only depended on salinity, but was also strongly associated with low cover of submergent vegetation. Unvegetated parts of shallow waters warm-up more quickly by solar heating than vegetated parts. Higher temperatures, and the increased production of benthic micro-organisms that may serve as food, may stimulate faster growth and development of Corixidae, explaining the preference for this habitat, at least during the cold winter months. We conclude that in southern Europe *T. verticalis* largely overlaps with the salinity niche of European halophilic species, and in addition may fill in the high end of the salinity gradient where autochthonous Corixidae are absent.

Native Corixidae and *T. verticalis*

We did not find indications for strong competition between *T. verticalis* and the autochthonous corixid community. However, corixid communities were mainly structured along a gradient from a low proportion of *T. verticalis* to dominance of the community by this alien species, as shown by the PCA on the proportional data. A similar observation led Rodríguez-Pérez et al. (2009) to suggest that *T. verticalis* changed the community through competitive exclusion of native species. However, a constrained analysis using the environmental data indicated that the *T. verticalis* gradient largely coincided with a salinity/anthropogenic disturbance gradient. When we explicitly tested for the effect of *T. verticalis*, taking into account the background changes in environmental variables, we found that *T. verticalis* did not have significant negative effects on native Corixidae (Fig. 3A).

Salinity was identified as the single most important environmental variable to predict *T. verticalis* abundance. However, anthropogenic disturbance was equally or more important in explaining variation in community structure of the other Corixidae. In fact, it appears that salinity mainly explains the presence of *T. verticalis*, while anthropogenic disturbance explains the absence of other corixid species (cf. Fig. 3A). Rather than specifically exploiting disturbed areas as repeatedly observed for other invading species (Daehler 2003), *T. verticalis* is resistant to these disturbances and becomes the dominant corixid under these circumstances. One explanation for this phenomenon may be the unusual resistance of *T. verticalis* eggs and their ability to overcome strong disturbances such as drought or hypersalinity (Kelts 1979), whereas native Corixidae are probably dependent on immigration from elsewhere for recolonization after local extinction. However, many of the natural systems dominated by native Corixidae are also subject to dry periods and/or seasonal variation in salinity, so more research is needed to identify the crucial disturbance parameter.

T. verticalis and the invertebrate community

In its native range, *T. verticalis* has been demonstrated to negatively affect other invertebrates, inducing trophic cascades and changes in water quality (Wurtsbaugh 1992). In our study, we could not detect effects of *T. verticalis* on the local invertebrate community. Neither did we observe any correlation between water transparency, invertebrate community structure and *T. verticalis* suggestive of a trophic cascade. Studies that did find community effects of *Trichocorixa* were all in hypersaline ecosystems with simple, species-poor food webs (Wurtsbaugh 1992, Herbst 2006). In these environments, *T. verticalis* is one of the few predators that can survive. By being almost the sole member of the highest trophic level, *T. verticalis* attains the role of a key-predator in these systems (Wurtsbaugh 1992). In our study we included only one hypersaline site (42 g/l) that had a typical species-poor community dominated by *Artemia* sp.. All other sites we studied exhibited more complex food webs, with several top predators and intermediate predators. Here, the ecological role of *T. verticalis* is less exclusive as it joins an existing functional group (almost all systems had native Corixidae present), and therefore may have had no detectable impact.

Conclusions

Ten years after its first discovery in Europe, *T. verticalis* is now a widespread and important component of the corixid communities in Doñana and surrounding areas of south-west Spain. It has reproductive populations at many different places from where it may colonize new ponds. Our study indicates that *T. verticalis* mainly develops dense populations in saline ponds where *S. selecta* also occurs. In addition, *T. verticalis* profits from open waters that are subject to human disturbance such as fish and shrimp farms and salterns, where they often are the dominant (if not only) Corixidae species. At present, *T. verticalis* has no detectable impact on the local Corixidae and the macroinvertebrate community as a whole. However, the correlative nature of our observational data, combined with the important fractions of unexplained variation urge for caution. More pronounced effects may also occur outside the winter season. Experiments designed specifically to assess the mechanisms of its success and to unravel species interactions and community-scale effects of *T. verticalis* are needed. Special attention should go to hypersaline environments, where *T. verticalis* has the potential to be a keystone predator. If *T. verticalis* is better able to tolerate hypersalinity than native corixids, it is likely to have a considerable impact on native *Artemia* populations in the Iberian peninsula, which are already severely threatened by competition with exotic *Artemia* (Amat et al. 2005). Several of the highly saline systems in Spain are wetlands of international importance designated by the RAMSAR convention, owing to their great importance for migratory waterbirds (Martí & del Moral 2002). The invasion by *T. verticalis* of these sites, possibly followed by strong internal trophic cascades and dramatic changes of the community, may also affect the waterbird populations that depend on these aquatic communities (Kelts 1979, Sánchez et al. 2006).

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