Global Change Biology

Global Change Biology (2012) **18**, 2135–2146, doi: 10.1111/j.1365-2486.2012.02691.x

Evaluating drivers of vulnerability to climate change: a guide for insect conservation strategies

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Abstract

Ongoing global climate change presents serious challenges in conservation biology, forcing us to revisit previous tools and principles based on how species may respond to novel climatic conditions. There is currently a major gap between predictions of species vulnerability and management strategies, despite the fact that linking these areas is fundamental for future biodiversity conservation. Herein, we evaluate what drives vulnerability to climate change in three Iberian endemic water beetles, representing three independent colonizations of the same habitat, employing comparative thermal physiology, species distribution models and estimations of species dispersal capacity. We derive conservation strategies for each species based on their differential capacity to persist and/or potential to shift their ranges in response to global warming. We demonstrate that species may be affected by climatic warming in very different ways, despite having broadly similar ecological and biogeographical traits. The proposed framework provides an effective complement to traditional species vulnerability assessments, and could aid the development of more effective conservation strategies in the face of global warming.

Keywords: adaptive management, conservation biology, dispersal capacity, geographical range shifts, global warming, Iberian Peninsula, risk determinants, species persistence, species sensitivity, water beetles

Received 23 February 2012; revised version received 23 February 2012 and accepted 24 February 2012

Introduction

Climate change is expected to become one of the greatest drivers of global biodiversity loss (Sala *et al.*, 2000; Thomas *et al.*, 2004), with impacts on species' ranges, phenology and physiology already widely documented (Parmesan, 2006). Furthermore, for threatened species, i.e., those species at risk of extinction due to the adverse effects of current natural or anthropogenic stressors, climate change may constitute a major additional threat, acting either alone or synergistically (Brook *et al.*, 2008). This additional impact on biodiversity presents major challenges to conservation biology, forcing us to revisit previous tools and principles based on how species are able to respond to climate change. As a consequence, studies arguing that conservation measures must take account of climate change have proliferated in recent years (e.g. Hannah *et al.*, 2002; Akcakaya *et al.*, 2006; Moss *et al.*, 2009; Thomas *et al.*, 2011). However, most such studies either refrain from making management recommendations, or simply refer to general conservation principles. Therefore, there remains a significant gap between predictions of species vulnerability and management strategies in the context of global warming, despite the fact that linking these areas is essential for future biodiversity conservation (Kareiva *et al.*, 2008; Heller & Zavaleta, 2009). To bridge this gap, it is fundamental that we are able to evaluate the main drivers of species sensitivity to climate change and subsequently, design specific conservation strategies focused on these determinants of species risk (McKinney, 1997; McMahon *et al.*, 2011).

Insects constitute the vast majority of terrestrial biodiversity. Like many ectotherms, they are often particularly sensitive to climatic warming as their basic physiological functions are strongly influenced by environmental temperature (Samways, 2007; Deutsch *et al.*, 2008). However, most insect orders are neglected in both conservation research and policy (Cardoso *et al.*, 2011), and our knowledge of the impact of climate change on much of insect biodiversity remains limited.

In general, the vulnerability of a species to global warming will depend on both, its capacity to maintain present populations (species persistence) and its capacity to shift its geographical range to suitable future environments (potential for range shift; Williams *et al.*, 2008). To date, most studies evaluating species vulnerability to climate change have focused on expected changes in habitat availability under future climatic

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scenarios using species distribution models (SDMs). However, SDMs often do not explicitly consider the differing abilities of species to persist and colonize in a changing world, and hence relevant species traits, such as physiological tolerance, dispersal ability and adaptive capacity are ignored. As a result, assessments of global warming impacts based only on SDMs could result in significant prediction errors, perhaps underestimating the persistence of species *in situ* and overestimating their potential to access and exploit predicted future climate space (Pearson & Dawson, 2003; Guisan & Thuiller, 2005; Elith & Leathwick, 2009). This partial consideration biases their derived conservation recommendations, which are mostly general strategies based on the selection of protected areas and measures to increase habitat connectivity (e.g., Hannah *et al.*, 2007; Krosby *et al.*, 2010; Araújo *et al.*, 2011; for a review see Heller & Zavaleta, 2009).

To evaluate how a species' traits may determine its vulnerability to climate change, we estimate both capacity to maintain present populations using data on thermal tolerance, and ability to shift geographical range to suitable future environments by coupling SDMs with measures of dispersal capacity. On the basis of this kind of information, we develop a decision framework that can be used to outline potential conservation strategies for individual species, as a function of their differential persistence capacity and/or potential to shift their ranges in response to global warming. As a case study, we focus on three threatened species of water beetles from different families, all restricted to the Iberian Peninsula and with similar ecological and biogeographical traits. These taxa, from lineages which colonized aquatic habitats independently, represent an ideal model system in which to explore how the intrinsic characteristics of species may determine their vulnerability to climate change. We use data from physiological experiments, ecological niche modeling and population phylogeography to elucidate the drivers of vulnerability to global warming, and define specific management strategies for each species. We demonstrate that despite having broadly similar ecology and biogeography, the studied species are likely to respond in very different ways to climate change due to differences in species-specific traits. The approach we outline here has the potential to significantly improve management strategies for threatened taxa in the face of climate change.

Materials and methods

Study species

We focused on three Iberian endemic water beetles: *Ochthebius glaber* (Montes & Soler 1988), *Nebrioporus baeticus* (Schaum 1864) and the Iberian lineage of *Enochrus falcarius* (Hebauer 1991; see Arribas *et al.*, in press), belonging to different families (Hydraenidae, Dytiscidae, and Hydrophilidae respectively). The three are all restricted to saline streams, themselves a threatened habitat, and are some of the most characteristic species of such systems in southern Iberia (Millán *et al.*, 2011). *Ochthebius glaber* is restricted to streams in the south of the Iberian Peninsula (Abellán *et al.*, 2007; Fig. 1, Table S1 in Supporting information) and *N. baeticus* is distributed from the south of the Iberian Peninsula to the Pyrenees (Fery *et al.*, 1996; Fig. 1, Table S1). Finally, *E. falcarius* has traditionally been viewed as a species occurring throughout the western Mediterranean (Schödl, 1998). However, a recent

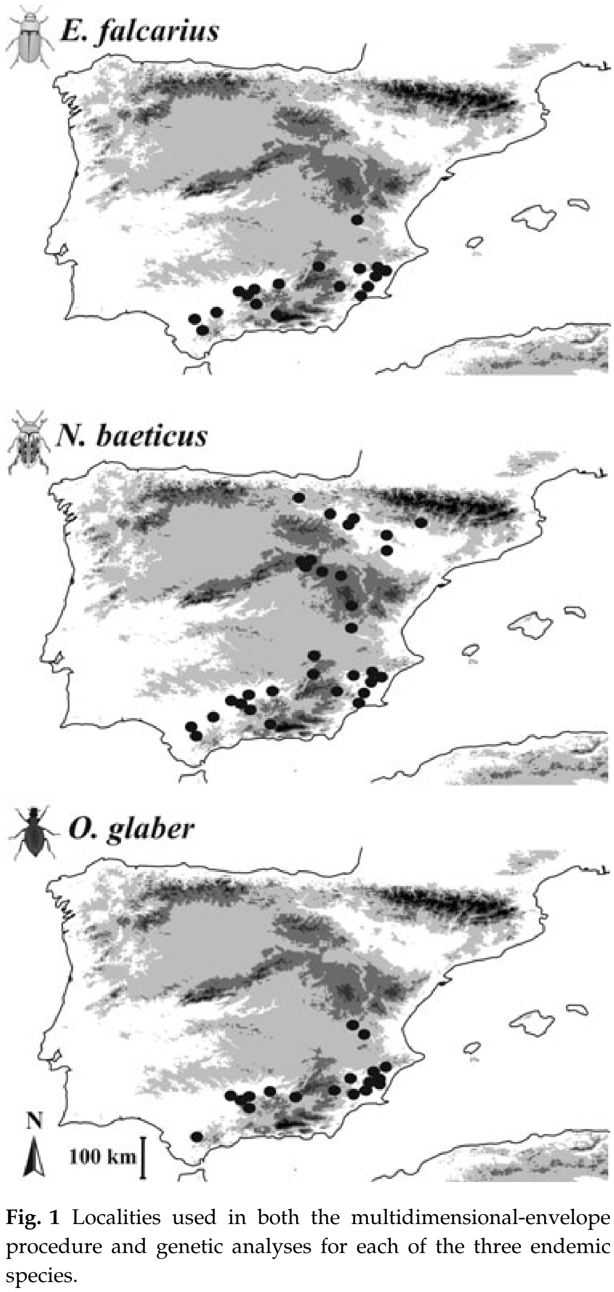

Fig. 1 Localities used in both the multidimensional-envelope procedure and genetic analyses for each of the three endemic species.

study has revealed that *E. falcarius* as currently understood comprises four very distinct lineages, each with restricted, disjunct distributions across the Mediterranean area (Arribas *et al.*, in press). In this study, we focused on the Iberian lineage ('*E. falcarius* IP' *sensu* Arribas *et al.*, in press; here *E. falcarius* for simplicity), which is restricted to the south of the Iberian Peninsula (Fig. 1, Table S1), and constitutes a phylogenetically, morphologically and ecologically independent entity from its sister lineages (Arribas *et al.*, in press). *Ochthebius glaber* and *N. baeticus* have been previously categorized as 'vulnerable species' according to several species (biogeographical and ecological) and habitat (habitat rarity and loss) attributes (for details see Abellán *et al.*, 2005 and Sánchez-Fernández *et al.*, 2008; see also Verdú & Galante, 2006 and Verdú *et al.*, 2011 for IUCN categorization of *O. glaber*). Similarly, the Iberian form of *E. falcarius* can also be viewed as a vulnerable taxon using the same criteria (Abellán & Millán, unpublished data).

Species persistence under climate change

We estimated relative persistence under climate change by determining species acclimation abilities and thermal tolerances via an experimental approach. Acclimation responses can provide a measure of species thermal plasticity, and therefore capacity to adapt to changing conditions (Calosi *et al.*, 2008a; Chown *et al.*, 2010; Somero, 2010). Similarly, the relationship between lethal thermal limits and environmental temperatures can be used to assess vulnerability to warming (e.g., Stillman, 2003; Deutsch *et al.*, 2008). Notably, the concept of a thermal safety margin (TSM) has previously been used to assess vulnerability to climate change, as it approximates the average amount of environmental warming an ectotherm could tolerate before performance drops to fatal levels (Deutsch *et al.*, 2008).

Herein, acclimation ability was assessed by investigating the effects of thermal acclimation on upper lethal limits (UTL; Chown & Nicolson, 2004). Adult beetles were collected as close as possible to the central point of their latitudinal ranges (all from close localities in the province of Murcia, Spain) to avoid possible confounding effects of local adaptation in range edge populations (see Kirkpatrick & Barton, 1997) and to minimize latitudinal differences between collection sites. Specimens were maintained for 7 days under constant conditions to minimize the effects of recent thermal history on measures of temperature tolerance (Sokolova & Pörtner, 2003). After this, specimens of each species were divided into two equal-sized groups (seven individuals in each one) and exposed to different acclimation temperatures (15 and 25 °C, respectively). Beetles were maintained under their corresponding thermal acclimation treatments for 6 days (Terblanche & Chown, 2006). Following this period individuals from each treatment were used to measure UTLs.

Thermal tolerance tests were carried out in air, using a dynamic method (Lutterschmidt & Hutchison, 1997), raising the temperature at 1 °C min^{-1} in a computer controlled water bath (Grant LTC 6–30, using the Grant COOLWISE software; Grant Instruments, Cambridge, UK). Heating commenced at the temperature at which a particular treatment group had previously been acclimated. UTL was estimated as a lethal point following the approach of other recent studies of aquatic beetles (see Calosi *et al.*, 2008a,b, 2010; Sánchez-Fernández *et al.*, 2010; Arribas *et al.*, in press). ANCOVAs were used with untransformed data to test for differences in UTL between the two acclimation temperatures, using body mass as covariate. Homoscedasticity of raw data was met, but for some treatments the assumption of normality was not. Despite this, we used raw data after verifying the distribution of GLM residuals (see Rutherford, 2001). In cases where significant differences between acclimation temperatures were found, acclimation capacity was estimated as the difference between mean UTLs for both acclimation treatments.

Thermal safety margins were estimated for each species and locality as the difference between species UTL (as estimated for the 25 °C acclimation treatment) and maximum temperature of the warmest month of each locality (i.e., BIO5 from WORLDCLIM, version 1.3, http://www.worldclim.org; see Hijmans *et al.*, 2005 for details) for both present and future scenarios. We used three general circulation models and different carbon emission scenarios (optimistic and pessimistic) for future estimates: CCM3 for the year 2100, GCGM2 and mk2 models, each using both A2a and B2a scenarios for the year 2080, and HadCM3 using A1b and B2a scenarios for the year 2080 (all with 30 arc-seconds resolution). The CCM3 scenario for the year 2100 assumes a duplication of greenhouse-gas emissions (Govindasamy *et al.*, 2003), being roughly equivalent to the average of the current IPCC scenario families (Dai *et al.*, 2001; Seavy *et al.*, 2008), and therefore represents a good baseline for conservative evaluations of species vulnerability under climate change. GCGM2, mk2 and HadCM3 models were used with both optimistic and pessimistic scenarios to cover the uncertainty of different predictions. Detailed explanation of these scenarios is available from the Intergovernmental Panel on Climate Change Data Distribution Center (IPCC, 2001; http://www.ipcc-data.org/). ANOVAs were used to test for differences between $TSM_{Present}$ and TSM_{Future} for each climate change scenario for each species, with untransformed data (as homoscedasticity and normality of raw data were met). All statistical analyses were conducted using SPSS for Windows, Version 15.0.1. 2006 (SPSS Inc., Chicago, IL, USA).

Species' potential for range shifts under climate change

Species could also adapt to novel climatic conditions by shifting their ranges into newly favorable areas (Parmesan, 2006). To evaluate species' potential to shift their ranges under climate change, we used both measures of change in climatically suitable area and estimates of dispersal capacity.

Identification of climatically suitable areas. Changes in climatic habitat suitability provide a fundamental estimate of species vulnerability (Guisan & Thuiller, 2005). They represent the change in potential area of species geographical ranges in the future. We used a multidimensional-envelope procedure (MDE) to estimate the climatically suitable area for each species at present and in different future scenarios (Jiménez-Valverde *et al.*, 2008), following Aragón *et al.* (2010) and Sánchez-Fernández *et al.* (2011).

Occurrence data (Table S1) were compiled from previous studies (Sánchez-Fernández *et al.*, 2008; Abellán *et al.*, 2009; Arribas *et al.*, in press) as well as from extensive sampling of saline running waters across the Iberian Peninsula carried out over the last decade (Velasco & Millán, unpublished database). Nineteen bioclimatic variables (see Table S2) were obtained from WORLDCLIM for the present, and seven future scenarios, at 30 arc-seconds resolution (see above). Both bioclimatic variables and occurrence data were aggregated onto 10×10-km grid cell resolution to account for uncertainties in presence data and the spatial configuration of aquatic lotic systems, which form hydrological basins within which most aquatic organisms can readily move.

As the distributional simulations obtained from MDE are highly dependent on the number of selected predictors (Beaumont *et al.*, 2005), we first tried to identify the minimum set of climatic variables related with the occurrence of each species via an ecological niche factor analysis (ENFA; Hirzel *et al.*, 2002); the number of retained factors being determined by comparing the eigenvalues to a 'broken-stick' distribution (Hirzel *et al.*, 2002). Finally, the relevant climatic variables for each species were selected as those showing the highest correlation with retained ENFA factors. We then calculated the extreme climatic values (maximum and minimum) of these relevant variables from known presences of each species. These values were used to derive binary maps of areas with climatically suitable conditions (i.e., potential distribution) in the Iberian Peninsula for present and future scenarios at a 10×10-km grid cell resolution.

By comparing these binary present and future maps, we estimated the percentage of change in suitable area (CSA) for each species in each future scenario and the percentage of future suitable area, which represented turnover (i.e., the number of new suitable grid cells as a fraction of the total suitable area in future). This variable was calculated as a surrogate measure of the degree to which species depend on dispersal capacity to shift their distributions under global warming.

Dispersal capacity. Despite the fact that dispersal ability will determine a species ability to track changing climate (Pearson & Dawson, 2003), comparative data on dispersal ability are scarce (but see Lester *et al.*, 2007) due to the difficulty of obtaining reliable and comparable measures. As population genetic structure is generally correlated with dispersal ability (Bohonak, 1999), we used a measure of the increase of phylogenetic distance with geographical distance among localities (i.e., phylogenetic beta diversity; Graham & Fine, 2008) to estimate the relative dispersal abilities of the three species.

MtDNA sequences (3′ end of Cytochrome c oxidase subunit 1, cox1) for *O. glaber*, *N. baeticus* and *E. falcarius* were obtained as described in previous studies (Abellán *et al.*, 2007, 2009; Arribas *et al.*, in press), with additional specimens of *E. falcarius* being sequenced for this study to approximately equalize numbers for each taxon. DNA was extracted using an Invisorb Spin Tissue Mini Kit (Invitek, Berlin, Germany) and *cox*1 gene was sequenced using the primers C1-J-2183 and L2-N-3014 (Simon *et al.*, 1994). Sequencing was conducted using the ABI PRISM BigDye Terminator Cycle Sequencing kit (Applied Biosystems, Carlsbad, CA, USA) and sequenced products were electrophoresed on ABI 310 and 3700 automated sequencers (Applied Biosystems). Sequences were assembled and edited with Sequencher 4.7 (GeneCodes Corporation) and submitted to GenBank (see Table S3 for accession numbers).

A total of 235 sequenced specimens of *E. falcarius*, *N. baeticus* and *O. glaber* were used, covering their known geographical ranges with a mean of five individuals per locality (Table S3, Fig. 1). Phylogenetic trees were constructed separately for each species using a range of related species from the same subgenera as outgroup taxa. Bayesian analyses (BA) were conducted with MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003), with 10×10^6 generations using default values, saving trees every 100 generations. The half compact consensus tree was calculated with the 'sumt' option of MrBayes. MrBayes searches were carried out on Bioportal (http://www.bioportal.uio.no).

We used the 'comdist' function as implemented in the Phylocom software (Webb *et al.*, 2008) with the phylogenetic trees obtained, to create a matrix of pairwise phylogenetic distances between localities for each species, based on the mean branch-length of all possible pairs of sequences (see Abellán *et al.*, 2009). To reduce possible confounding effects of species-specific differences in rates of molecular evolution on dispersal estimations, we standardized each species phylogenetic distances using its maximum phylogenetic distance. In parallel, a matrix of pairwise geographical distances between localities was created for each species and used to test the relationship between pairwise geographical and phylogenetic distances among populations of each species via Mantel tests (Mantel, 1967) with 9999 random permutations using the ade4 package for R (Thioulouse *et al.*, 1997). The increase of standardized phylogenetic distance with geographical distance (i.e., the slope of the regression line) was considered as an inverse proxy of each species dispersal capacity (Abellán *et al.*, 2009).

Results

Species persistence under climate change

Acclimation capacity. Of the three species studied, only *E. falcarius* showed a significant acclimation response, having a higher tolerance for high temperatures following acclimation at 25 °C than at 15 °C (ANCOVA *E. falcarius*, df = 1, $F = 323.94$, $P < 0.001$; $UTL_{15\,°C} = 51.66$ °C, $UTL_{25\,°C} = 54.77$ °C). *Nebrioporus baeticus* and *O. glaber* had similar UTLs following acclimation to both temperature treatments (ANCOVA *N. baeticus*, df = 1, $F = 4.94$, $P = 0.057$; $UTL_{15\,°C} = 45.08$ °C, $UTL_{25\,°C} = 45.60$ °C; *O. glaber*, df = 1, $F = 0.062$, $P = 0.807$; $UTL_{15\,°C} =$ 47.96 °C, $UTL_{25\,°C} = 47.93$ °C; see Fig. 2a, Table 1).

Thermal safety margins. The mean TSM decreased significantly for the seven future scenarios compared

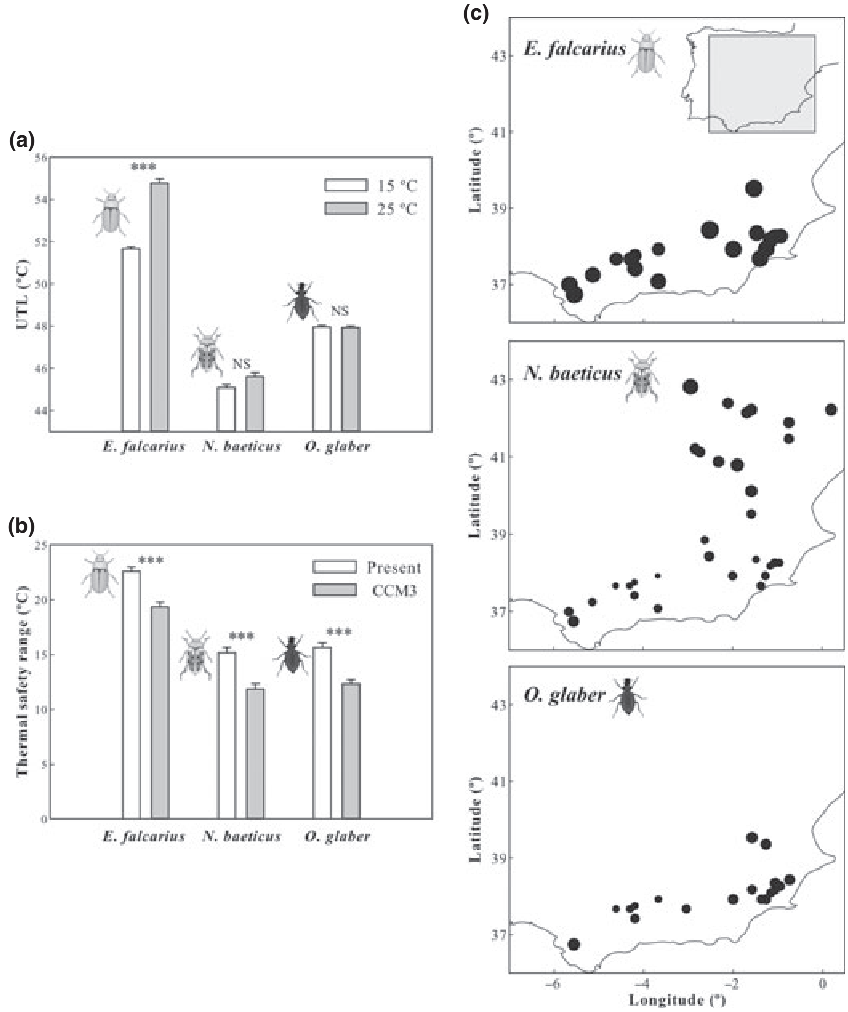

Fig. 2 Species persistence under climate change (CCM3 scenario for the year 2100). (a) The effect of temperature of acclimation on the upper thermal limits (UTL). (b) Differences between present and future mean thermal safety margins for localities (TSM). Histograms represent means + SE. Significantly different means are indicated by stars (***$P < 0.001$). (c) Geographic location and TSM_{Future} of each species locality. Circle diameter is proportional to TSM_{Future}.

with present for all three studied species ($P < 0.001$; see Fig. 2b for CCM3 scenario and Fig. S1 for the other future scenarios). *Enochrus falcarius* showed higher values of TSMs than *N. baeticus* and *O. glaber* for both present and future scenarios. Nevertheless, the magnitude of change in TSMs for present and each future scenario was quite similar between the three species and, in general, the different future scenarios resulted in comparable decreases in mean TSMs for all three species. The pattern of TSM_{Future} values across localities for all three species was also consistent across the different scenarios (Figs. 2c and S2): most *O. glaber* localities displayed low TSM_{Future} values (i.e., high risk under global warming); *N. baeticus* localities in the south of the Iberian Peninsula also showed low TSM_{Future} values, whereas northern localities displayed higher values; finally, most of the *E. falcarius* localities showed high TSM_{Future} values, indicating lower risk under global warming than the other two species (for details see Tables 1 and S4).

Species' potential to shift ranges under climate change

Identification of climatically suitable areas. Following the ENFA procedure, the 19th bioclimatic variables considered were reduced to five factors for *E. falcarius* explaining 100% of variance; three factors for *N. baeticus* explaining 67.7% and four factors for *O. glaber* explaining 99.3% of variance. Mean temperature of warmest quarter was the variable with highest marginality coefficients for *E. falcarius* and *O. glaber*, whereas for *N. baeticus* this was annual precipitation. Similarly, precipitation of the driest quarter, precipitation of the driest month and annual temperature range showed

Table 1 Assessment of different determinants of species vulnerability under climate change (CCM3 scenario for the year 2100)

	E. falcarius	*N. baeticus*	*O. glaber*
Species persistence			
Mean acclimation capacity (ºC)	3.11	No acclimation	No acclimation
Mean TSM_{Future} for localities (ºC)	19.36	11.87	12.33
Min–Max TSM_{Future} for localities (ºC)	16.4–22.4	7.2–18.9	9.5–15.5
Species' potential for range shifts			
CSA (%)	−29.47	−18.55	−32.82
Turnover in future suitable area (%)	47.80	25.80	79.66
Dispersal capacity [(km × 100)$^{-1}$]	0.078	0.029	0.109

Mean acclimation capacity is expressed as the difference in upper thermal limits following exposure to different acclimation temperatures. Mean, Min and Max TSM_{Future} represent average, minimum and maximum values of future thermal safety margins for localities of each species. CSA is the percentage of change in future climatically suitable area relative to the present, and turnover expresses the number of new suitable grid cells as a fraction of the total suitable area in the future. Dispersal capacity is expressed as the slope of the regression line between phylogenetic and geographical distances (higher values indicate lower dispersal abilities)

the highest coefficients of the specialization factor for *E. falcarius*, *O. glaber*, and *N. baeticus,* respectively.

For the three species, a comparison of the total area with climatically suitable conditions between present and the different future scenarios showed important habitat losses (i.e., negative CSA) and high turnover of suitable habitats (see Fig. 3 for CCM3 scenario and Fig. S3 for the other future scenarios). Despite congruence in the pattern of variation between the different scenarios, differences in CSA and turnover values were found between them, with HadCM3 predictions showing the highest losses of habitat and turnover compared to the other scenarios, which were much more similar. Among species, the pattern of habitat loss was consistent across the different future scenarios: *O. glaber* always showed the highest reductions in climatically suitable area (CSA) and the highest number of novel suitable grid cells (turnover), followed by *E. falcarius*, and *N. baeticus* (for details see Table 1 and S4).

Dispersal capacity. The standard deviation of split frequencies between the two runs of MrBayes reached a value of ca. 0.005 at 10 MY generations for all three species, and the half compact consensus tree was calculated removing 15% of initial trees as a 'burn-in'.

The pairwise measure of standardized phylogenetic diversity between populations was significantly correlated to linear geographical distance for all three

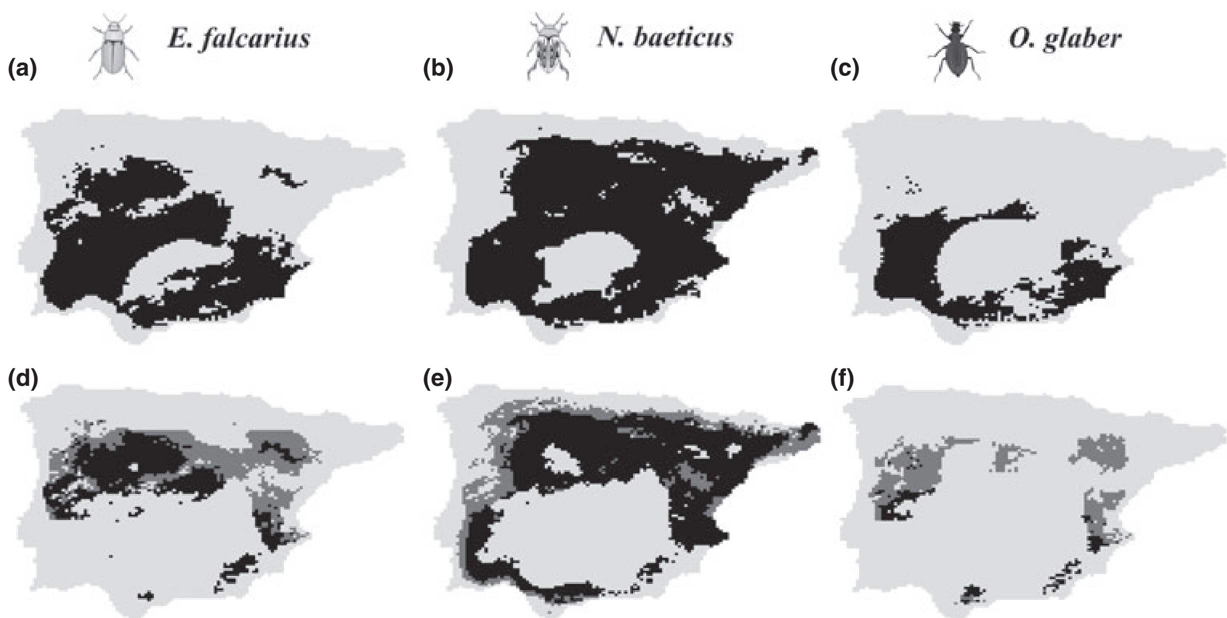

Fig. 3 Climatically suitable areas of each species as estimated by the multidimensional-envelope procedure for present (a, b and c) and future (CCM3 scenario for the year 2100; d, e and f). Grid cells representing turnover are shown in gray.

species (Mantel test *E. falcarius* $R = 0.571$, $P < 0.001$; *N. baeticus* $R = 0.244$, $P = 0.012$; *O. glaber* $R = 0.466$, $P < 0.001$), indicating an increase of genetic distance with geographic distance across localities (see Table S5 for distance matrices). In *O. glaber*, the rate of increase of standardized phylogenetic distance with geographical distance was higher [0.109 $(\text{km} \times 100)^{-1}$] than for *E. falcarius* [0.078 $(\text{km} \times 100)^{-1}$] and noticeably higher than in *N. baeticus* [0.029 $(\text{km} \times 100)^{-1}$; Fig. 4, Table 1].

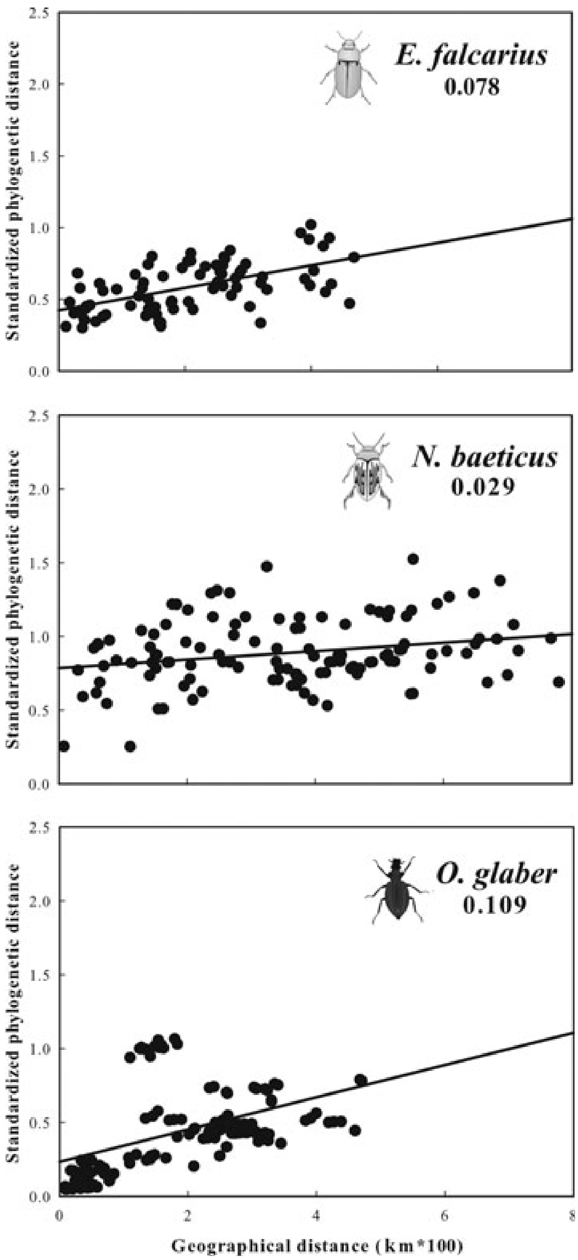

Fig. 4 Dispersal capacity of each species as estimated by the increase of standardized phylogenetic distance with geographical distance among localities. The slope of regression line is indicated in the upper-right corner of each graph.

Discussion

Evaluation of drivers for species vulnerability under climate change

Species persistence under climate change. Experimentally derived measures of thermal tolerance such as those used here (i.e., acclimation capacity and TSM), are crucial for understanding species persistence, since warming-induced stress is the most proximate effect of global warming (Pörtner & Farrell, 2008; Tewksbury *et al.*, 2008; Barnes *et al.*, 2010), preceding behavioral or evolutionary responses to climate change (Chown & Nicolson, 2004). Experimental approaches to obtain such data are well developed for a wide range of taxa, from marine invertebrates to mammals (see Lutterschmidt & Hutchison, 1997; Bozinovic *et al.*, 2011) and data on thermal biology have the potential to contribute greatly to our understanding of the effects of climate change (Bernardo & Spotila, 2006; Wikelski & Cooke, 2006; Helmuth, 2009). Indeed for some taxa such data may already be present in the existing literature (see Chown & Nicolson, 2004 for review), and while there may occasionally be difficulties or ethical considerations involved in obtaining extensive data of this type from endangered taxa, many threatened invertebrates are common locally, making data on thermal biology relatively easy to collect, even for rare species.

The three species studied displayed contrasting persistence capabilities according to the measures used, and *O. glaber* seems to be the most vulnerable in this regard. This species showed low values for TSM_{Future} for most of its localities and did not show any acclimation response in the laboratory. *Nebrioporus baeticus,* despite having comparable $TSMs_{Future}$ to *O. glaber* in southern localities, had noticeably higher values in its northern localities. In general, the risk of high-temperature episodes adversely affecting population viability seems to be higher in southern localities for both species. Conversely, *E. falcarius* could be less compromised by an increase in temperature, as most of its localities showed TSM_{Future} values above 15 °C across all future scenarios. The elevated persistence of *E. falcarius* is mainly due to its high mean UTL, which is notably higher than for all other water beetles studied to date (Calosi *et al.*, 2008a,b, 2010; Sánchez-Fernández *et al.*, 2010), but consistent with that recorded in related *Enochrus* species (Arribas *et al.*, in press). Moreover, *E. falcarius* seems to have good UTL acclimation capacity, a trait that has been inversely related with vulnerability to climate change in a range of taxonomic groups (e.g., Stillman, 2003; Calosi *et al.*, 2008a; Donelson *et al.*, 2011).

The TSM_{Future} differences found in the species studied are likely to be highly relevant to their population persistence, particularly when considering their biology and ecology. Although these are aquatic animals, these beetles do spend some of their life-cycle on land (in the pupal stage and as a teneral adult), where they are exposed to greater temperature fluctuations than when they are submerged. In addition, saline streams are characterized by scarce riparian vegetation and very low flow, meaning that water temperatures follow air temperatures closely (Millán *et al.*, 2011).

Identification of climatically suitable areas. Measures of CSA and turnover have been applied previously to estimate macro-scale extinction risks under climate change (e.g., Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Araújo *et al.*, 2011). These measures seem to be highly informative about the habitat matrix, which species could face in the future, especially in combination with estimates of dispersal ability and persistence. Nevertheless, other important factors could be incorporated, such as the distance of potentially suitable future environments from current ones (affecting establishment success) and the degree of climatic suitability or habitat quality in already occupied and new locations (affecting population viability; see e.g., Ohlemuller *et al.*, 2006).

Estimates of CSA showed significant future reductions in suitable habitat areas for all three species and across all scenarios, although in some cases these were moderate compared with those predicted in some other groups (e.g., Thuiller *et al.*, 2005). Nevertheless, the small range size and high specialization of these species highlight their vulnerability under any future expected reduction in suitable habitat area. Turnover percentages were markedly higher for *O. glaber* and *E. falcarius*, irrespective of the future scenario used. In both species, suitable areas showed major shifts northward, with currently suitable southern areas being dramatically reduced.

Dispersal capacity. Pronounced differences in dispersal capacity were estimated between the studied species. As revealed by previous molecular studies (Abellán *et al.*, 2007, 2009), the dispersal ability of *O. glaber* seems to be markedly limited, with *E. falcarius* also showing reduced dispersal capacity when compared with *N. baeticus*, which shows little geographical structure in its phylogenetic diversity. Despite the fact that all three studied species are able to fly, little is known regarding their dispersal strategies, which could play a fundamental role in the different dispersal abilities of the three studied species (Bilton *et al.*, 2001). The predicted changes in habitat availability referred to above suggest that, *O. glaber* and *E. falcarius* would be highly dependent on dispersal to shift their ranges under the future climatic predictions, something which may be beyond their capabilities. The results of our study emphasize that, species occupying habitats in semiarid areas of the Mediterranean region could undergo major reductions in climatically suitable area and experience high turnover as consequence of global warming, and that some Mediterranean macroinvertebrates may have a lower northward expansion potential than previously proposed due to dispersal limitation (e.g., Bonada *et al.*, 2007).

Conservation strategies

On the basis of evaluation of a species persistence, and its ability to shift its range under climate change (i.e., the drivers of each species vulnerability), we propose a framework to guide conservation strategies, which ultimately try to mitigate climate change impacts on species (see Fig. 5). Given the need for species-specific data, such an approach is most appropriate for the conservation of threatened taxa, such as those studied here, and could be especially relevant to reserve managers, who have the resources to hone conservation strategies for particular 'flagship' species.

For species showing high capacities to deal with future climate conditions without the need to disperse, the concentration of conservation efforts in actual localities (i.e., *in situ* management), could be a more efficient and practical strategy than others (e.g., connectivity, Hodgson *et al.*, 2009). In our case study, *E. falcarius* seems to have a high-persistence capacity in its current localities. Protection and conservation measures should therefore be focused on the maintenance of current populations and the minimization of other threats, also taking into account the relatively low dispersal capacity and the anticipated climate-driven habitat reduction for this species. Conservation measures should be especially focused on southern localities, in which the interaction of intense climate change with more localized anthropogenic threats (e.g., nutrient and freshwater inputs, Millán *et al.*, 2011) could result in local extinctions. Similarly, climate adaptation and mitigation measures at the habitat scale could be fundamental to improve the persistence of populations in current localities under climatic warming. In aquatic habitats, increased shading is a commonly proposed measure in this regard (Ormerod, 2009), but its real value is only partially understood (Wilby *et al.*, 2010).

For species with reduced capacity to deal with temperature rise *in situ* (e.g., *O. glaber* and *N. baeticus*), the potential for range shifts is fundamental in determining viability under climate change. When species show substantial reduction or displacement in future suitable habitat with respect to present, species dispersal capacity should determine which conservation strategies to

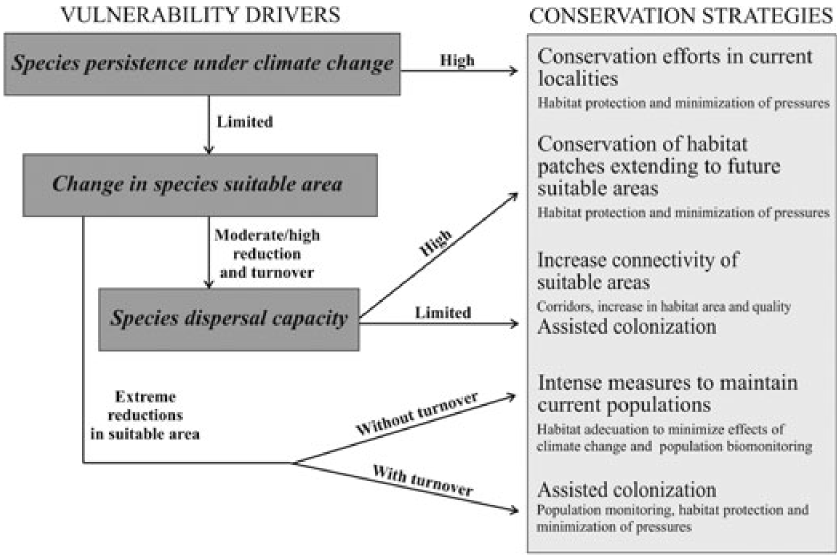

Fig. 5 Decision framework to guide conservation strategies based on the different drivers of vulnerability to climate change.

apply. In this sense, an important increase in suitable habitat connectivity would be required for species with low-dispersal ability (Krosby *et al*., 2010), especially for highly fragmented habitats such as aquatic systems (Sala *et al*., 2000). Conservation and restoration of riparian corridors and the creation of a network of habitats within and between present and future suitable areas (including artificial ones if the natural habitat matrix is not enough), could be essential measures for poorly dispersing aquatic species. Furthermore, the management of the spatial arrangement of habitat and matrix characteristics, together with increases in protected habitat area and habitat quality could also be effective conservation measures, as they serve to improve connectivity (Hodgson *et al*., 2009, 2011).

In extreme situations where species are unable to migrate (i.e., severe habitat turnover and/or limited dispersal capacity), assisted colonization has emerged as a conservation strategy aimed at reducing the negative effects of climate change on defined biological units such as populations (Hoegh-Guldberg *et al*., 2008). This measure has triggered intense debate (e.g., Ricciardi & Simberloff, 2009; Schlaepfer *et al*., 2009), mainly because of its associated uncertainties and risks. However, one cannot disregard the use of translocations under an extreme probability of extinction scenario, although it should be always implemented after a multidimensional evaluation of its relative costs and benefits to other conservation strategies (Richardson *et al*., 2009).

Ochthebius glaber seems to be the most endangered of the three species considered here, showing low persistence, low-dispersal capacity and very high turnover percentages in future suitable area. Increases in protected suitable habitat area and connectivity will be required for this species, especially for southern populations, including restoration of traditional inland saltpans, which could act as stepping stones for this species and other fauna inhabiting saline aquatic ecosystems. Moreover, intensive biomonitoring programs and analyses conducted at the landscape scale should be applied to check population viability and define more precise conservation measures (Cabeza *et al*., 2010). For species showing a higher dispersal capacity, increased habitat connection should not be required, and so conservation strategies could promote the maintenance and restoration of future suitable habitat patches. During the area selection for possible future range shifts, it should be taken into account that conservation measures appropriate for vertebrates and insects (or invertebrates in general) are not always the same. A selection of small, but appropriately distributed, habitat patches in future suitable areas could represent a low cost, but highly effective strategy in conserving insect species (Dunn, 2005). In the case of *N. baeticus*, despite its low potential persistence in southern localities, its higher dispersal capacity and relatively lower reduction in suitable habitat area could allow populations to follow the predicted shift in suitable habitat to the north of the Iberian Peninsula. In this case, special attention to the maintenance and restoration of saline habitats into future suitable northern areas could provide an effective strategy to facilitate its predicted movements, and so increase its viability in the face of future climate change.

In summary, our findings highlight that species may be affected by climatic warming in widely differing ways, despite having similar ecological and biogeographical traits. On the other hand, we demonstrate how an exploration of the different drivers of species vulnerability to climatic warming (i.e., species persistence and potential for range shift) could guide conservation strategy decisions to help species cope with this impact. In this way, the proposed framework could become an effective complement for other species vulnerability categorizations already in use (e.g., IUCN, 2001; Abellán *et al.*, 2005; Sánchez-Fernández *et al.*, 2008; Thomas *et al.*, 2011). Such an approach achieves an equilibrium between the quantity of data required and the possibility of defining concrete conservation strategies, something which is of fundamental practical importance, especially for taxa where information is limited, such as most insects. Although other biotic (e.g., Araújo & Luoto, 2007) or spatial factors (e.g., Opdam & Wascher, 2004) may influence the vulnerability of species to climate change, our approach could be used as a framework within which to explore the impacts of such additional factors, as data become available for individual taxa.

Acknowledgements

We thank all collectors for proving material for study, especially I. Ribera and A. Cieslak; C. Andújar, F. Picazo, C. Gutiérrez-Cánovas, J.A. Carbonell, J. Lencina, A. Hidalgo-Galiana, J. Arribas, L. Blázquez for field assistance; J. Hemprich, R. Haslam and R. Alonso for technical support; I. Ribera, C. Andújar, P. Calosi, G. Massamba-N'Siala and the members of the Aquatic Ecology research group (Universidad de Murcia, Spain) for help at various stages of this project. We also thank five anonymous referees for their useful comments on an earlier version of this manuscript. This work was supported by funding from a predoctoral grant (FPU) from the Ministerio de Educación to P. Arribas, a postdoctoral grant from the Fundación Séneca to D. S.-F. and a postdoctoral grant from the Ministerio de Educación to P.Ab., and projects CGL2006-04159, 023/2007 (A.M.) and CGL2010-15378 (J. V.).

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Supporting Information

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

Table S1. Localities used in the multidimensional-envelope procedure for each of the three species and populations included in the genetic analyses.
Table S2. Bioclimatic variables used in the multidimensional-envelope procedure (MDE).
Table S3. List of sequenced specimens for *N. baeticus*, *E. falcarius* and *O. glaber*.
Table S4. Assessment of different determinants of species vulnerability under climate change (six additional future scenarios for the year 2080).
Table S5. Matrices of raw phylogenetic distance (below diagonal) and geographical distance [above diagonal; (km $\times$ 10^{-2})] between localities for each of the three species.
Figure S1–S2. Species persistence under climate change (six additional future scenarios for the year 2080).
Figure S3. Climatically suitable areas of each species as estimated by the multidimensional-envelope procedure for present and seven future scenarios (CCM3 scenario for the year 2100, the rest for the year 2080).

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