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Preserving the evolutionary history of freshwater biota in Iberian National Parks

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ABSTRACT

The establishment of protected areas is one of the main strategies to reduce losses of biodiversity. While a number of studies have evaluated the effectiveness of existing reserves in preserving representative samples of ecosystem and species diversity, there has been no systematic assessment of their effectiveness in terms of conserving evolutionary history. We used comprehensive phylogenies of four lineages of aquatic Coleoptera to investigate (i) the performance of National Parks (NPs) in representing the phylogenetic diversity (PD) of the Iberian Peninsula; (ii) the representation in NPs of the species with the highest conservation priority, as identified from a combination of their evolutionary distinctiveness and vulnerability; and (iii) whether species richness may be a good surrogate of PD when selecting new conservation areas. Our results show that Iberian NPs perform poorly in the preservation of freshwater PD. In most cases PD was not different from a random expectation, but when it did differ, PD in NPs was always lower than that obtained by a random selection of the same number of species. We also found that most of the highly evolutionarily distinct and vulnerable taxa were not covered by any NP. Finally, when additional conservation areas were selected maximizing the number of unrepresented species, the variation in PD could be very high, and as a consequence, depending on the group and the number of areas added, they could preserve much less evolutionary history than when they were specifically selected to maximize PD.
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1. Introduction

Conservation biologists are increasingly incorporating phylogenetic information when evaluating conservation priorities, both using species-based and area-based approaches (Rolland et al., 2012). When the focus is on species, the assumption is that not all species are equal in terms of evolutionary distinctiveness, as the extinction of phylogenetically singular taxa would result in a larger loss of evolutionary history (Vane-Wright et al., 1991; Redding and Mooers, 2006). These measures of evolutionary distinctiveness can also be extended to incorporate extinction risk for assessing conservation worth (e.g., Redding and Mooers, 2006; Isaac et al., 2007).

When the focus is the conservation of an area, the evolutionary relationships of the species it contains reveal their shared evolutionary history. One of the most frequently used statistics, phylogenetic diversity (PD), can be quantified by summing the branch lengths of a phylogeny that subtend all the species in the subset to be measured (Faith, 1992). Conservation efforts can then be directed towards those areas hosting the subset of species that maximizes PD (see e.g., Forest et al., 2007). The rationale underlying this approach is the assumption that, since closely related taxa will tend to be also similar in their physiologies and ecologies (Harvey, 1996), by maximizing PD we likely maximize the representation of genotypic, phenotypic and functional diversity, thus providing biological systems with the best options to respond to a changing world (Vane-Wright et al., 1991; Faith, 1992). Despite evidently strong theoretical grounds for incorporating PD into conservation prioritization schemes, the benefits of the use of PD metrics has been called into question because it tends to scale in a predictable way with taxon richness, which is more easily obtained. In practical terms, conservation decision making based on richness or PD might be largely indistinguishable (Polasky et al., 2001; Rodrigues and Gaston, 2002; Rodrigues et al., 2005, 2011). Nevertheless, empirical studies (e.g., Forest et al., 2007; Devictor et al., 2010) have shown that taxon richness maybe decoupled from PD (i.e. some areas have more or less PD than expected given their number

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of species), and this decoupling could have important implications for conservation planning (Forest et al., 2007; Strecker et al., 2011).

Although protected areas play a key role in conservation strategies to reduce losses of biological diversity (Chape et al., 2005), they are often not selected to meet specific biodiversity objectives, and historical, socio-economic or aesthetic criteria have dominated the choice of their locations (Pressey, 1994). While a number of studies have evaluated the effectiveness of protected areas in preserving representative samples of ecosystem and species diversity (e.g. Rodrigues et al., 2004; Araújo et al., 2007; Branquart et al., 2008), there has been no systematic assessment of their effectiveness in preserving evolutionary history (but see Devictor et al., 2010) nor the extent to which the PD captured by existing reserves shows departures from what it would be expected based solely on their species richness. This is particularly the case for non-charismatic groups – such as invertebrates – and for freshwater biota, which is especially threatened but generally neglected (Abell et al., 2007; Cardoso et al., 2011).

Here we investigate how the existing network of National Parks (NPs) represents the evolutionary history of the Iberian freshwater biota. In the Iberian Peninsula, a global biodiversity hotspot (Brooks et al., 2006), NPs are at the core of the conservation polices and are committed to preserve the best representation of its natural heritage (Morillo and Gómez-Campo, 2000). We use water beetles as a surrogate of the wider freshwater biota, as it is one of the most diverse and best known groups of aquatic invertebrates in this region (Ribera, 2000; Sánchez-Fernández et al., 2008b). They exhibit a high level of endemism, but also include species widely distributed across the Palearctic and Holarctic regions. They have been shown to be good indicators of the wider diversity in aquatic ecosystems (Bilton et al., 2006; Sánchez-Fernández et al., 2006) and to be useful to select priority areas for conservation (Sánchez-Fernández et al., 2004; Abellán et al., 2005).

More specifically, we use comprehensive phylogenies of four lineages of aquatic Coleoptera to investigate: (i) the performance of the Iberian NPs in representing PD (i.e. do NPs include more or less PD than expected given their number of species or their area?); (ii) the representation in NPs of the species with the highest conservation priority, as identified from a combination of its evolutionary distinctiveness and vulnerability; and (iii) whether species richness is a good surrogate of PD in the selection of new protected areas. Since NPs are not the only protected areas in Spain and Portugal, which have several other heterogeneous regional or international categories of protection, our aim was not to evaluate the extent to which the whole phylogenetic diversity of the Iberian Peninsula is protected. We rather focused on the performance of this concrete reserve network, which represents the most charismatic and exigent protection category in the region and whose areas are linked by a common focus and similar management approaches.

2. Methods

2.1. Studied groups

We used four monophyletic lineages of aquatic Coleoptera belonging to three different families in two suborders, representing three independent invasions of the aquatic medium. Sampling aimed to maximize the presence of western Palearctic – and in particular Iberian – species, but with the inclusion of species from other geographical areas when morphological or molecular data suggested they could be closely related to some Iberian ones. The full list of taxa and data used in this study is provided in the Appendix A.

1. Suborder Adephaga, family Dytiscidae, subfamily Agabinae: in the West Palearctic it includes the genera *Agabus*, *Ilybius* and *Platambus* (Nilsson, 2001). They are mostly species inhabiting standing water and with generally wide geographical ranges throughout the Palearctic or Nearctic realms, although they also include a number of narrow-range endemics (Table 1).
2. Suborder Adephaga, family Dytiscidae, Hydroporini *sensu lato*: a clade including tribes Hydroporini and Hygrotini (Ribera et al., 2008), with 20 genera in the western Palearctic (Nilsson, 2001; Appendix A). It encompasses a heterogeneous set of species inhabiting a wide spectrum of aquatic habitats and geographic ranges.
3. Suborder Polyphaga, family Hydraenidae: in the western Palearctic it includes six genera (Hansen, 1998) encompassing a heterogeneous set of species inhabiting a wide spectrum of aquatic habitats, with a high number of narrow endemics but also with widespread species.
4. Suborder Polyphaga, family Hydrochidae: includes a single genus (*Hydrochus*) with ca. 180 described species. In the west Mediterranean (Iberian Peninsula, Italy, south France and North Africa) the species of the genus form a monophyletic group that also includes one species (*H. roberti*) so far recorded only from the Caucasus and Turkey (Hidalgo-Galiana and Ribera, 2011).

In the phylogenies we included all Iberian species of Agabinae, Hydroporini and Hydrochidae (Table 1). Missing endemics of Hydraenidae were in general very rare, some only known from the types and never collected since their description. All the endemic species present in the NPs were included in the phylogenies with the exception of *Ochthebius cantabricus*, although we included specimens from a morphologically very similar species from Turkey recorded as *O. cantabricus* but likely to be a separate species (M.A. Jäch per.com., 2011). We did not consider *Agabus nevadensis*, an endemic to Sierra Nevada, as it is nested within the widespread *A. bipustulatus* (Drotz et al., 2010).

2.2. Species inventories in the National Parks

Our study focused on the NPs (IUCN category II) located within the Iberian Peninsula (Fig. 1). In mainland Spain, the National Park network is an integrative system for the protection and management of eight areas selected to represent the Spanish natural heritage (Morillo and Gómez-Campo, 2000). It started in 1918 with the NP of Covadonga (now Picos de Europa) and Ordesa (Fig. 1), and new parks had been added in a process still underway (the last one, Monfragüe, in 2007, although a new one – Guadarrama – is planned to be established in 2013). We also included in the study the only designated NP in Portugal (Peneda-Gerês) (Fig. 1).

We obtained species distribution data for the NPs from fieldwork and from ESACIB, an exhaustive database of Iberian water beetle occurrences (Sánchez-Fernández et al., 2008b). Field data were collected during 2008–2010 from a total of 111 localities which represent the diversity of water body types present within

Table 1
Number of Iberian species, Iberian endemics, Iberian subspecies (all endemic), and total number of taxa included in the phylogenies in the four studied lineages (as for August 2012). All Iberian species and subspecies were included in the phylogenies with the exception of the Hydraenidae (with the included number in parentheses). See Appendix A for a complete species list.

Lineage	Iberian sp	Endemic sp	Iberian ssp	Total
Agabinae	26	4	0	98
Hydroporini s.l.	96	41	8	280
Hydraenidae	148 (128)	62 (49)	1	245
Hydrochidae	11	4	0	12

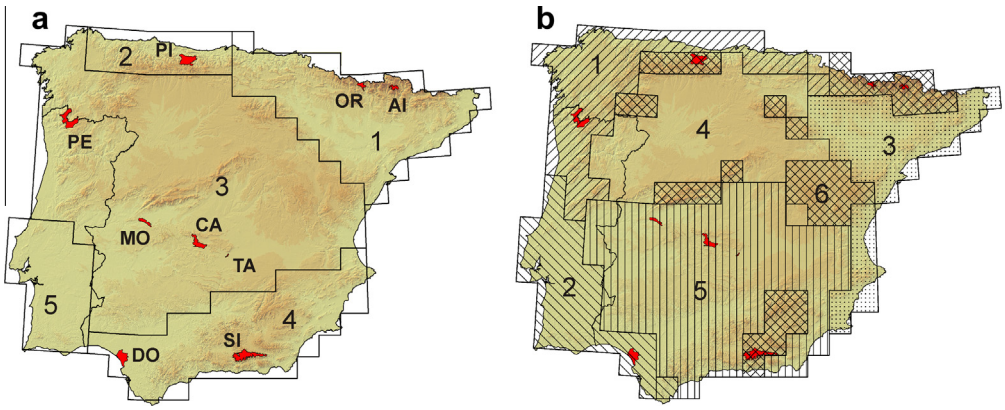

Fig. 1. Geographical location of the National Parks (solid polygons) in the Iberian Peninsula (Codes: TA, Tablas de Daimiel; AI, Aigüestortes i Estany de Sant Maurici; CA, Cabañeros; DO, Doñana; MO, Monfragüe; OR, Ordesa y Monte Perdido; PE, Peneda-Gerês; PI, Picos de Europa; SI, Sierra Nevada). (a) Biogeographical subregions according to Ribera (2000) (codes: 1, Pyrenean; 2, Cantabrian; 3, Hercynian Iberia; 4 Southeastern Iberia; 5, Southwestern Iberia). (b) Physicoclimatic subregions defined by Lobo and Martín-Piera (2002) (codes: 1, Eurosiberian; 2, West Mediterranean; 3, East Mediterranean; 4, North Plateau; 5, South Plateau; 6, Montane).

the NPs (see Millán et al., 2012 for details). ESACIB, which represents the most complete information available for a major group of freshwater invertebrates in the Iberian Peninsula, includes all available geographical and biological data for water beetles from the literature as well as from museum and private collections, PhD theses and other unpublished sources. The database contains over 60,000 records with associated location data (10 × 10 UTM squares) for 510 species.

2.3. Phylogenetic analyses

For Hydrochidae we used the phylogeny of Hidalgo-Galiana and Ribera (2011), pruning outgroups to leave only the western-Mediterranean clade and a single specimen for *H. interruptus* (see this reference for methodological details and Appendix A for the sequences used). For the other three lineages we reconstructed the phylogenetic relationships from a combination of two continuous fragments encompassing four mitochondrial genes (3′ end of Cytochrome c oxidase subunit 1 and 3′ end of the large ribosomal unit plus the Leucine tRNA plus the 5′ end of NADH dehydrogenase subunit 1). Sequence data were obtained from previous studies (Abellán and Ribera, 2011 and references therein) or newly obtained (441; EMBL accession numbers HF931106-HF931546, Appendix A). Specimens were killed and preserved in absolute ethanol in the field. We employed for DNA isolation a standard phenol–chloroform extraction or the DNeasy Tissue Kit (Qiagen GmbH, Hilden, Germany). Sequencing was conducted using the ABI PRISM BigDye Terminator Cycle Sequencing kit (Applied Biosystems) in an external facility. Sequences were assembled and edited with Sequencher 4.7 (GeneCodes Corporation) (see Appendix A for details of the data used for each lineage, and Appendix B for the phylogenetic trees used in the analyses).

We aligned length-variable regions with MAFFT v5.8 (Katoh et al., 2002). For Agabini and Hydraenidae no outgroups were used, and trees were rooted according to previously published topologies (Ribera et al., 2008, 2011). The Hydroporini tree was rooted with the genus *Laccornis*, following Ribera et al. (2008). We obtained ultrametric trees for each lineage (i.e. a tree in which branch lengths are scaled in units of time) using the Bayesian relaxed phylogenetic approach implemented in BEAST v1.6 (Drummond and Rambaut, 2007), which allows variation in substitution rates among branches. We implemented a GTR + I + G model of DNA substitution with four rate categories using a single partition, as the a priori rate used was estimated for a combination of protein-coding and ribosomal mitochondrial genes (see below). We fixed the root according to the outgroups or previous topologies (see above), and used an uncorrelated lognormal relaxed molecular clock model to estimate substitution rates and the Yule process of speciation as the tree prior. We sampled the run each 1000 generations and used TRACER v1.5 to determine convergence, measure the effective sample size of each parameter and calculate the mean and 95% highest posterior density interval for divergence times. After removing the fraction of trees considered as burn-in (see Appendix B for details on number of generations and burn-in), consensus trees were obtained using median values for branch lengths with TREEANNOTATOR v1.5.4. To estimate the evolutionary rate for the combined mitochondrial sequence (including protein coding and ribosomal genes) we used as prior a normal distribution with average 0.0115 substitutions/site/MY and a standard deviation of 0.0001. This is the standard arthropod mitochondrial clock of 2.3% (Brower, 1994), close to recent estimations of different groups of Coleoptera when using a combination of protein-coding and ribosomal genes (Papadopoulou et al., 2010; Ribera et al., 2011; Andújar et al., 2012).

2.4. Phylogenetic diversity coverage and random expectations

Phylogenetic diversity within each park was quantified as the minimum total branch length connecting all species of each of the four lineages to the root of the phylogenetic tree (Faith, 1992). We then assessed whether they have more or less PD than would be expected at random given their number of species. To do this we calculated the standardized effect size of PD (PD_{SES}) in each park by comparing the observed PD to the values expected from 10,000 random draws of an equal number of species from a given regional species pool (see below). PD_{SES} describes the difference between PD in the observed and randomly generated null samples, standardized by the standard deviation of PD in the null samples (Kembel et al., 2010). Positive values of PD_{SES} indicate that PD is higher, and negative values lower, than expected by chance. The significance of PD_{SES} was assessed using the rank of observed values relative to the values in the 10,000 null samples. PD and randomization tests were performed in R (R Development Core Team, 2011) with functions from the package PICANTE (Kembel et al., 2010). To account for topological uncertainty in the phylogenies we also computed the PD and the randomization tests for each of the 1000 last trees obtained with BEAST.

We used three different regional species pools to obtain the null expectations for (i) the Iberian species pool; (ii) the set of species occurring in the physicoclimatic subregion in which each park is

located, as defined in Lobo and Martín-Piera (2002); and (iii) the set of species occurring in the Iberian biogeographical subregion in which each park is located, as defined in Ribera (2000) according to their geological history and their present topography. We used the first null distribution to assess the role of the NPs in the conservation of the overall Iberian diversity of each of the beetle groups studied, as the recognized aim of the Iberian network of NPs is to preserve the best representation of the biodiversity of mainland Spain and Portugal. With the second and third distributions we assessed to what extent the NPs represent each of the subregional diversity pools according to two different regionalization schemes. The first regionalization allows us to consider differences in macroenvironmental characteristics, while the second reflects isolation due to geographical barriers or historical factors. By considering these alternative subregional species pools we tried to assess how the spatial structure of diversity in the Iberian Peninsula influences the estimated phylogenetic representation of NPs.

To better characterize possible patterns of phylogenetic structure we identified the clades that exhibit nonrandom patterns of representation in the NPs using the nodesig module in Phylocom (Webb et al., 2008). Nodesig tests whether a particular node in the phylogeny has significantly more or less descendent taxa in a sample (a NP in our case) than a null model predicts. The null model is a random draw of n taxa from the Iberian phylogeny, where n is the number of taxa in the sample (Webb et al., 2008). In this way, we were able to identify clades that contributed significantly to the decoupling between PD and species richness and to detect whether multiple patterns of phylogenetic structure are present within a given park.

We also compared the level of PD representation within the NPs with what would be expected by chance alone given the area they cover. Species distribution data for the Iberian Peninsula were obtained from the ESACIB database (see above), which are georeferenced at a spatial resolution of 100 km^2 (UTM 10×10 km grid cells). Because NPs are encompassed within polygons, we conservatively assigned protected areas to grid cells overlapping with NPs or parts of them. We then obtained 1000 random sets of equivalent number of grid cells where species have been recorded across the Iberian Peninsula, which were used as an estimate of the maximum PD that could be expected to be represented by chance. The rank of observed values of PD relative to the values in the 1000 random sets were used to assess the significance of differences in the effectiveness of NPs from random expectations.

2.5. Identifying species with high conservation value

We assessed to what extent the NPs protect species of high conservation value, as identified by a combination of their evolutionary distinctiveness and vulnerability. We first calculated the evolutionary distinctiveness (ED) of all Iberian endemic species using the metric proposed by Isaac et al. (2007), implemented in the R package PICANTE. The ED of a species is calculated as the length of its terminal branch plus its weighted share of ancestral branches. Hence, ED takes into account the evolutionary redundancy present in the surrounding tree, giving greater value to species whose genetic history is not shared with many other species. To account for phylogenetic uncertainty, for each species we averaged the ED values in the 1000 last trees obtained with BEAST (see above).

As a proxy of extinction risk we obtained estimates of species vulnerability from Sánchez-Fernández et al. (2008a), who ranked the Iberian endemic aquatic Coleoptera according to their conservation priority or degree of vulnerability using a combination of species' and habitat attributes. For the Iberian endemics not included in Sánchez-Fernández et al. (2008a) (recently described species, or species subject to taxonomic changes) we evaluated their vulnerability following the same methodology. In each lineage we identified the species of high conservation priority as those displaying both the highest evolutionary uniqueness (upper quartile) and high vulnerability ("high" and "very high" vulnerability categories according to Sánchez-Fernández et al., 2008a). We opted for this approach instead of Red List category weights (as in e.g. Isaac et al., 2007) as the vulnerability criteria of Sánchez-Fernández et al. (2008a) were specifically developed for aquatic Coleoptera and include a semi-quantitative assessment, trying to avoid qualitative judgments of extinction risk. We finally determined to what extent the existing network of Iberian NPs covered the species of high conservation value.

We also tested for phylogenetic clustering in the degree of vulnerability of the species in Hydroporini and Hydrenidae, the lineages with the highest number of endemic species. We used Blomberg's K-statistic (Blomberg et al., 2003) with the R package PICANTE (Kembel et al., 2010). Significance was calculated by randomizing the tips of the tree and recalculating K (1000 replicates). The K statistic compares the distribution of phylogenetically independent contrasts across nodes within the tree into the expectation under a Brownian motion model of trait evolution.

2.6. Species richness as a surrogate of phylogenetic diversity in the selection of conservation areas

Previous studies have suggested that species inventories are generally good surrogates of PD for spatial conservation planning purposes (Polasky et al., 2001; Rodrigues et al., 2005, 2011). However, the surrogacy value of species complementarity in the selection of additional conservation areas to extend the existing protection of PD has not yet been evaluated. Complementarity methods are used to select areas that in total have the highest representation of diversity (e.g. species richness; Vane-Wright et al., 1991). We explored whether taking into account evolutionary history for selecting new potential areas to add to the extant network of Iberian NPs increased the overall PD with respect to just maximizing species richness. For this purpose, we compared the overall PD represented when new areas were selected maximizing the unrepresented PD versus the PD represented as a by-product of maximizing the number of unrepresented species.

Species distribution data for the Iberian Peninsula were compiled from the ESACIB database, which are georeferenced at a spatial resolution of 100 km^2 (10×10 km cells). We then obtained two complementary sets of cells outside the existing NP network maximizing (1) the representation of the PD not included in the existing network of NPs, and (2) the number of unrepresented species. For the second, we also quantified how much overall PD was captured. We used an iterative heuristic algorithm, also known as a "greedy algorithm" (e.g., Csuti et al., 1997), that selected the site with the greatest value of diversity (either species or PD) not already represented in the NPs. The process was then iterated until the overall diversity was included. For the species richness, different cells can add the same number of species at a given step during the selection process. In these cases, we obtained all the possible complementary sets and calculated the PD captured in each of them. We also quantified how much PD is expected to be incidentally represented if sites were selected at random among unprotected cells, by obtaining sets of sites (1000 replicates) of variable size and calculating the mean PD and limits of the 95% confidence interval.

We evaluated the surrogacy value of species diversity in relation to PD by comparing the PD represented when maximizing species richness (the surrogate curve) with the one that directly maximizes PD (the optimal curve), taking into account the expected PD incidentally represented when sites are selected at random (the random curve). We measured the area under the

surrogate (S), optimal (O) and random (R) curves and these three values were combined into an index, SAI = (S − R)/(O − R) (Ferrier and Watson, 1997; see also Rodrigues et al., 2005, 2011). SAI equals one if there is perfect surrogacy (i.e. if the surrogate data produce results as good as the perfect data), zero if there is null surrogacy (using the surrogate data is as good as a random selection), and less than zero if there is negative surrogacy (using the surrogate data is worse than a random selection). We conservatively calculated SAI based on the upper 95% confidence interval of the random curve. We also calculated SAI for the range of values of PD covered when maximizing species representation at each number of selected areas. All analyses were performed with the R software.

3. Results

3.1. Phylogenetic diversity

Most of the NPs had less PD than expected at random according to their number of species for all four considered taxonomic groups and the three regional species pools, as indicated by the negative PD_{SES} values (Table 2 and Fig. 2). However, only ca. a fourth of these comparisons were statistically significant, in all cases showing a lower PD than expected by chance. When considering all NPs together, the representation of PD with respect to the Iberian species pool was always not significantly different from random (Table 2). In all cases, results were consistent when phylogenetic uncertainty was taken into account by using the last 1000 trees obtained in BEAST (Appendix C).

The nodesig algorithm identified which clades were causing a mismatch between observed and expected PD values (Appendix B). In Agabinae, only Sierra Nevada exhibited a nonrandom pattern of representation when compared to the Iberian phylogeny. This park had one significantly unrepresented clade (the genus *Ilybius*, with none of the nine Iberian species occurring in the park) and five nested clades with significant overrepresentation. In Hydroporini, most of the parks had at least one clade with significant over- or underrepresentation when compared to the Iberian phylogeny (Appendix B). Among those parks with significantly less PD than expected, Cabañeros and Monfragüe showed overrepresentation for clades encompassing species from the genera *Graptodytes* and *Stictonectes*, and underrepresentation for the remaining main clades. In the case of Peneda-Gerês and Sierra Nevada, they had more species than expected for several clades within the genus *Hydroporus*. With respect to Hydraenidae, all the parks had at least one clade with significant over- or underrepresentation. Among those parks with significantly less PD than expected, in Cabañeros, Peneda-Gerês and Picos de Europa patterns of decoupling between PD and species richness were caused especially by the underrepresentation of clades within the genus *Ochthebius*. For this genus, the overall PN network showed significant underrepresentation for a clade encompassing mostly species living in saline environments. Finally, none of the clades of Hydrochidae exhibited nonrandom patterns of representation in the NPs.

When the phylogenetic or species diversity represented within the NPs network was compared with what would be expected given the area they cover, for all groups except Hydraenidae NPs did not differ from a random selection ($p > 0.05$; Appendix C). In the case of Hydrenidae, NPs cover significantly less PD than expected by chance (only 11 of the 1000 random sets showed less PD than the observed value for NPs).

3.2. Coverage of vulnerable taxa with high evolutionary distinctiveness

We identified 22 Iberian endemic taxa with a high evolutionary distinctiveness (ED) and 53 taxa displaying high vulnerability, as assessed by the categorization system proposed by Sánchez-Fernández et al. (2008a) (Table 3). Values of ED and vulnerability scores were not significantly correlated (Spearman's correlation coefficient: $rs = 0.18$, $p = 0.46$ and $rs = 0.11$, $p = 0.28$ for the most diverse groups, Hydroporini and Hydraenidae respectively; $rs = 0.004$, $p = 0.96$ for the complete species pool). The phylogenetic signal of species vulnerability was negligible, as K values were not significantly different from zero (Hydroporini $P = 0.58$, $K = 0.0001$; Hydrenidae $P = 0.90$, $K = 0.039$). Among the highly vulnerable species, only 17 (32%) occur in the NPs (Table 3). When the two criteria were combined, 15 taxa were identified as both highly evolutionarily distinct and highly vulnerable (Table 3). Notably, most of these species (12, 80%) are not covered by the existing network of NPs.

3.3. Species richness as a surrogate of PD

The PD represented in the selection of new potential areas to be included in the network of NPs based on species richness was distinctly superior to that represented when sites were randomly selected, and tended to be similar to the values obtained when sites were specifically selected to maximize PD (Fig. 3). However, there was a large variation in the amount of PD included (and hence in the surrogacy value) across the range of complementary sets, as indicated by the SAI values (from 0.57 to 0.91 for Agabinae; 0.67–0.94 for Hydroporini; 0.80–0.94 for Hydraenidae; 0.93–1.00 for Hydrochidae). Discrepancies were maximal in the first steps, for which richness-based complementary sets gave suboptimal results in the representation of PD. As expected, most of the diversity, either PD or species richness, was represented after the first few 10×10 km cells were added (Fig. 3). The selected additional areas maximizing unprotected PD did not tend to match across groups (Appendix C), but were mainly located in arid areas of southern Spain, the Central and Iberian mountain systems, and the Cantabrian Mountains and Pyrenees in the north.

4. Discussion

4.1. Representation of phylogenetic diversity in the Iberian network of NPs

Our results show that Iberian NPs perform poorly in representing freshwater phylogenetic diversity, as assessed with aquatic Coleoptera. Across the four groups of beetles studied, the amount of PD included in NPs either did not depart significantly or was lower than what could be expected given their number of species. A similar result was obtained when the NPs network was considered as a whole. Although the extent to which these results are applicable to other reserve networks in both Iberia and other geographical areas remains to be investigated, they highlight the potential limitations of protected area systems in preserving PD. Furthermore, we also found substantial variation in the performance of the different NPs in the preservation of the PD of the different studied lineages. If this pattern of high variability among groups were confirmed to be a general trend, the objective of finding a low number of reserves able to maximize PD across multiple taxa could be unfeasible, suggesting the need of alternative conservation strategies (e.g. based on a more diffuse level of protection of wider geographical areas; Hernández-Manrique et al., 2012).

The observed mismatch between the observed and expected PD could be the result of processes acting at different geographical scales. An area showing comparatively low PD contains taxa that are, on average, more closely related to each other than the average species present in the regional pool. Density-dependent interactions and environmental filtering generally act at local scales,

Table 2
Phylogenetic diversity (PD) included in the Iberian national parks and expected (average) PD (PD_{ran}) based on 10,000 samples of the same number of species (*N*; number of Iberian endemic species in parentheses) randomly drawn from the pool of species present in the Iberian peninsula, and the species pool of the physicoclimatic and biogeographical subregion in which the park is located. The standardized effect size of PD (PD_{SES}) and *P*-value (*P*) based on the randomization test (proportion of random values with less than observed PD) are also shown. Codes as in Fig. 1. NPs, whole national park network; IBE, Iberian species pool; WP, whole species pool.

Park	*N*	PD	Iberian pool			Physicoclimatic subregional pool			Biogeographic subregional pool		
			PD_{ran}	PD_{SES}	*P*	PD_{ran}	PD_{SES}	*P*	PD_{ran}	PD_{SES}	*P*
Agabinae											
AI	11 (1)	113.6	113.2	0.05	0.494	111.5	0.25	0.579	99.1	0.80	0.786
CA	6 (0)	80.3	74.4	0.70	0.740	67.0	1.47	0.936	71.7	0.94	0.844
DO	6 (0)	67.8	74.4	−0.78	0.191	67.5	0.04	0.474	67.0	0.09	0.516
MO	5 (0)	73.4	65.0	0.96	0.854	58.9	1.50	0.970	62.4	1.21	0.928
OR	5 (0)	50.7	65.1	−1.68	0.073	62.4	−1.21	0.144	54.3	−0.30	0.342
PE	8 (0)	82.5	91.3	−1.05	0.144	88.0	−0.65	0.253	88.7	−0.68	0.232
PI	12 (0)	113.8	119.9	−0.69	0.240	117.8	−0.48	0.308	123.2	−1.38	0.094
SI	9 (0)	68.4	99.0	−3.58	0.002	97.2	−3.23	0.003	87.0	−2.42	0.007
TA	2 (0)	36.9	28.7	0.86	0.686	26.4	0.98	0.920	27.0	1.06	0.960
NPs	18 (1)	150.1	153.2	−0.42	0.333						
IBE	26 (4)	186.5									
WP	98	453.8									
Hydroporini											
AI	16 (5)	356.5	383.6	−0.88	0.191	376.0	−0.64	0.255	389.2	−1.12	0.133
CA	16 (2)	316.0	384.1	−2.17	0.020	387.6	−2.41	0.011	382.1	−2.19	0.019
DO	14 (1)	311.5	350.5	−1.30	0.102	339.0	−1.09	0.142	354.5	−1.48	0.074
MO	12 (3)	250.8	314.1	−2.20	0.018	319.1	−2.53	0.009	313.8	−2.23	0.017
OR	11 (4)	274.4	296.1	−0.81	0.209	289.2	−0.54	0.284	299.3	−0.96	0.175
PE	20 (12)	363.0	430.4	−2.22	0.017	430.1	−2.42	0.012	429.0	−2.29	0.014
PI	34 (15)	672.4	621.0	1.07	0.861	610.1	1.42	0.924	651.6	0.43	0.657
SI	16 (7)	330.2	383.5	−1.68	0.054	376.2	−1.45	0.080	387.6	−1.86	0.035
TA	7 (1)	202.9	213.5	−0.49	0.297	217.1	−0.66	0.252	212.9	−0.46	0.304
NPs	67 (26)	1033.5	971.3	1.43	0.931						
IBE	96 (40)	1222.4									
WP	280	2673.3									
Hydraenidae											
AI	3 (1)	68.6	68.0	0.05	0.447	67.7	0.07	0.463	67.1	0.11	0.478
CA	15 (10)	211.3	233.3	−1.06	0.145	246.1	−1.94	0.033	240.0	−1.50	0.075
DO	14 (1)	242.6	222.8	1.00	0.838	242.8	−0.01	0.475	232.8	0.57	0.703
MO	16 (7)	239.9	245.3	−0.26	0.385	257.7	−0.96	0.169	251.7	−0.60	0.267
OR	8 (2)	133.0	147.9	−0.96	0.164	146.5	−0.85	0.188	147.4	−0.90	0.175
PE	17 (12)	208.3	255.8	−2.19	0.020	251.4	−2.00	0.026	263.1	−2.73	0.006
PI	23 (13)	255.1	316.8	−2.54	0.009	312.2	−2.47	0.010	297.1	−2.47	0.009
SI	21 (5)	277.7	297.2	−0.84	0.202	292.7	−0.68	0.241	313.3	−1.75	0.049
TA	5 (0)	114.7	103.5	0.83	0.796	106.9	0.68	0.736	105.1	0.74	0.763
NPs	65 (29)	611.6	646.4	−1.27	0.105						
IBE	126 (60)	994.7									
WP	245	1656.0									
Hydrochidae											
AI	0										
CA	3 (0)	36.5	34.2	0.58	0.529	35.1	0.45	0.441	34.5	0.53	0.482
DO	3 (0)	35.3	34.2	0.28	0.390	35.6	−0.11	0.251	35.1	0.08	0.297
MO	4 (0)	44.7	44.0	0.19	0.365	45.4	−0.27	0.235	44.3	0.11	0.304
OR	0										
PE	0										
PI	3 (1)	36.5	34.2	0.59	0.858	33.9	0.65	0.859	34.3	0.69	0.750
SI	1 (1)	13.2									
TA	0										
NPs	7 (2)	72.7	69.8	0.71	0.722						
IBE	11 (4)	106.8									
WP	12	114.6									

whereas processes such as speciation, extinction, and trait evolution occur through longer time periods and at regional scales (Vamosi et al., 2009; Losos, 2008). Interestingly, our results were consistent across spatial scales, from the subregional to the Iberian species pools. It can be expected that at smaller scales ecological sorting processes within subregions should play a stronger role, while historical factors must be more determinant when the comparison is made with the Iberian species pool. Unfortunately, our data do not allow to disentangle between these two potential confounding factors, although further studies considering the phylogenetic distribution of ecological traits in conjunction with the geographical distributions of species might help to explain the phylogenetic aggregation found in some of the NPs (Losos, 2008; Cardillo, 2011). When pooling the data across the different NPs, which should reduce the effect of local species sorting due to ecological differences, the low PD can be partly attributed to the underrepresentation in the NPs network of habitats typical of specific lineages, as indicated by the nodesig algorithm. This seems to be the case of the genus *Ochthebius* (Hydraenidae), for which none of the habitats with the highest diversity of this genus, such as the arid streams of southern Spain (Millán et al., 2011), is represented within the Iberian NP network. Our results were also consistent across the two considered subregional pools (biogeographic and physioclimatic), showing that the estimated phylogenetic

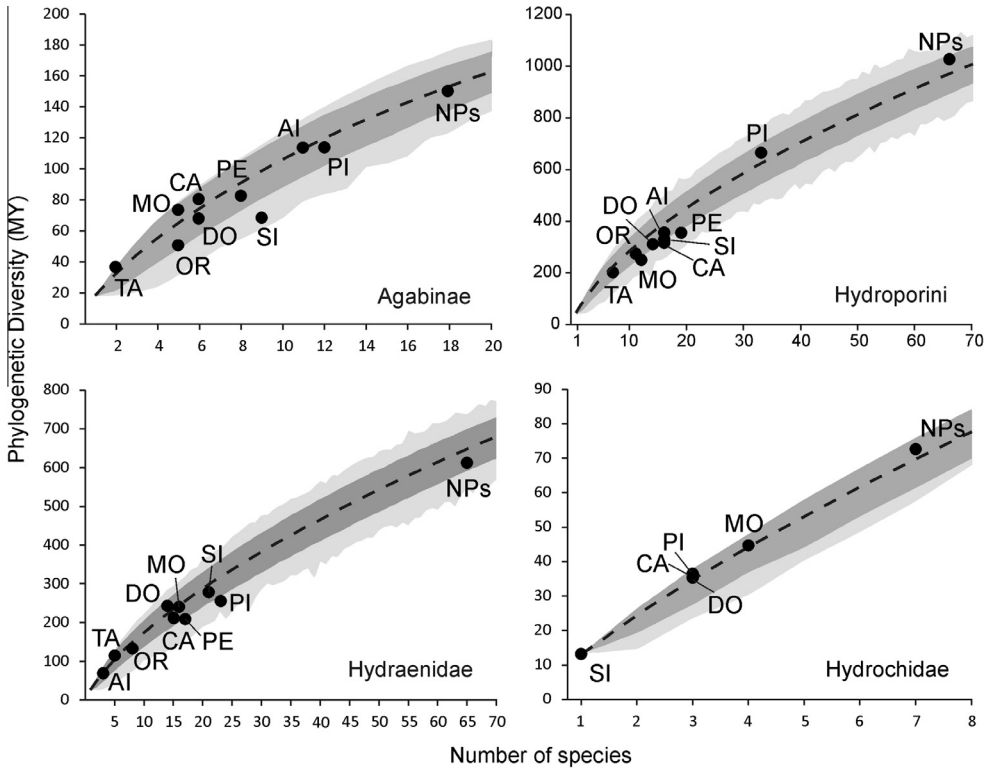

Fig. 2. Relationship between the phylogenetic diversity (PD) protected in the Iberian national parks and species richness (i.e. relative to a null model of random drawing species from the pool of species occurring in the Iberian phylogeny with equal probability). The dashed lines show mean PD from 10,000 randomizations at each species richness level, dark gray indicates the range of the 95th percentiles, and light gray shows the extent of the randomized data. Codes as in Fig. 1. NPs, whole National Park network. MY, millions of years.

representation of NPs is analogous when considering them in either an ecological or historical and geographic context.

Another difficulty is the trade-off between protecting relict species, with high PD values, or species clusters with low PD but restricted geographical distributions, which are potential sources of evolutionary novelty. Some authors (e.g., Cowling and Pressey, 2001) have suggested that conservation goals should also consider the evolutionary future of biodiversity, because prioritizing areas that maximize PD means prioritizing evolutionary 'relicts', i.e. lineages that have few close relatives, which could lead to the neglect of areas where a recent radiation has occurred. These areas, potentially containing more recent speciation events (and a lower global PD), could be active centers of biodiversity generation ("evolutionary fronts"; Erwin, 1991). In the Iberian Peninsula many of the endemic species among the studied families are of recent, Pleistocene origin (Ribera and Vogler, 2004; Ribera et al., 2011; Trizzino et al., 2013), and so their presence in NPs will add little to the overall PD. In agreement with this, some of the NPs with the highest number of Iberian endemics (e.g. Sierra Nevada, Picos de Europa or Peneda-Gerês, the first one with two subspecies of Hydroporini endemic to the park) have significantly lower PD than expected at random, although other NPs with low numbers of endemics (e.g. Doñana, Cabañeros or Monfragüe) also show significantly lower PD than expected for some groups.

Interestingly, when we compared the recorded level of PD representation in the NPs network with that expected from an equivalent number of areas selected at random, we found again that NPs do not represent PD at a rate higher than expected by chance. In other words, the level of PD representation achieved by this protected area system is not better than the outcome expected from selecting protected areas with little regard for the distribution of freshwater biodiversity. Similar results were found for just species representation (Appendix C2). These results partially disagree with those coming from former studies that assessed the effectiveness of Iberian protected areas in conserving terrestrial vertebrate and plant diversity (e.g. Araújo et al., 2007), which showed that, in general, protected areas represent more species than expected by chance for some of these groups. Although in that study all protected areas were included (not just NPs), our general results suggest that protected areas, usually designated with terrestrial vertebrate and plant diversity in mind, could be largely inefficient in preserving invertebrate aquatic biodiversity. Thus, our results stress the importance of explicitly taking into account freshwater and invertebrate biodiversity data in designing protected areas, something that has been largely ignored (Abellán et al., 2007).

4.2. Species with the highest conservation value

For the aquatic Coleoptera endemic to the Iberian Peninsula, evolutionary distinctiveness and vulnerability were not correlated (in consistency with the negligible phylogenetic signal in species vulnerability), and hence the two variables provide complementary information in the assessment of their conservation worth. This result is in contrast to previous reports of nonrandom distribution of extinction risks across phylogenies (Purvis, 2000), implying that biological traits shared between closely related species may affect their response to human impact (e.g. Davies et al., 2008; Huang, 2012). The lack of correlation in our case could be partially due to the use of a vulnerability measure including a mixture of heterogeneous factors, some of which may not be related to phylogeny (Sánchez-Fernández et al., 2008a). The decoupling between distinctiveness and vulnerability stress the necessity of applying a diversity of measures for the design of conservation areas.

Table 3
Conservation priority of the Iberian endemic species included in the study (as for August 2012) according to their evolutionary distinctiveness and extinction risk. ED, evolutionary distinctiveness (average and range of values for the 1000 trees). EDq, ED quartile. VS and VU, vulnerability score and category of vulnerability (H, high; M, moderate; L, Low), respectively, according to Sánchez-Fernández et al. (2008a). CP, species of high conservation value (i.e. displaying both high evolutionary uniqueness and high vulnerability). NP, inclusion in the network of Iberian NPs (0, no; 1, yes). Asterisks indicate species for which their vulnerability has been assessed in this study for the first time.

Taxa	ED	EDq	VS	VU	CP	NP
Agabinae						
Agabus picotae (Foster and Bilton, 1997)	1.84 (1.44–2.38)	1	12	H		0
Ilybius dettneri (Fery, 1986)	6.41 (4.84–8.71)	4	9	H	x	0
Hydroporini						
Deronectes algibensis (Fery and Fresneda, 1988)	10.08 (8.07–13.13)	4	9	H	x	0
Deronectes angusi (Fery and Brancucci, 1990)	8.17 (6.48–10.39)	2	8	M		1
Deronectes aubei sanfilippoi (Fery and Brancucci, 1997)	5.35 (4.46–6.61)	2	9	H		1
Deronectes bicostatus (Schaum 1864)	9.80 (7.54–12.63)	4	7	M		1
Deronectes costipennis (Brancucci 1983)	8.60 (6.96–10.70)	2	8	M		1
Deronectes delarouzei (du Val, 1857)	5.35 (4.46–6.61)	2	8	M		1
Deronectes depressicollis (Rosenhauer, 1856)	9.38 (7.38–12.28)	3	8	M		1
Deronectes ferrugineus (Fery and Brancucci, 1987)	5.59 (4.23–6.63)	3	7	M		1
Deronectes fosteri (Aguilera and Ribera, 1996)	9.38 (7.38–12.28)	3	10	H		0
Deronectes wewalkai (Fery and Fresneda, 1988)	5.59 (4.23–6.63)	3	9	H		0
Graptodytes castilianus Fery 1995	4.30 (3.48–5.07)	2	7	M		0
Hydroporus brancuccii (Fery, 1987)	3.80 (2.75–5.58)	2	8	M		0
Hydroporus brancoi brancoi (Rocchi, 1981)	4.04 (3.25–5.56)	2	8	M		1
Hydroporus brancoi gredensis (Fery, 1999)	3.07 (2.47–3.93)	1	5	M		1
Hydroporus cantabricus (Sharp, 1882)	3.16 (2.40–4.08)	1	9	H		0
Hydroporus constantini (Hernando and Fresneda, 1996)	3.07 (2.47–3.93)	1	9	H		0
Hydroporus decipiens (Sharp, 1878)	6.41 (4.74–9.29)	3	4	L		1
Hydroporus necopinatus (Fery, 1999)	5.37 (3.82–7.35)	2	7	M		0
Hydroporus nevadensis (Sharp, 1882)	2.70 (2.10–3.38)	1	9	H		1
Hydroporus normandi alhambrae (Fery, 1999)	3.16 (2.40–4.08)	1	7	M		1
Hydroporus paganettianus (Scholz, 1923)	6.33 (4.68–8.18)	3	8	M		0
Hydroporus sabaudus sierranevadensis (Shaverdo, 2004)	2.92 (2.10–3.88)	1	12	H		1
Hydroporus vagepictus (Fairmaire and Laboulbène, 1854)	5.82 (4.72–7.51)	2	6	M		1
Hydroporus vespertinus (Fery and Heindrich, 1988)	5.49 (4.28–6.95)	2	7	M		1
Hygrotus fresnedai (Fery, 1992)	8.42 (6.98–10.19)	3	10	H		1
Iberoporus cermenius (Castro and Delgado, 2000)	14.01 (10.34–19.58)	4	11	H	x	0
Nebrioporus baeticus (Schaum 1864)	6.47 (5.24–7.98)	2	10	H		0
Nebrioporus bucheti cazorlensis (Lagar, Fresneda and Hernando, 1987)	5.55 (4.33–7.18)	2	6	M		1
Nebrioporus carinatus (Aubé, 1836)	4.04 (3.33–5.05)	1	6	M		1
Nebrioporus croceus (Angus, Fresneda and Fery, 1992)	4.07 (3.33–5.05)	1	11	H		0
Nebrioporus fabressei (Régimbart, 1901)	4.14 (3.38–5.30)	2	7	M		0
Oreodytes davisii rhianae (Carr, 2001)	6.78 (5.79–8.16)	2	5	M		1
Rhithrodytes agnus agnus (Foster, 1993)	10.17 (8.17–12.95)	4	9	H	x	1
Rhithrodytes agnus argaensis (Bilton and Fery, 1996)	10.17 (8.17–12.95)	4	9	H	x	0
Rhithrodytes bimaculatus (Dufour, 1852)	11.71 (9.44–15.04)	4	9	H	x	1
*Stictonectes sp.**	12.88 (8.26–17.24)	4	10	H	x	1
Stictonectes rebeccae (Bilton, 2012)*	3.73 (3.21–4.37)	1	8	M		1
Stictonectes occidentalis (Fresneda and Fery, 1990)	3.73 (3.21–4.37)	1	8	M		0
Stictotarsus bertrandi (Legros, 1956)	16.39 (12.51–22.38)	4	7	M		1
Hydraenidae						
Hydraena afussa (Orchymont, 1936)	1.53 (1.26–1.87)	1	5	M		1
Hydraena albai (Sáinz–Cantero, 1993)	4.88 (3.69–6.18)	3	10	H		1
Hydraena alcantarana (Ieniesta, 1985)	5.38 (4.22–7.26)	3	11	H		0
Hydraena altamirensis (Díaz Pazos and Garrido, 1993)	2.37 (1.82–3.12)	1	11	H		1
Hydraena bolivari (Orchymont, 1936)	4.88 (3.69–6.18)	3	8	M		1
Hydraena catalonica (Fresneda, Aguilera and Hernando, 1994)	2.23 (1.65–2.69)	1	9	H		0
Hydraena corinna (Orchymont, 1936)	3.62 (2.89–4.27)	2	6	M		1
Hydraena delia (Balfour-Browne, 1978)	2.68 (1.99–3.56)	2	9	H		1
Hydraena diazi (Trizzino, Jäch and Ribera, 2011)*	1.15 (0.90–1.47)	1	9	H		0
Hydraena fosterorum (Trizzino, Jäch and Ribera, 2011)*	1.15 (0.90–1.47)	1	8	H		0
Hydraena gaditana (Lagar and Fresneda, 1990)	2.25 (1.72–3.00)	2	9	H		0
Hydraena gavarrensis (Jäch, Díaz and Martinoy, 2005)	7.91 (6.27–9.93)	4	8	M		0
Hydraena hispanica (Ganglbauer, 1901)	1.33 (1.01–1.70)	1	7	M		1
Hydraena iberica (Orchymont, 1936)	2.38 (1.82–3.12)	2	8	M		1
Hydraena isabelae (Castro and Herrera, 2001)	7.81 (6.27–9.86)	4	10	H	x	0
Hydraena lucasi (Lagar, 1984)	1.48 (1.24–1.82)	1	12	H		0
Hydraena lusitana (Berthélemy, 1977)	3.15 (2.40–4.24)	3	10	H		1
Hydraena madronensis (Castro García and Ferreras, 2000)	2.59 (1.88–3.37)	2	9	H		0
Hydraena manfredjaechi (Delgado and Soler, 1991)	2.76 (2.11–3.78)	2	8	M		0
Hydraena marcosae (Aguilera, Hernando and Ribera, 1997)	7.88 (6.27–9.81)	4	9	H	x	0
Hydraena marinae (Castro, 2004)	6.78 (5.55–8.85)	3	11	H		1
Hydraena mecai (Millán and Aguilera, 2000)	2.89 (2.13–4.04)	2	10	H		0
Hydraena monstruosipes (Ferro, 1986)	2.88 (2.22–3.78)	2	9	H		0
Hydraena servilla (Orchymont, 1936)	7.46 (5.64–9.16)	4	10	H	x	0
Hydraena sharpi (Rey, 1886)	10.38 (8.18–12.72)	4	6	M		1
Hydraena tatii (Sáinz-Cantero and Alba-Tercedor, 1989)	2.25 (1.72–3.00)	2	9	H		1

(*continued on next page*)

Table 3 (*continued*)

Taxa	ED	EDq	VS	VU	CP	NP
Hydraena unca (Valladares, 1989)	7.92 (6.39–10.24)	3	5	M		1
Hydraena zezerensis (Díaz, Pazos and Bilton, 1994)	2.88 (2.22–3.78)	2	10	H		0
Limnebius cordobanus (Orchymont, 1938)	5.86 (4.84–7.72)	3	6	M		0
Limnebius gerhardti (Heyden, 1870)	1.48 (1.16–1.70)	1	5	M		1
Limnebius hilaris (Balfour-Browne, 1976)	1.45 (1.19–1.76)	1	12	H		0
Limnebius hispanicus (Orchymont, 1941)	4.45 (3.42–5.74)	3	7	M		0
Limnebius ibericus (Balfour-Browne, 1978)	5.97 (4.36–8.46)	3	7	M		1
Limnebius ignarus (Balfour-Browne, 1978)	4.39 (3.61–5.49)	2	10	H		1
Limnebius lusitanus (Balfour-Browne, 1978)	11.45 (8.71–15.02)	4	7	M		1
Limnebius millani (Ribera and Hernando, 1998)	1.61 (1.23–2.12)	1	10	H		0
Limnebius monfortei (Fresneda and Ribera, 1998)	1.46 (1.20–1.79)	1	10	H		1
Limnebius montanus (Balfour-Browne, 1978)	2.20 (1.77–2.68)	2	9	H		1
Limnebius ordunyai (Fresneda and Ribera, 1998)	1.48 (1.17–1.73)	1	11	H		0
Ochthebius aguilerai (Ribera, Castro and Hernando, 2010)*	12.35 (9.57–15.38)	4	10	H	x	0
Ochthebius andalusicus (Jäch and Castro, 1999)	10.90 (8.11–15.15)	4	13	H	x	0
Ochthebius caesaraugustae (Jäch Ribera and Aguilera, 1998)	11.16 (7.81–14.86)	4	13	H	x	0
Ochthebius glaber (Montes and Soler, 1988)	12.82 (9.78–15.89)	4	11	H	x	0
Ochthebius heydeni (Kuwert, 1887)	8.23 (6.86–9.85)	4	7	M		1
Ochthebius irenae (Ribera and Millán, 1998)	5.77 (4.84–7.00)	3	10	H		0
Ochthebius montesi (Ferro, 1984)	9.98 (7.01–13.07)	4	13	H	x	0
Ochthebius sanabrensis (Valladares and Jäch, 2008)	7.59 (6.04–10.16)	3	11	H		0
Ochthebius tudmirensis (Jäch, 1997)	5.09 (3.92–6.38)	3	11	H		0
Hydrochidae						
Hydrochus angusi (Valladares, 1988)	6.01 (4.36–8.74)	3	9	H		1
Hydrochus ibericus (Valladares, Díaz-Pazos and Delgado, 1999)	6.01 (4.36–8.74)	3	7	M		0
Hydrochus interruptus (Heyden, 1870)	8.61 (6.10–12.01)	3	10	H		0
Hydrochus nooreinus (Henegouven and Sáinz-Cantero, 1992)	8.76 (6.25–14.77)	4	7	M		1

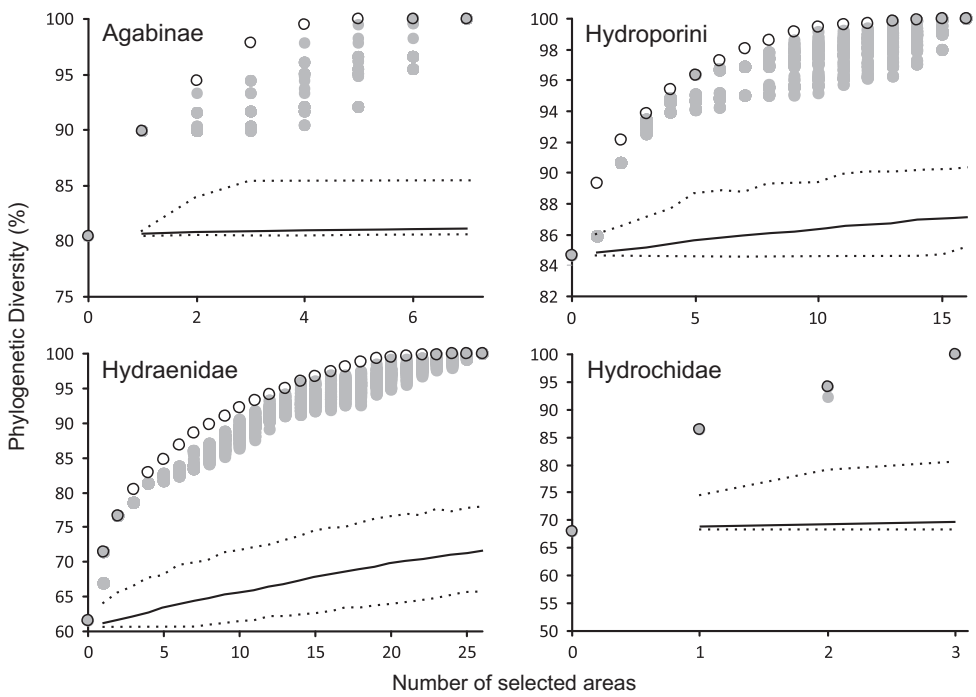

Fig. 3. Percentage of Iberian phylogenetic diversity (PD) included by selecting new areas (10 × 10 km grid cells) that maximize protected diversity. Open circles represent the PD represented when new protected areas are selected maximizing the unrepresented PD and gray circles represent the PD incidentally represented when new protected areas are selected maximizing the number of unrepresented species (all the possible complementary sets). The circles on the *y*-axis represents the PD already included in the Iberian National Park network. Solid and dashed lines represent, respectively, mean PD and limits of the 95% confidence interval included when sites are selected at random among unprotected cells (1000 replicates).

None of the species of aquatic Coleoptera occurring in the Iberian Peninsula is included in the National Catalogue of Threatened Species of Spain or Portugal, Annex II of the Bern convention or Annex II and IV of the Habitats Directive (92/43/EEC). In the current situation, the only protection available for these species is the extent to which they occur in protected areas designated on the basis of other taxa or habitat features. However, we found that most of the highly vulnerable and evolutionarily distinct taxa were not covered by any NP (see Lawrence et al., 2011 for similar findings evaluating the representation of highly imperiled fish species

in NPs from USA). As already noted, NPs are not the only protected areas in Spain and Portugal, with several other regional (e.g. Natural Parks) or international (e.g. the Natura 2000 network) categories of protection, and hence from a global point of view some of the priority species could still be considered protected if they occur in some of these other areas. Nevertheless, since NPs aims to represent a comprehensive and representative network of protected areas constituting the best representation of the Iberian natural heritage, our results point to their limited role in preserving highly vulnerable and evolutionarily distinct taxa of aquatic invertebrates in this region. In agreement with this, previous work (Hernández-Manrique et al., 2012) has shown that many of the species and populations of Spanish endangered invertebrates are not represented in the current network of protected reserves.

4.3. Phylogenetic diversity in the selection of additional protected areas

Predictions from simulated data (Rodrigues et al., 2005) and some vertebrate studies (Polasky et al., 2001; Rodrigues et al., 2011) have showed that species richness tends to be a good surrogate of phylogenetic diversity in the selection of conservation areas, putting into question the need of incorporating measures of PD in conservation planning. Nevertheless, as shown by Rodrigues et al. (2005), the structure of the phylogenetic tree and the patterns of species spatial distribution affect the performance of species diversity as a surrogate of phylogenetic diversity. In lineages with highly unbalanced trees, a high proportion of the total PD is concentrated in the most ancient species, so when these species have distributions restricted to species-poor areas complementary sets maximizing species diversity may perform as poor surrogates of PD.

Our results show that, depending on the group and the number of additional protected areas to be considered, the variation in the PD represented when selecting new conservation areas to maximize species richness could be very high. As a consequence, new protected areas selected maximizing the number of unrepresented species could add much less evolutionary history than if areas were specifically selected to maximize PD, especially with the first areas added to the NP network. When the number of protected areas is low, and the number of areas that are realistically likely to be added is even lower (as is the case of the Iberian network of NPs), these differences could be critical for maximizing the protection of biodiversity. Because even small gains can be important in the context of conservation planning (Faith, 1992; Forest et al., 2007), our results suggest that datasets that include information on the evolutionary relationship between species should be used whenever available (see also Rodrigues et al., 2011). Thus, although the new additional areas that were selected to maximize unprotected PD varied across groups, they provided useful information about the environments underrepresented in the Iberian network of NPs. Among the first areas selected for the most diverse groups were arid streams in southern Spain, highlighting the lack of coverage of the evolutionary history of these singular habitats.

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Appendix A–C. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.04.001.

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