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Abstract: Protected area networks represent one of the mainstays of global conservation polices and are therefore central to current efforts to maintain biodiversity. However, a major limitation of most conservation strategies is their bias towards particular taxonomic groups and ecosystems, meaning that many taxa and habitats are often only incidentally protected as a by-product of inclusion within reserves. Here we investigate how effectively protected area networks, not specifically designated for freshwaters, support aquatic biodiversity in the Iberian Peninsula (Spain and Portugal), using data for water beetles, surrogates of overall macroinvertebrate diversity in these habitats. We explore the behaviour of different measures (alpha, beta and gamma) of both taxonomic and functional diversity at different spatial scales. Overall our findings highlight the contrasting performance of reserve systems in the maintenance of either taxonomic or functional diversity, as well as the importance of spatial scale. Iberian reserves perform relatively well in supporting taxonomic diversity of water beetles at the peninsular scale, but the same protected areas poorly represent functional diversity. Such a mismatch cautions against the use of any one diversity component as a surrogate for others, and emphasizes the importance of adopting an integrative approach to biodiversity conservation in aquatic ecosystems. Furthermore, our results often show contrasting patterns at smaller spatial scales, highlighting the need to consider the influence of scale when evaluating the effectiveness of protected area networks.

Dear Dr. Vincent Devictor,

Many thanks for your e-mail of 23 December 2014 regarding our MS entitled "How well do protected area networks support taxonomic and functional diversity in non-target taxa? The case of Iberian freshwaters" (Ms. Ref. No.: BIOC-D-14-01399).

We are very pleased that both you and the referees have seen considerable merit in our work and MS. We found the comments provided to be very helpful, and following these suggestions, the MS has been modified accordingly. We are now resubmitting a revised version that we would like you to consider for publication in *Biological Conservation*.

In this letter we address all comments (text in blue proceeded by >>>), as well as details about changes introduced in the text.

Yours sincerely,

Simone Guareschi (on behalf of all co-authors)

simone.guareschi@um.es

Aquatic Ecology Group
Department of Ecology and Hydrology
University of Murcia, Espinardo Campus, Murcia
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EDITOR'S COMMENTS

As you will see, the reviewers are quite positive about the work but also found important limits. I also appreciated the general framework and think you could make a nice contribution. Pay particular attention to the request for better a priori expectation/meaning of decrease or increase in each of your indices and of their implications for conservation. I would add that it is crucial to distinguish spatial and temporal trends in such approach. In time, it is for instance not obvious that an increase in any indices is synonym of conservation improvement. Some habitats may host low taxonomic or functional diversity and that is a good thing. Disturbing these habitats may increase many indices due to the arrival of generalist species but this will not make any improvement. So some cautious is needed as you only work with spatial data where temporal trends would be needed. To really show that protected areas have a true effect on the dynamics of each indices, one should test whether temporal trends are better or less negative in protected areas. Spatial trends are indicative but not conclusive. So please clarify your expectations and conservation implications. Also, unless I have missed it, providing the correlations between each of the indices used might be interesting? (for instance the link between beta-TD versus beta-FD might reveal functional redundancy or originality).

>>> Many thanks for your useful comments. In the new version of the manuscript we have tried to clarify the conservation implications of our results. Indeed, while high levels of gamma diversity covered by a reserve network are indicative of good performance or effectiveness, the conservation implications for high/low levels of alpha and beta diversity are less straightforward. In this context, we totally agree in that a high local diversity (e.g. species richness) in a given site does not necessarily indicate high conservation value. We have now noted this in the Discussion (page 8 L397-401):

> "Nevertheless, it should be noted here that a high local diversity in a given site does not necessarily indicate high conservation value. For instance, some habitats support few species, but contain many endemic or exclusive taxa. Similarly, local diversity is often maximized at a certain level of human disturbance (Wilkinson 1999), rather than in pristine sites."

On the other hand, in the case of beta diversity, please note that we already discuss its conservation implications (page 10, L476):

> "Ideally, protected area networks should maximize the species/trait turnover amongst protected sites within the network, as this would denote high complementarity among protected sites. On the other hand, the nestedness component of β diversity (β_{NES}) provides information about redundancy in biodiversity attributes in the network, which also may be relevant for the persistence of biodiversity over time, as multiple representations of species within the set of sites would increase the probability of regional persistence (i.e. maintain each species within the reserve network, even if local extinctions occur (Cabeza and Moilanen, 2001)".

Concerning possible correlations between TD and FD, we have now indicated in the text (page 9, L448) that the correlation between TD and FD across Iberian protected cells (i.e. alpha diversity) was low (Pearson's correlation coefficient $r = 0.29$ and $r = 0.32$ for RNAs and N2000, respectively; $P < 0.001$ in both cases). In the case of gamma and beta diversity in protected areas it is not possible to assess potential correlations, as we obtained a single value of TD and FD for each one of the protected area networks. In any case, our results show throughout the manuscript a mismatch between gamma and beta TD and FD, which reveal disproportionate levels of functional redundancy in protected areas relative to those of taxonomic diversity.

REVIEWERS' COMMENTS

Reviewer #1:

Dear Authors

I've now read your MS entitled "How well do protected area networks support taxonomic and functional diversity in non-target taxa? The case of Iberian freshwaters" that aims at testing whether or not protected areas in Spain and Portugal accurately cover the taxonomic and functional diversity of freshwater beetles. The strenght of this MS is to use both functional and taxonomic proxies of diversity and it analyses diversity at the alpha, beta and gamma levels.
Overall, I appreciated reading this MS; it is relatively well-written and easy to follow. I particularly appreciated the decomposition of beta diversity and the explanation of the two components (nestedness and turnover). In my opinion the statistics are correctly used. I regret you did not mention the statistics related to the Mann-Whitney tests (degree of freedom and U) as it might be used by others for future meta-analyses. In the same vein I would try to add an effect size in Table 1 and 2 of the differences you reported between observed and random values. For instance, how biologically is it to observe differences of 0.005 in term of beta-diversity.

>>> Thanks for the positive evaluation of our manuscript and your useful comments. Please note that the W-statistic values (Wilcoxon–Mann-Whitney test) for all the thresholds are provided in Appendix A. Because no parameters are estimated in this test, each group's size (see Appendix A) can be taken as degrees of freedom.

We agree about very small but significant differences between observed and random values for beta diversity. However, in the Discussion (page 9, L461) we try to explain that:

"In case of β diversity (both TD and FD) at the Iberian scale, although the overall value obtained in both protected area networks was very high (close to 1), it was always significantly lower than expected by chance, i.e. communities in protected areas were more similar than would be expected from a random draw of equivalent area. This result may reflect the wide environmental heterogeneity in the Peninsula, which, despite being reasonably well represented in protected areas, may still be insufficient to cover the full spectrum of environments and associated faunas."

Furthermore, and following the reviewer's suggestion, we have now added in tables 1 and 2 the standardized effect sizes of the diversity measures, which describe the difference between the observed value of diversity in the protected area network and the mean value obtained from random draws, divided by the standard deviation of null data.

Beyond these statistical issues (that are absolutely not lethal) I provided a series of comments directly in the pdf file attached. The major comments are:

- in the discussion you need to stick on the fact that you only consider a very small part of freshwater biodiversity. Notably in the discussion you should remind that it is probably difficult to extrapolate our findings to other freshwater taxa. This would be fair from you and would not deserve your main message

- try to more provide a biological interpretation of what a small value of dissimilarity index means (for those who are not familiar)

- try to provide information on the type of traits that make these differences (in term of beta functional) between protected and unprotected areas.

>>> We have addresses these concerns in the new version of the manuscript. Briefly: concerning the first point, we explain more clearly the utility of water beetles as biodiversity surrogates in inland waters, and we now use the terms "water beetles" or "macroinvertebrate biodiversity" instead of "freshwater biodiversity"; concerning the second point, we have tried to provide a biological interpretation of what a small value of dissimilarity index means; and finally, with respect to the third point, we explain that such information cannot be directly inferred from our results, but we now discuss in the text the potential effects of our results on ecosystem processes and services. Below we answer in detail each one of the reviewer's comments provided in the annotated pdf and which deal with these three concerns.

L129-132. I do not completely agree as the conservation planning framework (e.g. Maxan software) is more or less based on this idea, at least not only on richness but rather on representation of the diversity. This should be acknowledge here or somewhere else on the MS.

>>> We completely agree. In fact, we already noted this in several parts of the manuscript, both the Introduction (page 4, L173-174):

"Finally, the third question deals with dissimilarity amongst protected sites within the network, which is related to their complementarity, a principle widely used in conservation planning (Justus and Sarkar, 2002)"

and the Discussion (page 10):

"Although rarely recognized, the principles behind most approaches to systematic planning, such as complementarity, are driven by patterns of β diversity (Magurran, 2004; Justus and Sarkar, 2002). As the turnover component of β diversity (β_{SIM}) quantifies the change in biodiversity attributes across space, it provides critical information to represent all biodiversity within practical constraints such as area and cost (Margules and Pressey, 2000)."

L222. Please provide a Table (supplementary material) with the 11 traits you considered.

>>> In the new version of the Manuscript the list of functional traits considered and the scores for each catery are now available as suggested (in Appendix).

L254. Why not using the same approach (resampling approach) than for beta diversity? I guess this will give similar results but this would homogenize the statistics employed in the MS. It would also permit accounting for area.

>>> It should be noted here that we aimed to address two different kinds of questions for alpha diversity, on the one hand, and gamma and beta diversities, on the other hand. While in the case of alpha diversity we aim to address if individual protected cells are, on average, more diverse than unprotected ones, in the case of both gamma and beta diversity we aim to address if the whole network of protected cells include disproportionate levels of diversity relative to the area they cover in the study area. Thus, these two kinds of questions require two different approaches. In the first case it is not necessary to account for area, as all the cells are equivalent in size (10x10 km) and we assess if there are differences in local diversity of protected and unprotected cells. In contrast, in the second case, we do need to account for area, as we aim to know if the observed levels of diversity (total diversity and inter-site diversity) covered by a reserve network (i.e. a set of cells) is different than would expected by chance alone given their area (i.e. the number of cells they occupy). By using the resampling procedure we built a null model that drew random sets of cells from the study area and compared the diversity included in these random pseudo-networks to the observed in the protected area network.

L283. As is dissimilarity index, I think you should provide a short biological explanation (interpretation) of what a lower value means: there are less dissimilar than expected at random; does it means the are more similar?

>>> Effectively, it means that communities in protected areas were more similar than would be expected from a random draw of equivalent area. We have clarified this in the Discussion section (page 9, L460):

> "In case of β diversity (both TD and FD) at the Iberian scale, although the overall value obtained in both protected area networks was very high (close to 1), it was always significantly lower than expected by chance, i.e. communities in protected areas were more similar than would be expected from a random draw of equivalent area".

L 286. I guess it is the values from the random pool? please specify. If yes the observed and simulated values are extremely closed (even if significantly different). Can you express this difference as an effect size to make clear how biologically important is this difference?

>>> We have now indicated in the text that these numbers represent the values from the random samples. Furthermore, as indicated above, we have added in tables 1 and 2 the standardized effect sizes of the diversity measures.

L422. It would be nice to have a better understanding of why FD is mis-represented. Of the 11 traits what the ones contributing the most to the under-reppresentation? are they "true" functional traits (trophically-related) or life-history traits (e;g. fecundity)? in the later case (life-history) the effect on ecosystem functions is probably less.

>>> Indeed it would be interesting to know what traits are contributing the most to the under-representation of FD in protected areas. Unfortunately, such information cannot be directly inferred from our results. The measure of PD used here relies on a functional dendrogram, which clusters species based on the similarity of their functional-trait characteristics. This measure links all the species in a multi-dimensional trait space, and hence little information is available about the relative importance of individual traits in the obtained values of FD (see e.g. Petchey and Gaston 2002 for the general properties of dendrogram-based measures of FD).

As our results suggest a relationship between the under-representation of FD by protected areas and a bias in environmental representation within the Iberian reserve networks, in the new version of the manuscript we discuss the potential effects of this bias on ecosystem processes and services (page 9, L455):

> "Our results suggest that important ecosystem processes (e.g. energy flow, nutrient cycling and biomass production) and services (e.g. mosquito control, food source to species of commercial interest) in which water beetles (and aquatic macroinvertebrates in general) are involved in some lowland freshwater habitats could remain under-represented by protected areas."

Petchey, O.L. and Gaston, K.J. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5, 402–411.

L437. As a general comment on beta diversity, please provide a clear interpretation of what a high index of dissimilarity means. This is sometimes confusing as they are often called "similarity" index whereas they actually measure dissimilarity.

>>> As indicated above, we have now clarified this throughout the text.

L503. Another general comment: you sometimes forget that you are "just" considering a single taxonomic group of invertebrates (beetles): how this can be extended to other groups (e.g. ephemeroptera, trichoptera, mollusks...): you absolutely don't know. So please avoid over-generalization and keep in mind that you "just" consider one group of species.

>>> We used here water beetles as surrogates of wider freshwater biodiversity. Water beetles have been shown to be good biodiversity surrogates of overall aquatic macroinvertebrate biodiversity in Iberia and elsewhere because their diversity patterns are correlated with those of other freshwater invertebrates, and can also adequately represent the diversity of these other groups when used to design reserve systems (Bilton et al., 2006; Guareschi et al., 2012; Sánchez-Fernández et al., 2006). Additionally, they meet many of the criteria proposed in the literature for such purposes. For instance, they comprise a great number of species, their taxonomy and distribution is well known in the study area, and they occupy the complete range of aquatic habitats, inhabiting virtually every kind of fresh and brackish water body.

   In the new version (Introduction, page 4, L155-164) we explain more clearly the utility of water beetles as biodiversity surrogates in inland waters, and their key role in aquatic ecosystems. Furthermore, and following the reviewer's recommendation, we have moderated our claims in the Discussion section using the terms "water beetles" or "macroinvertebrate biodiversity" instead of "freshwater biodiversity".

Tables 1 and 2. Please provide the meaning of the index of variation for the random values: is it SE, SD or CI? It would be preferable to provide 95% CI

>>> We have now indicated that the index of variation for random values is SD. Furthermore, as indicated above, we have added in tables 1 and 2 the standardized effect sizes of the different diversity measures.

Other comments are more minor but should however be considered before publication.
>>> We have considered all the minor changes suggested by the referee in the annotated pdf.

Reviewer #2: Comment to the authors:

The authors investigate the performance of the Iberian reserve system at representing water beetles richness and functional diversity. In particular they investigate the behaviour of alpha, beta and gamma components of these two facets of diversity at different spatial scale.
The questions they address are as follow:
1)   Do the current protected areas have higher local diversity (alpha) than the non-protected areas?
2)   Do the current network of protected areas represent gamma diversity better than by chance?
3)   Do the current network of protected areas have higher beta diversity than random? - where beta is partitioned into turnover and nestedness

I found this study interesting especially because I think that the performance of current protected areas at representing functional diversity has not been addressed often so far. I think the authors use appropriate and up-to-date methods to measure and partition diversity. Globally the article is well written and the story easy to follow. I have a couple of concerns/suggestions that I have listed below.

>>> Thank you for your positive evaluation and your useful comments.

My main concern is about functional diversity (FD). While the author explain clearly in the introduction why FD is important to account for in conservation and how this can complement an approach based on species richness, they do not say much about why water beetles are good surrogates and what are their key role in the ecosystem.

>>> Water beetles have been shown to be good biodiversity surrogates of overall aquatic macroinvertebrate biodiversity in Iberia and elsewhere because their diversity patterns are correlated with those of other freshwater invertebrates, and can also adequately represent the diversity of these other groups when are used to design reserve systems (Bilton et al., 2006; Guareschi et al., 2012; Sánchez-Fernández et al., 2006). Additionally, they meet many of the criteria proposed in the literature for such purposes. For instance, they comprise a great number of species, their taxonomy and distribution is well known in the study area, and occupy the complete range of aquatic habitats, inhabiting virtually every kind of fresh and brackish water body.

Furthermore, aquatic Coleoptera species show considerable diversity in life histories and ecological strategies, and consequently high functional diversity (e.g. they encompass a wide variety of sizes, food types, feeding habits, respiration modes, reproduction and locomotion types, etc). As a result, despite the fact that invertebrates and their ecological services are mostly unknown to the general public (Cardoso et al. 2011), water beetles play a key functional role in aquatic habitats and are involved in ecosystem processes such as nutrient cycling and recourse processing, as well as biomass production (as are one of the most important invertebrate groups in freshwater ecosystems in terms of richness and abundance).

In the new version (Introduction) we explain more clearly the importance of water beetles as biodiversity surrogates in freshwaters, and their key role in aquatic ecosystems.

Cardoso P, Erwin TL, Borges PAV, New TR. 2011. The seven impediments in invertebrate conservation and how to overcome them. Biological Conservation 144: 2647–2655.

Related to that, I would have liked in the discussion to have a couple of more words regarding the implications of having functional redundancy in protected areas in terms of ecosystems processes. Indeed the authors make a good job in explaining what could be the drivers of the low FD but they do not make much link to ecosystem processes and services while they argue in the introduction that FD is a key component to maintain ecosystem processes.

>>> Following reviewer's suggestions, we have now discussed this issue in the manuscript (page 9 L455):

"Our results suggest that important ecosystem processes (e.g. energy flow, nutrient cycling and biomass production) and services (e.g. mosquito control, food source to species of commercial interest) in which water beetles (and aquatic macroinvertebrates in general) are involved in some lowland freshwater habitats could remain under-represented by protected areas."

My second concern is about semantic. The authors use the term taxonomic diversity while they actually measured species richness, I would avoid using taxonomic diversity as no abundance data were used in this work.

>>> We think that it is important to differentiate here between diversity itself and a diversity index: an index of something is just a surrogate for the thing itself. Whilst community diversity is often expressed as indices that weight both the richness and equitability (evenness of abundance across species), for many authors (e.g. Magurran 2004) species richness is one of several possible measures of species diversity (or biodiversity more generally). In any case, and recognizing that there is some controversy about this in the ecological literature, we think that it is necessary to ensure that the terms used have clear and discrete meanings. Because of this, we explain in the text (page 5, L228-229) that we use species richness (and dissimilarity in species composition in the case of beta diversity) to describe taxonomic diversity:

"Both α and γ TD were calculated as species richness, whilst β TD was measured as the change in species composition amongst sites (grid cells in our case)."

Magurran, A. E., 2004. Measuring biological diversity, Blackwell Publishing: Oxford.

Minor comments
(P refers to the page number and L to the line number)

P5- L189: Why including Natural monument?
>>> We considered all the types of natural protected areas in the Iberian Peninsula. Despite of its name, "Natural Monuments", which are included in the legislation of some Spanish regions, are not areas protected just for scenic or landscape value, but also for biodiversity value.

P5-L203: Why choosing a 50% threshold and not the 1% or 90%?
>>> As it was already indicated in the manuscript, we think that a 50% threshold can be considered appropriate, as most aquatic habitats are highly influenced by processes occurring in their catchments and similar thresholds have been used elsewhere in comparable evaluations (e.g. Araújo, 2004; D'Amen et al., 2013; Sánchez-Fernández et al., 2013). In any case, and in order to assess the sensitivity of results to this choice of threshold, alternative values (1%, 25%, 75% and 90%) were also considered and their results are presented in Appendix A.

P5 - L222: A table with the traits and their different modality to be in the sup materials would be nice.
>>> Done as suggested. In this version the reader can found in the appendix a complete table with all the biological traits considered in the analysis.

P7 - L296 replace focussed by focus
>>> Done as suggested.

P10 - L465 to 470 long sentence, I don't understand the end.
>>> We have now reworded this sentence.

P10-L479 replace showed by show
>>> Done as suggested.

References:

The authors should carefully check their references; the style is not consistent from one reference to another. (e.g: misspelled firstname P12 - L558, use of an acronym for the journal P13-L606 etc)

>>> In the new version of the manuscript the References list was carefully checked and now the style is consistent.

How well do protected area networks support taxonomic and functional diversity in non-target taxa? The case of Iberian freshwaters

S. Guareschi [a*], D. Bilton [b], J. Velasco [a], A. Millán [a], P. Abellán [a, c]

Highlights

- We explore how well protected areas support non target taxa

- We study α, β and γ components of taxonomic *and* functional diversity

- Protected areas perform differently for taxonomic and functional diversity

- Poor performance of protected areas in representing functional diversity

- Results also highlight the importance of spatial scale when evaluating reserves

1 **How well do protected area networks support taxonomic and functional diversity**

2 **in non-target taxa? The case of Iberian freshwaters**

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Abstract

Protected area networks represent one of the mainstays of global conservation polices and are therefore central to current efforts to maintain biodiversity. However, a major limitation of most conservation strategies is their bias towards particular taxonomic groups and ecosystems, meaning that many taxa and habitats are often only incidentally protected as a by-product of inclusion within reserves. Here we investigate how effectively protected area networks, not specifically designated for freshwaters, support aquatic biodiversity in the Iberian Peninsula (Spain and Portugal), using data for water beetles, surrogates of overall macroinvertebrate diversity in these habitats. We explore the behaviour of different measures (alpha, beta and gamma) of both taxonomic and functional diversity at different spatial scales. Overall our findings highlight the contrasting performance of reserve systems in the maintenance of either taxonomic or functional diversity, as well as the importance of spatial scale. Iberian reserves perform relatively well in supporting taxonomic diversity of water beetles at the peninsular scale, but the same protected areas poorly represent functional diversity. Such a mismatch cautions against the use of any one diversity component as a surrogate for others, and emphasizes the importance of adopting an integrative approach to biodiversity conservation in aquatic ecosystems. Furthermore, our results often show contrasting patterns at smaller spatial scales, highlighting the need to consider the influence of scale when evaluating the effectiveness of protected area networks.

Keywords: biodiversity conservation, macroinvertebrates, aquatic ecosystems, reserves, beta diversity, functional diversity

1. Introduction

Protected area networks represent one of the mainstays of worldwide conservation polices and are therefore central to current efforts to maintain biodiversity (Chape et al., 2005). Numerous species are highly dependent on protected areas for their continued persistence; occurring either entirely or largely within their bounds (Jackson and Gaston, 2008). However, the implementation of nature reserves is only the start of the task and evaluating how effective they are is a global research priority to better understand their effectiveness in protecting wider biodiversity (Bertzky et al., 2012). A major limitation of most conservation strategies is their bias towards particular taxonomic groups (Martín-López et al., 2009), meaning that many taxa and habitats are often only incidentally protected as a by-product of their inclusion within reserves. Freshwaters, for example, are key hotspots of biodiversity (Strayer and Dudgeon, 2010), and are recognized as amongst the most endangered habitats in the world with important needs of protection, research and public awareness (e.g. Dudgeon et al., 2006; Geist, 2011; Kingsford and Neville 2005; Monroe et al., 2009; Strayer and Dudgeon, 2010). Despite this, very few protected areas have been planned specifically for freshwaters (Abell et al., 2007) and the effectiveness of incidental protection in representing aquatic features and taxa remains poorly and incompletely known (e.g. Abellán et al., 2007). Additionally, the groups which have been the focus of most conservation efforts (e.g. vertebrates or plants) are likely to be poor surrogates for diversity patterns in many freshwater organisms (see Darwall et al., 2011). Given this, assessing the extent of both intentional and incidental representation of freshwaters within existing protected area networks is a major prerequisite for identifying and plugging conservation gaps (Herbert et al., 2010).

To date, most conservation efforts have focused on protecting areas that ensure adequate representation of taxonomic diversity (TD), such as species richness (e.g. Rodrigues et al., 2004). Despite this, it is increasingly well recognized that protected areas should strive to preserve all components of biodiversity including the ecological and evolutionary processes that generate and maintain it and the goods and services that humans obtain from nature (Mulongoy and Chape, 2004). Functional diversity (FD), which reflects the range of biological, physiological and ecological traits within natural communities (Petchey and Gaston, 2006), has been advocated as an important facet of diversity for ensuring the provision of goods and services (Díaz et al., 2006), and has been shown to be a key driver of ecosystem processes (e.g. Mokany et al., 2008); essential in understanding relationships between biodiversity, ecosystem functioning and environmental constraints (Mouchet et al., 2010). In addition, incorporating functional information into conservation strategies allows for this approach to go beyond simple species representation. Indeed, human activities may have an impact on FD and alter species interactions and ecosystem functioning regardless of the change in taxonomic diversity (Díaz et al., 2006). Similarly, regions of high TD may be incongruent with regions of high FD (Cumming and Child, 2009), and such spatial mismatch between different aspects of diversity may result in protected area networks that do not fully represent biodiversity (Abellán et al. 2013; Devictor et al., 2010).

Effective protected area systems in a changing world should also ensure the maintenance of species and functional processes at different spatial scales (Brooks et al., 2006; Devictor et al., 2010; Gering et al., 2003). Both taxonomic and functional diversity can be broken down into local, regional and among-site components (so-called alpha, gamma and beta diversities; Whittaker, 1972). Whilst the effectiveness of protected areas in representing alpha (e.g. species richness in a given site, or local diversity) and gamma biodiversity (the total taxa represented in a protected area network, or regional diversity) have often been assessed (e.g. Araújo et al., 2007; Branquart et al., 2008; Rodrigues et al., 2004), very few studies have explored how well existing protected area networks represent beta diversity (and its components), despite the fact that it is the rate of species (or trait) turnover between sites that dictates the optimal spatial arrangement of conservation areas (Nekola and White, 2002). As beta diversity quantifies the change in species (or traits) across space, it provides information about variation in species assemblages, which can be very useful to preserve ecological and evolutionary processes as well as the underlying environmental heterogeneity necessary for long-term persistence (Fairbanks et

al., 2001; Margules and Pressey, 2000). Furthermore, beta diversity itself is comprised of two components: spatial turnover and nestedness (see Baselga, 2010). Whilst both nestedness (i.e. a pattern characterized by depauperate sites being strict subsets of richer ones) and turnover (i.e. species/trait replacement from site to site) are components of beta diversity, they have different conservation implications (Wright and Reeves, 1992). A preponderance of nestedness within a network would permit the prioritization of just a small number of the richest sites, whilst high turnover would require conservation of a larger number of different sites, not necessarily the richest ones (Baselga, 2010).

In this study we investigate how effectively protected area networks, not specifically designated for freshwaters, support aquatic macroinvertebrate biodiversity in the Iberian Peninsula. We explore the behaviour of both taxonomic and functional diversity measures, at local (α), inter-site (β) and regional (γ) scales. In addition to making up the bulk of freshwater animal biodiversity, macroinvertebrates play a key role in freshwater ecosystem processes (Covich et al., 1999) but are still less studied and protected compared to other, more publicly appealing, taxa (Strayer, 2006). We specifically use water beetles as a surrogate of overall macroinvertebrate diversity, as these represent one of the most diverse and best known groups of aquatic invertebrates in the region (Millán et al., 2014; Ribera 2000), living across the complete spectrum of inland water habitats. Aquatic beetles have been shown to be excellent surrogates for wider macroinvertebrate biodiversity in Iberia (Guareschi et al., 2012; Sánchez-Fernández et al., 2006) and elsewhere (Bilton et al., 2006) and have been used to select priority areas for aquatic conservation (Foster et al., 1989; Sánchez-Fernández et al., 2004). Furthermore, aquatic Coleoptera show considerable diversity in life histories and ecological strategies (Jäch and Balke, 2008), and are therefore functionally important in aquatic habitats, being involved in ecosystem processes such as biomass production, nutrient cycling and recourse processing.

Specifically, we use aquatic beetle data from the Iberian Peninsula to address the following questions: i) do protected areas have significantly higher α-diversity than non-protected areas? ii) do protected area networks include more total diversity (γ) than expected by chance, given their area? and iii) do protected area networks include more inter-site diversity (β) than expected by chance alone, given their area? Addressing the first question we explore whether protected areas include those cells with the highest diversity (e.g. species richness), whilst answering the second question provides information about the effectiveness of the whole network in representing overall freshwater diversity. Finally, the third question deals with dissimilarity amongst protected sites within the network, which is related to their complementarity, a principle widely used in conservation planning (Justus and Sarkar, 2002). Our study has wider implications for the design of protected area networks, being the first investigation to explore how well such networks support both taxonomic and functional measures of biodiversity in a non-target group across different spatial scales.

2. Methods

2.1 Study area and data

This study focuses on the Iberian Peninsula, a biodiversity hotspot located in south-western Europe, which is mainly composed of the mainland territories of Portugal and Spain (Fig. 1). The region, which extends nearly 600 000 km^2, includes a variety of biomes, relief, climates, and soil types, where altitude ranges from sea level to 3 483 m. The study area is one of the richest European regions in terms of animal species diversity (Williams et al., 2000) and is characterised by a wide variety of ecosystem types, including aquatic environments, some of which are rare on a European context (Millán et al., 2011).

Distributional data of Iberian water beetles at 10x10 km resolution were obtained from the ESACIB database (see Sánchez-Fernández et al., 2008a; Millán et al., 2014), which represents the most complete information available for a group of freshwater macroinvertebrates in the study area. The database currently contains over 60 000 records with associated location

194 data (10x10 km UTM cells) for 484 water beetle species. Species level was used for taxonomic
195 diversity measures whilst genus level information was used to assess functional diversity
196 (Dolédec et al., 2000; Gayraud et al., 2003).
197　　　Two different protected area networks were investigated: the extant regional and
198 national protected area network (RNAs) and the wider and incompletely implemented Natura
199 2000 network of protected areas (N2000) (see Fig. 1). RNAs are at the core of national and
200 regional conservation policies, and include National and Natural Parks, Natural Reserves,
201 Natural Monuments, Protected Landscapes, Protected Marine Areas (not included in this study)
202 as well as different types of local protected areas (i.e. those included in Spanish and Portuguese
203 laws). The N2000 network represents a key tool for biodiversity conservation at the European
204 scale and aims to guarantee the long-term survival of Europe's most valuable and threatened
205 species and habitats. It includes Special Areas of Conservation (SACs) designated under the
206 Habitats Directive (92/43/EC), and Special Protection Areas (SPAs) which are designated under
207 the Birds Directive (79/409/EC, 2009/147/EC). GIS data layers supplied by the national
208 conservation agencies of Spain and Portugal, were edited and combined to produce single layers
209 of Iberian RNAs and N2000 networks, respectively.
210　　　Since species distribution information is available at a resolution 10x10 km UTM cells,
211 whereas protected areas are polygons, often smaller than these grid cells, we applied a filter to
212 identify grid cells that can be considered protected (see Araujo et al.,2007; Sánchez-Fernandez
213 et al., 2013 for similar approaches). We calculated the area of each 10x10 km UTM cell
214 included within the two different protected area scenarios and a cell was considered protected
215 when at least 50% of its area was within RNA or N2000 sites (Fig. 1). This threshold can be
216 considered appropriate, as most aquatic habitats are highly influenced by processes occurring in
217 their catchments and similar thresholds have been used elsewhere in comparable evaluations
218 (e.g. Araújo, 2004; D'Amen et al., 2013; Sánchez-Fernández et al., 2013). Nevertheless, to
219 assess the sensitivity of results to this choice of threshold alternative values (1%, 25%, 75% and
220 90%) were also considered (see Appendix A in Supplementary materials).
221
222 *2.2 Diversity measures*
223
224 We calculated values describing the different components (α, β and γ) of water beetle TD and
225 FD included in protected areas. Thus, for each protected area network (RNAs or N2000) we
226 assessed the diversity (either TD or FD) within each protected cell (α diversity), the change in
227 diversity amongst protected cells (β diversity) and the total diversity in the whole network of
228 protected cells (γ diversity). Both α and γ TD were calculated as species richness, whilst β TD
229 was measured as the change in species composition amongst sites (grid cells in our case). β TD
230 was measured as both spatial turnover in species composition (β_{SIM} Simpson's dissimilarity) and
231 variation in species composition due to nestedness (β_{NES} nestedness-driven dissimilarity), with
232 overall β diversity (β_{SOR}, Sørensen's dissimilarity) being the sum of these components (Baselga,
233 2010). For a given set of grid cells, overall β diversity and its two components were calculated
234 using multiple-site dissimilarity measures following Baselga (2010).
235　　　To characterise the functional diversity of coleopteran communities, 11 biological traits
236 (considering 40 modalities, see appendix A) were considered following Tachet et al. (2010),
237 which relate to morphology, life history, dispersal ability and trophic role. Tachet et al.'s trait
238 database summarises expert knowledge on European freshwater invertebrates by assigning an
239 affinity score for each taxon to each modality using a fuzzy coded approach. Selection of values
240 was conducted using information developed for Mediterranean ecosystems by Bonada and
241 Dolédec (2011) and Picazo et al. (2012), with some scores being modified on the basis of the
242 authors' own fieldwork.
243　　　A matrix of trait pairwise dissimilarity among taxa was generated using Gower
244 distance, and a functional dendrogram constructed from this distance matrix using Ward linkage
245 and hierarchical clustering (Petchey and Gaston, 2002 - alternative methods gave qualitatively
246 similar results). Subsequently FD was calculated for each grid cell (α diversity) and for each
247 protected area network (γ diversity), as the mean pairwise distance amongst species – i.e. the
248 average of the branch lengths in the trait dendrogram joining all pairs of species in a given

5

community (Webb et al., 2002). Furthermore, functional β diversity was computed using the Functional Sørensen's Index (F_{sor}; Swenson et al., 2011), which is an analogue of the traditional Sørensen's Index. F_{sor} is a dissimilarity metric that provides an overall indicator of the shared function between two communities and, like its phylogenetic analogous metric (*PhyloSor,* Bryant et al., 2008), can be broken down into both turnover (F_{sim}) and nestedness (F_{nes}) components of functional β diversity (Leprieur et al*.,* 2012). We therefore also partitioned these components of β diversity using the framework proposed by Baselga (2010).

2.3 Assessment of protected areas performance

In order to assess the performance of protected area networks in representing γ and β taxonomic and functional freshwater diversity, we compared the level of TD and FD representation within both networks with what would be expected by chance alone, given the area they cover. To do this, we compared observed γ and β TD or FD to expected values from 1,000 random draws of an equal number of cells, taken from the pool of grid cells where species have been recorded (including both protected and unprotected cells). The proportion of random samples with higher or lower diversity values than those observed for protected area networks allowed us to obtain a significance value (see e.g. Araujo 2007). In the case of α TD and FD, we assessed whether values of TD and FD in protected grid cells were significantly greater than in unprotected cells using nonparametric Wilcoxon–Mann–Whitney tests.

We investigated the effectiveness of protected area networks in representing macroinvertebrate biodiversity at two different spatial scales. First, we assessed α-, β- and γ-diversity represented by the whole reserve networks for the entire Iberian Peninsula. Second, as network planning is often carried out at an intermediate spatial scale, we assessed protected area performance at a subregional scale according to the following procedure (see also Devictor et al., 2010): a circle with a radius of 100 km (Fig. 1) was centred on each 10x10 km cell (so that all grid cells are the centre of one 100 km radius window - such windows are overlapping and therefore some plots included in one window will be included in neighbouring ones). Then, for each of these 100 km radius windows we calculated α-, β- and γ-diversity in protected cells and compared them with random expectations as described above (for example, we compared the observed γ-diversity of protected cells within a given window to the values expected from 1 000 random draws of an equal number of grid cells within that window).

All analyses were performed using R (R-Development-Core-Team, 2010) with packages "ade4" (Chessel, 2011), "Betapart" (Baselga and Orme, 2012), "picante" (Kembel et al., 2010) and "FD" (Laliberté and Legendre, 2010).

3. Results

3.1 Representation of taxonomic diversity in protected areas

In terms of α diversity at the Iberian Peninsula scale, species richness of water beetles was significantly higher in protected than in unprotected cells for both RNAs and N2000 (Wilcoxon–Mann–Whitney test $P < 0.001$ – See Appendix A). Furthermore, Iberian protected areas (both RNAs and N2000) represented significantly more total species (γ diversity) than expected given the area they cover. In total, RNA cells ($n = 352$) included 419 water beetle species (86.6% of the Iberian species pool) and this value was significantly higher than those obtained by chance (Table 1). This pattern is even clearer for N2000 cells ($n = 690$) that supported 458 species (94.6% of the Iberian species pool).

Overall β TD of water beetles in RNAs ($\beta_{SOR} = 0.9940$) mainly results from spatial turnover ($\beta_{SIM} = 0.9866$), with only a small contribution from nestedness (Table 2). Despite the high value of overall β diversity, it was significantly lower than values generated by random sampling of cells ($\beta_{SOR} = 0.9944 \pm 0.0001$ in random samples; $P= 0.002$). In terms of the two components of β diversity, observed nestedness was significantly lower than random values, whilst turnover was not significantly different from random expectations (Table 2). A similar pattern was found for N2000, with overall β diversity mainly due to turnover. Again, both β_{SOR}

and β_{NES} were significantly lower than expected by chance, whilst in this case β_{SIM} was significantly higher than random (Table 2).

At a smaller spatial scale, i.e. in the 100 km radius windows, α- diversity was significantly higher in protected cells than in unprotected ones for 50% of windows in the case of RNAs, and 68% in the case of the N2000 network. Windows with non-significant differences in α TD were mainly located in Eastern Iberia and along the central boundaries between Portugal and Spain (Fig. 2a, d). When we focus on γ diversity within windows, an opposite and more marked pattern was detected: for most of the windows (86% for RNAs; 83% for N2000) protected area networks did not perform significantly better in term of total species richness than an equal number of random cells within the same windows (see also Fig. 2b, e).

Focussing on β diversity, again for most of the windows (99.6%) overall β diversity among RNAs protected cells (average $\beta_{SOR} = 0.9082 \pm 0.0528$ across windows) was mainly caused by spatial turnover ($\beta_{SIM} = 0.7939 \pm 0.1051$), with only a small contribution from nestedness ($\beta_{NES} = 0.1143 \pm 0.0698$). Furthermore, RNA protected cells did not perform especially well in terms of overall β TD; 61.3% of windows having values of β_{SOR} in protected cells significantly lower than random expectations, and just 0.04% of windows having significantly higher values for protected cells (Fig. 2c). In the case of turnover, only 2.1% of windows had significantly higher β_{SIM} values in protected cells than random expectations (these cells being clustered between Galicia and the Cantabrian Mountains, at north and north-western of Iberian Peninsula), whilst 19.6% had significantly lower values (Fig. 3a). Finally, 4.3% of the windows had significantly higher nestedness in their network of protected cells than expected by chance, whilst 4.0% had significantly lower values (again grouped between Galicia and the Cantabrian Mountains; Fig. 3b).

In the case of N2000, similar patterns of β diversity were obtained. Overall β diversity amongst N2000 protected cells ($\beta_{SOR} = 0.9445 \pm 0.0276$) was mainly (99.9% of windows) due to spatial turnover ($\beta_{SIM} = 0.8699 \pm 0.0673$ *versus* $\beta_{NES} = 0.0746 \pm 0.044$). Here 66.2% of windows had β_{SOR} values significantly lower in the network of protected areas than random expectations, and none had significantly higher values (Fig. 2f). 14.8% of windows had significantly lower β_{SIM} values in the protected network than expected by chance (clustered in the Cantabrian Mountains), and just 0.09% higher (Fig. 3e). Finally, 3.6% of windows had significantly higher values of β_{NES} in their network of protected cells, whilst 0.6% had significantly lower values than those obtained by chance (Fig 3f).

All these results were basically consistent across thresholds used to consider a cell as protected (see Appendix A).

3.2 Representation of functional diversity in protected areas

In terms of α diversity at the Iberian Peninsula scale, FD was significantly higher in protected (both RNA and N2000 networks) than in unprotected cells (Wilcoxon–Mann–Whitney test; *P* < 0.001; Appendix A). However, both protected area networks did not include significantly more γ FD than expected by chance at this scale (Table 1). Again, in the case of β diversity, for both RNAs and N2000 overall β diversity mainly resulted from spatial turnover (β_{SIM}), with only a small contribution from nestedness. For both protected area networks, β_{SOR} and β_{SIM} were significantly lower than random expectations, whilst β_{NES} was significantly higher (Table 2).

At a smaller spatial scale, i.e. in the 100 km windows, α FD was significantly higher in protected cells than in unprotected ones for just 26% of windows in the case of RNAs, and 30% in the N2000 network. These windows were basically located in southern Iberia, northern Iberian (Cantabrian Mountains) and the Pyrenees (Fig. 4a, d). Furthermore, in most of the windows (98.6% for RNAs and 95.3% for N2000) protected area networks did not perform significantly better in term of γ FD than expected by chance. In the case of N2000, windows with significantly higher values of γ FD were mainly clustered in the southernmost part of the Iberian Peninsula (Fig. 4e). Focussing on β FD, again for the most of the windows (88%), overall β diversity amongst RNA protected cells ($\beta_{SOR} = 0.8019 \pm 0.1015$) was mainly due to spatial turnover ($\beta_{SIM} = 0.5542 \pm 0.1648$), with a smaller contribution from nestedness ($\beta_{NES} = 0.2477 \pm 0.0981$). 50.9% of windows had values of β_{SOR} significantly lower in RNA

protected cells than random expectations, and no windows had significantly higher values (Fig. 4c). Also, no windows had significantly higher β_{SIM} values amongst protected cells than random, whilst 30.4% had significantly lower values (mainly clustered in the Cantabrian Mountains and the south of Spain, Fig. 3c). Finally, 15.0% of windows had significantly higher values of β_{NES} amongst protected cells (with a similar geographic pattern, Fig. 3d), whilst 1.17% had significantly lower values than random expectations.

With the Natura 2000 network, similar patterns of β FD were obtained: for most of the windows (98.7%) overall β diversity (average $\beta_{SOR} = 0.8858 \pm 0.0674$ across windows) was mainly driven by spatial turnover (average $\beta_{SIM} = 0.7135 \pm 0.1156$ *versus* $\beta_{NES} = 0.1724 \pm 0.0638$). 56.9 % of windows had values of β_{SOR} significantly lower in the N2000 network, and no windows had significantly higher values for protected cells (Fig. 4f). Only 0.34% of windows had significantly higher β_{SIM} values in protected cells than random, whilst 36.8% had significantly lower values (Fig. 3g). Finally, 24.2% of windows had significantly higher values of β_{NES} in their network of protected cells, whilst 1.3% had significantly lower values than expected by chance (Fig. 3h).

Again, all these results were consistent across the different thresholds used to consider a cell as protected (see Appendix A).

4. Discussion

Our research represents the first attempt to assess the effectiveness of protected areas in representing different components of invertebrate biodiversity at different spatial scales, despite the fact that invertebrates make up the bulk of global animal diversity, in both taxonomic and functional senses. Ramos et al. (2001) have estimated that about 98% of the total Iberian fauna is made up of invertebrates, for example, and similar values apply elsewhere. Biodiversity knows no political boundaries and in this context evaluations of protected areas at biogeographical scales (like the Iberian Peninsula) are desirable, but as we demonstrate these should be combined with studies at different scales which will assist in the design and management of protected areas.

Our results show that, at the Iberian scale, protected areas (both RNAs and N2000) tend to include those cells of highest diversity (both taxonomic and functional), as revealed by α diversity assessments. Protected areas usually tend to over-represent mountainous areas and under-represent lowlands, probably because the former provide less conflict with human land uses (Joppa and Pfaff, 2009). This is true for the two studied protected area networks in the Iberia Peninsula (mean altitude of RNA cells 892 m versus 588 m in unprotected ones, and 807 m in N2000 cells versus 561 m in unprotected ones; Wilcoxon-Mann-Whitney test, $P < 0.001$ in both cases), something which is common in many countries (e.g. Maiorano et al., 2007). These mountainous areas usually include a high density of relatively unimpacted localities with, in general, the highest water beetle diversity (Ribera, 2000; Millán et al., 2014). Nevertheless, it should be noted here that a high local diversity in a given site does not necessarily indicate high conservation value. For instance, some habitats support few species, but contain many endemic or exclusive taxa. Similarly, local diversity is often maximized at a certain level of human disturbance (Wilkinson 1999), rather than in pristine sites.

When we focus on γ diversity, protected area networks capture a relatively large proportion of the Iberian water beetle species pool (87% and 95% in RNAs and N2000, respectively); significantly more than expected by chance, given their area, despite the fact that they were established with little or no consideration of their freshwater biodiversity. These results are congruent with those for Iberian plant and terrestrial vertebrate species (Araújo et al., 2007), which show that, in general, protected areas conserve more species than expected by chance. Nevertheless, it should be noted that the distribution and extent of existing reserves is still inadequate or insufficient to protect some water beetles of conservation concern in the study area (see also Sánchez-Fernández et al., 2008b). Among the 64 species (13%) that occur completely outside the RNA network, 14 are Iberian endemics with high vulnerability (Millán et al., 2014; Sánchez-Fernández et al., 2008b). Moreover, in the case of the 25 species excluded from the N2000 network (5%), four (*Iberoporus cermenius,* Castro & Delgado 2000,

Nebrioporus croceus Angus, Fresneda & Fery 1992, *Rhithrodytes agnus argaensis* Bilton & Fery 1996 and *Ochthebius irenae* Ribera & Millán 1999) are also vulnerable Iberian endemics. In a similar vein, a recent study has shown that current protected sites in Spain do not allow a complete representation of endangered invertebrates (Hernández-Manrique et al., 2012). Most of the detected gap-species (i.e. those not represented in any protected area at a threshold of 50%) are distributed along the Mediterranean coast and eastern Iberia, inhabiting small lentic, coastal or/and mineralized ecosystems (Fig. A1) and their localities should be considered for future protection. Interestingly, these patterns were not congruent for α and γ diversity at smaller scale, with a considerable percentage of 100-km-radius windows (50-30% for TD and ca. 70% for FD) showing no significant differences in α diversity between protected and unprotected areas, and most (80-95%) with no significant differences in total species representation (γ diversity). This suggests that in some areas of the Peninsula protected areas are not biased towards the most speciose localities or zones, and they do not cover sufficiently subregional diversity. The size of our 100-km-radius windows can be considered as a valid approximation to the scale of conservation management that often occurs on the ground, being more realistic in many cases than a biogeographical or national scale. For example, in many countries with federal distribution of powers, each region may have its own system of protected areas (EEA, 2012). In the case of Spain, most nature conservation responsibilities are devolved to regional autonomous governments (Morillo and Gómez-Campo, 2000), and most of current protected areas have been designated under this regional setting. The mean size of the Spanish autonomous regions is around 30 000 km^2, approximating to that of our windows (31 400 km^2).

In contrast to TD, the overall FD included in both protected area networks was not significantly higher than chance expectations, given the areas they cover. In other words, the level of FD representation achieved is no better than that expected by chance. Furthermore, this pattern was consistent across the two spatial scales for γ diversity. These findings illustrate the relative failure of both protected area systems in preserving freshwater functional diversity, despite this component of biodiversity being a better predictor of ecosystem productivity and vulnerability than species diversity (Hooper et al., 2005) and illustrate the importance of explicitly taking all types of diversity into account when designing protected areas (Cumming and Child, 2009; Devictor et al., 2010; Forest el al., 2007; Strecker et al., 2011).

This incongruence in the performance of protected areas in representing either TD or FD could result from a bias in habitat representation within reserve networks. This could result, for example, if certain aquatic habitats (e.g. headwaters) are overrepresented within protected areas, and these contain relatively higher species diversity than functional diversity (the correlation between TD and FD across Iberian protected cells was low; Pearson's correlation coefficient r = 0.29 and r = 0.32 for RNAs and N2000, respectively; *P* < 0.001 in both cases). This appears to be the case of headwater streams in mountain areas, which have a rich, and often locally endemic, but functionally specialized, and rather homogenous fauna (Picazo et al., 2012). This situation could be due to environmental and biogeographical factors affecting the two diversity components in different ways. Environmental filtering will limit community members to those that are preadapted, and thus functionally similar, creating a functional structure of communities that is not necessarily reflected in their taxonomic structure (Poff, 1997). Our results suggest that important ecosystem processes (e.g. energy flow, nutrient cycling and biomass production) and services (e.g. mosquito control, food source to species of commercial interest) in which water beetles (and aquatic macroinvertebrates in general) are involved in some lowland freshwater habitats could remain under-represented by protected areas.

In case of β diversity (both TD and FD) at the Iberian scale, although the overall value obtained in both protected area networks was very high (close to 1), it was always significantly lower than expected by chance - i.e. communities in protected areas were more similar than would be expected from a random draw of equivalent area. This result may reflect the wide environmental heterogeneity in the Peninsula, which, despite being reasonably well represented in protected areas, may still be insufficient to cover the full spectrum of environments and associated faunas. Deconstructing β diversity into its spatial turnover and nestedness components provides crucial insights here, showing that spatial turnover is responsible for most

β diversity amongst protected sites, with only a small contribution from nestedness. β diversity within Iberian reserve systems is therefore mainly the result of species/trait replacement between sites. Although rarely recognized, the principles behind most approaches to systematic planning, such as complementarity, are driven by patterns of β diversity (Magurran, 2004; Justus and Sarkar, 2002). As the turnover component of β diversity (β_{SIM}) quantifies the change in biodiversity attributes across space, it provides critical information to represent all biodiversity within practical constraints such as area and cost (Margules and Pressey, 2000). Ideally, protected area networks should maximize the species/trait turnover amongst protected sites within the network, as this would denote high complementarity among protected sites. On the other hand, the nestedness component of β diversity (β_{NES}) provides information about redundancy in biodiversity attributes in the network, which also may be relevant for the persistence of biodiversity over time, as multiple representations of species within the set of sites would increase the probability of regional persistence (i.e. maintain each species within the reserve network, even if local extinctions occur (Cabeza and Moilanen, 2001).

When we compared both spatial turnover and nestedness components with expectations based on the surface covered by protected areas, we again found contrasting results between TD and FD. Whilst protected area networks showed significantly less turnover and more nestedness than random for FD, they generally displayed the opposite pattern for TD, suggesting that the processes underlying these β diversity values are different. Spatial turnover implies the replacement of some biodiversity attributes by others as a consequence of environmental sorting or spatial and historical constraints (Qian et al., 2005). The fact that we found lower functional turnover amongst protected areas than expected at random, despite higher taxonomic replacement, seems to suggest that spatial turnover within reserve networks is mainly driven by spatial and historical constraints and less so by environmental sorting. The same would apply for species/traits loss (or gain) between protected sites, which suggest a higher functional redundancy within reserve systems than expected at random, despite lower taxonomic redundancy. These results point again to a bias in environmental representation within protected area networks, in agreement with γ and α diversity assessment. Although the results for 100-km-radius windows were more equivocal, they generally point to the same pattern. They also show that the performance of protected area networks in representing β diversity at this smaller spatial scale differs between regions of the Iberian Peninsula, since windows significantly departing from random were usually geographically clustered.

Finally, it is worth noting that our results did not show important qualitative differences between the two studied protected area networks. The complete implementation of the proposed Natura 2000 network may mean an important increase of the area of protected land in the study area (e.g. from around 12% of RNAs up to 28% in Spain; Europarc-España, 2010), with a subsequent increase in the taxonomic diversity represented at Iberian scale (e.g. up to 95% of the Iberian species pool). However, and despite the important potential of this reserve system enhancing the protection of European endangered species and habitats (European Commission 1992) we found that Natura 2000 network did not often over performed RNAs in relative terms, this is, when compared to that would be expected given the area it covers (for instance, in the conservation of γ functional diversity). These findings highlight some limitations of this network in preserving numerous components of freshwater biodiversity (see also Hermoso et al., 2014; Sánchez-Fernández et al., 2013) and the need of explicitly consider their biota and environments into conservation planning at European level (Hermoso et al., 2014). In any case, it is worth noting also that, in the case of inland waters, the inclusion in protected areas does not automatically guarantee protection because they often fail to address important aquatic concerns such as whole-catchment integrity, hydrology, and introductions of non-native species (Moyle and Randall, 1998). In this context the expansion of protected areas beyond their terrestrial comfort zone and the change towards catchment-based conservation planning (e.g. Nel et al., 2009; Bruno et al., 2014) seems crucial if we aim to improve protected area performances in terms of freshwater biodiversity conservation.

5. Conclusions

Our approach represents a synthetic view of the performance of protected area networks in representing different facets (taxonomic and functional) and components (α, β and γ) of water beetles biodiversity at different spatial scales.

Overall, our findings highlight the contrasting performance of reserve systems in the maintenance of either taxonomic and functional diversity, as well as the importance of spatial scale. First, results show that, despite the fact that Iberian reserves were often set up without any consideration of non-target organisms, they perform relatively well for taxonomic diversity of water beetles at Iberian Peninsula scale. Although the extent to which these results are applicable to other geographical areas and freshwater taxa remains to be investigated, they seem to highlight the potential role of protected area systems in representing the taxonomic diversity of non-target groups.

Second, our results show a poor performance of Iberian protected areas in representing the functional diversity of water beetles at Iberian scale, in contrast to findings for taxonomic diversity. Such mismatch between results for taxonomic and functional diversity call for caution against the use of any one diversity component as a surrogate for others, and emphasize the importance of adopting an integrative approach to biodiversity conservation in aquatic ecosystems (Abellán et al., 2013; Devictor et al., 2010; Strecker et al., 2011). And third, our results point contrasting results at smaller spatial scale, highlighting the importance to consider the influence of spatial scale when evaluating the effectiveness of protected area systems (Andelman et al., 2002; Caro et al., 2009; Gaston et al., 2006).

Acknowledgements

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885 Figure 1. Study area (Iberian Peninsula) showing the two different protected area networks
886 considered (a) regional and national protected areas (RNAs), (b) Natura 2000 (N2000) and the
887 cells considered as protected by RNAs (c) or N2000 (d) at a threshold of 50% coverage. Dashed
888 circle in (c) represents an example of a 100 km radius window.

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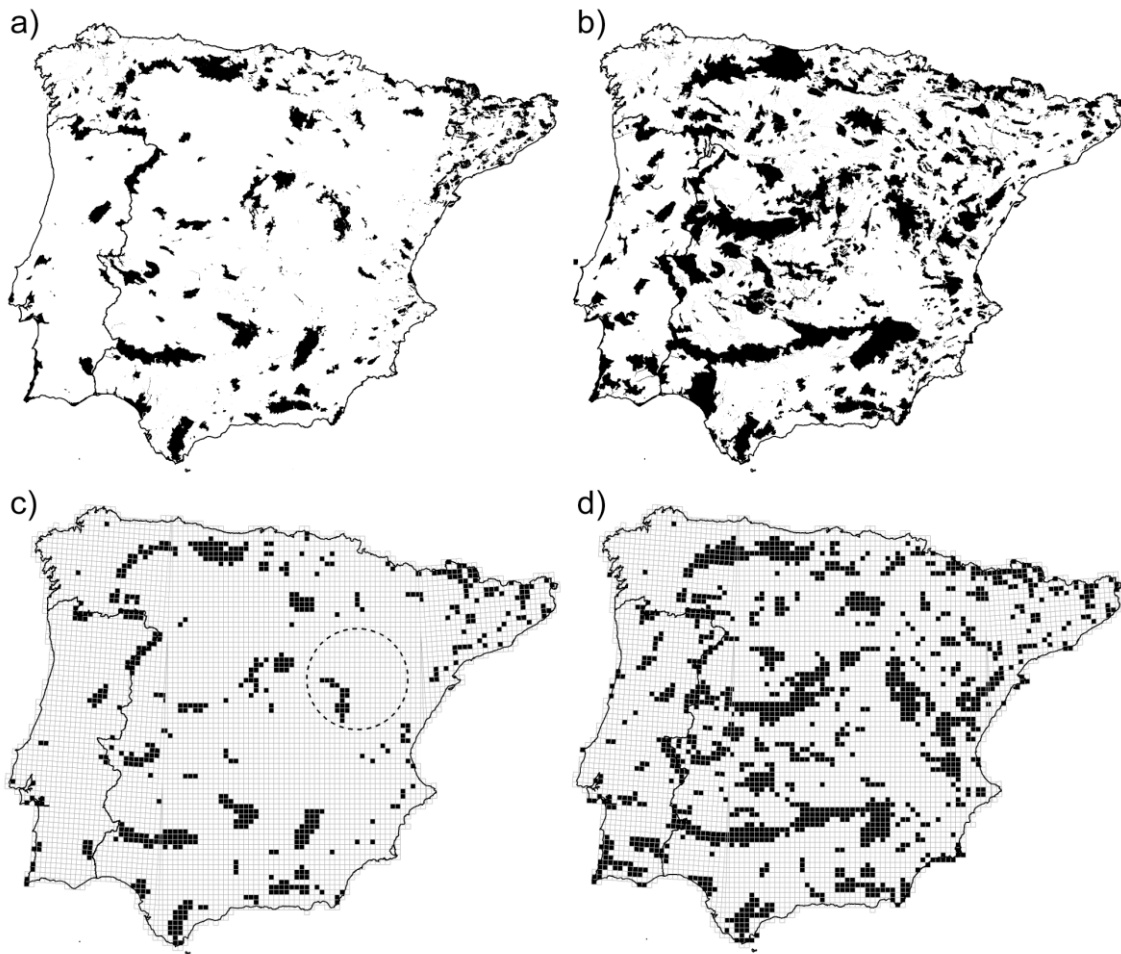
Figure 2. Performance of RNAs (a-c) and N2000 (d-f) networks in representing α, β and γ
taxonomic diversity at subregional scale (100 km radius windows): a) and d) windows for
which α diversity is significantly higher in protected than in unprotected cells; b) and e)
windows for which γ diversity was significantly higher than random; c) and f) windows for
which overall beta diversity (β_{SOR}) was significantly higher (black cells) and lower (grey cells)
than random. Each grid cell represents the centre of the window.
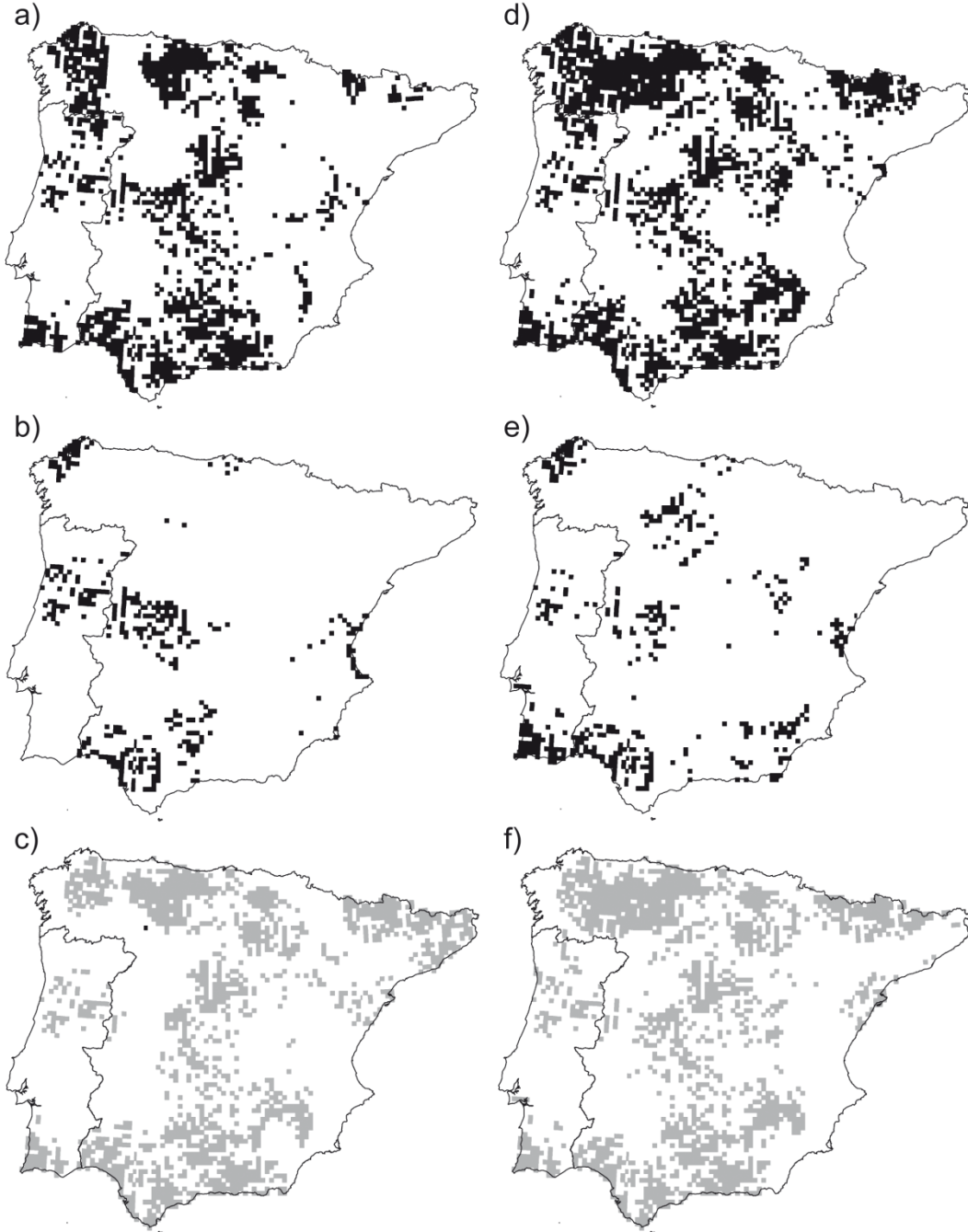
Figure 3. Performance of RNAs (a-d) and N2000 (e-h) networks in representing taxonomic and functional beta diversity components (turnover and nestedness) at subregional scale (100 km radius windows). Grid cells representing the centre of those 100-km-radius windows with significantly higher (black cells) and lower (grey cells) values than random are shown. a) and e) taxonomic β_{SIM}; b) and f) taxonomic β_{NES}; c) and g) functional β_{SIM}; d) and h) functional β_{NES}.
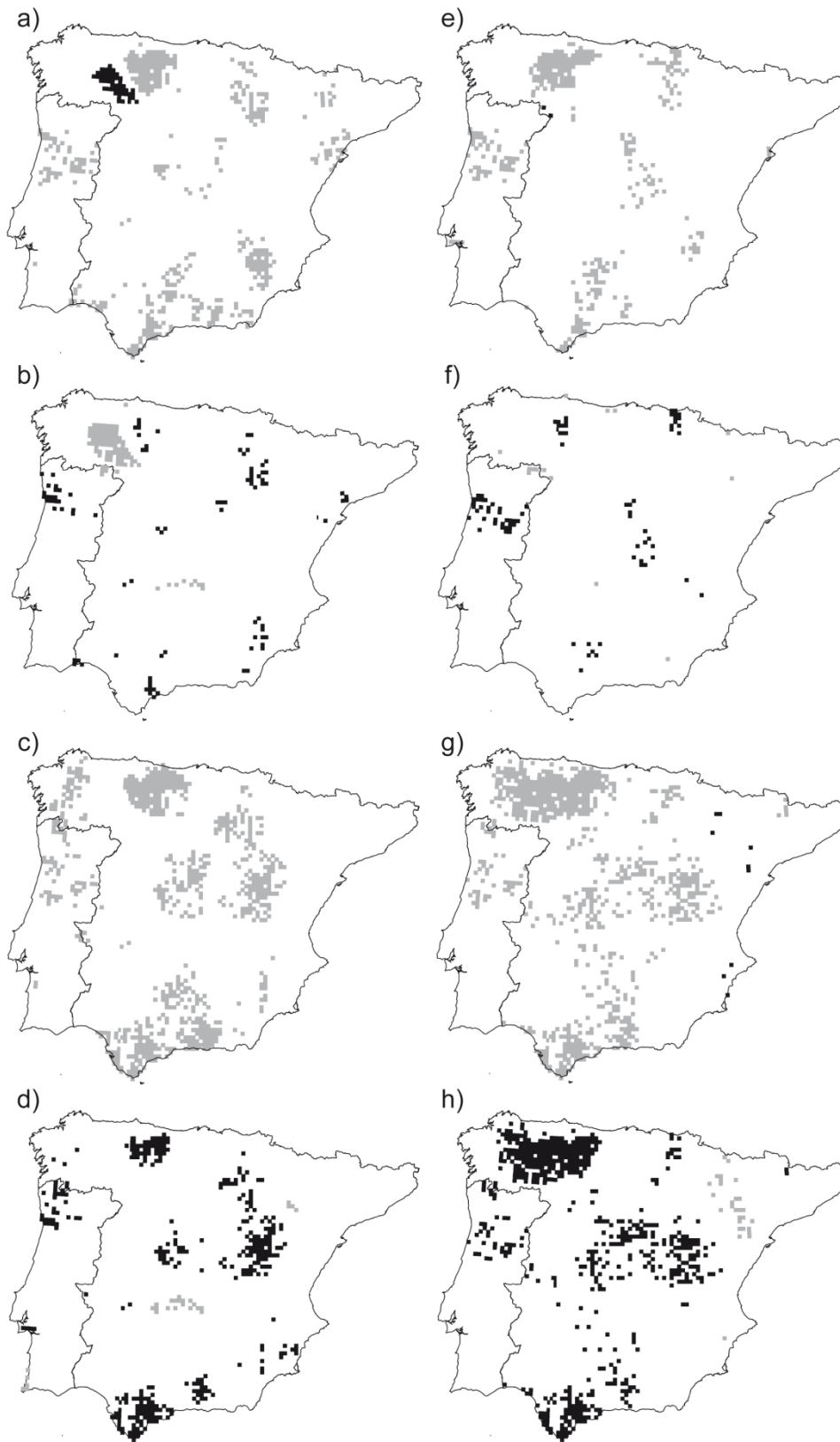
906 Figure 4. Performance of RNAs (a-c) and N2000 (d-f) networks in representing α, β and γ
907 functional diversity at subregional scale (100-km-radius windows). a) and d) windows for which
908 α diversity is significantly higher in protected than in unprotected cells; b) and e) windows for
909 which γ diversity was significantly higher than random; c) and f) windows for which overall
910 beta diversity (β_{SOR}) was significantly higher (black cells) and lower (grey cells) than random.
911 Each grid cell represents the centre of the window.

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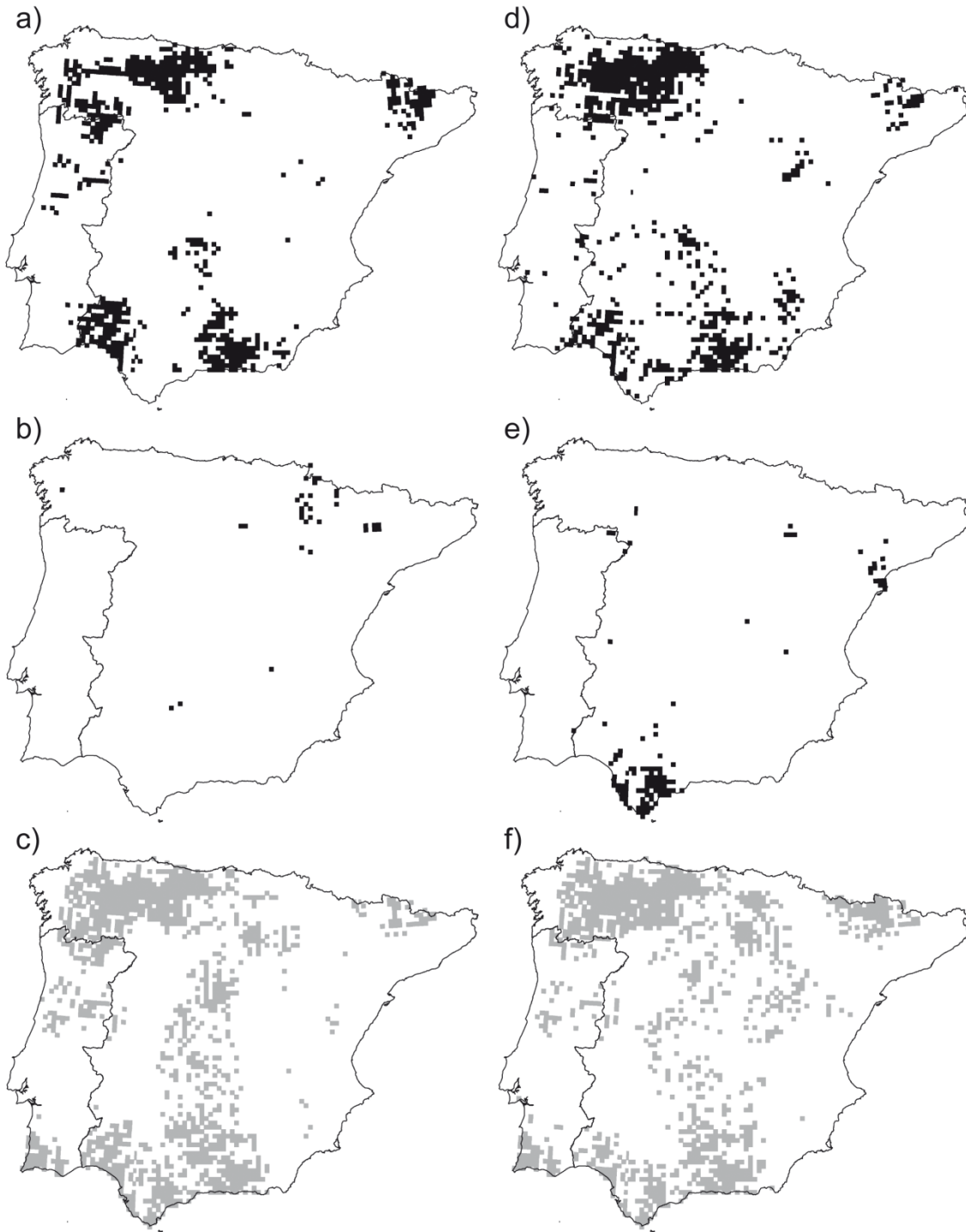
Table 1. Representation of taxonomic and functional γ diversity in protected area networks at Iberian scale (Protected) and comparison with the values expected from 1 000 random draws of an equal number of grid cells (Random, mean value ± SD). Standardized effect sizes (SES; which describe the difference between the observed value of diversity in the protected area network versus the mean value obtained from random draws, divided by the standard deviation of null data) and the p values are shown.

	Protected	Random	SES	p
Taxonomic diversity				
RNAs	419	404.2 ± 8.4	1.76	0.04
N2000	458	442.7 ± 5.9	2.60	0.002
Functional diversity				
RNAs	0.283	0.283 ± 0.002	0.00	0.692
N2000	0.284	0.283 ± 0.001	1.00	0.131

Table 2. Representation of taxonomic and functional beta diversity (β_{SOR}) and its decomposition in nestedness (β_{NES}) and turnover (β_{SIM}) in protected area networks at Iberian scale (Protected) and comparison with the values expected from 1 000 random draws of an equal number of grid cells (Random). Standardized effect sizes (SES; which describe the difference between the observed value of diversity in the protected area network versus the mean value obtained from random draws, divided by the standard deviation of null data) and the p values are shown.

	RNAs				N2000			
	Protected	**Random**	**SES**	***p***	**Protected**	**Random**	**SES**	***p***
Taxonomic diversity								
β_{SOR}	0.9940	0.9944	-4.20	0.002	0.9969	0.9970	-9.61	0.002
β_{SIM}	0.9866	0.9859	1.34	0.180	0.9928	0.9925	1.80	0.038
β_{NES}	0.0074	0.0086	-0.28	0.022	0.0040	0.0046	-3.02	0.008
Functional diversity								
β_{SOR}	0.9890	0.9907	-11.43	0.002	0.9946	0.9952	-12.56	0.002
β_{SIM}	0.9671	0.9722	-4.76	0.002	0.9835	0.9855	-5.63	0.002
β_{NES}	0.0220	0.0186	3.43	0.001	0.0111	0.0097	4.20	0.002

Figure1
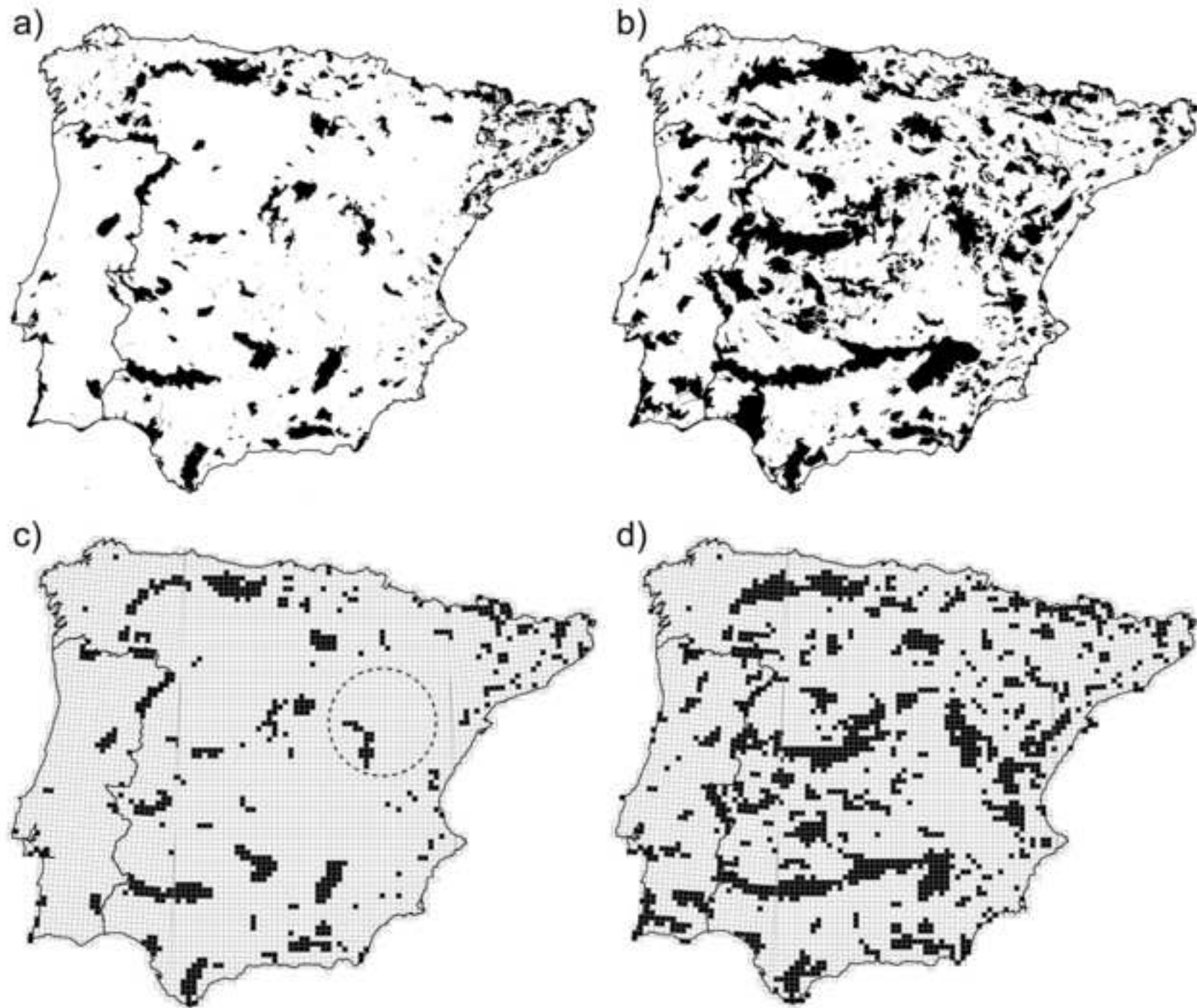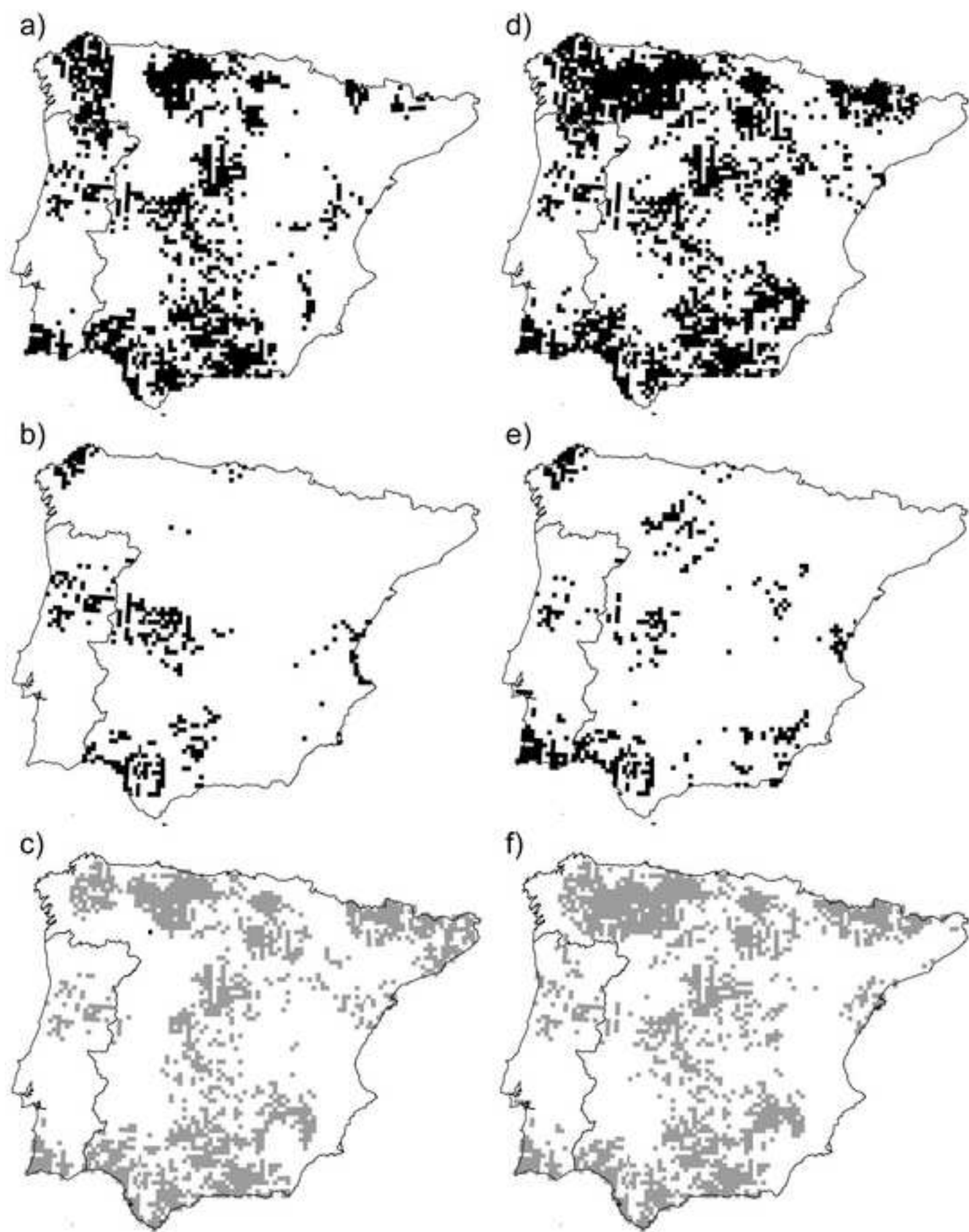**Click here to download high resolution image**

Figure2
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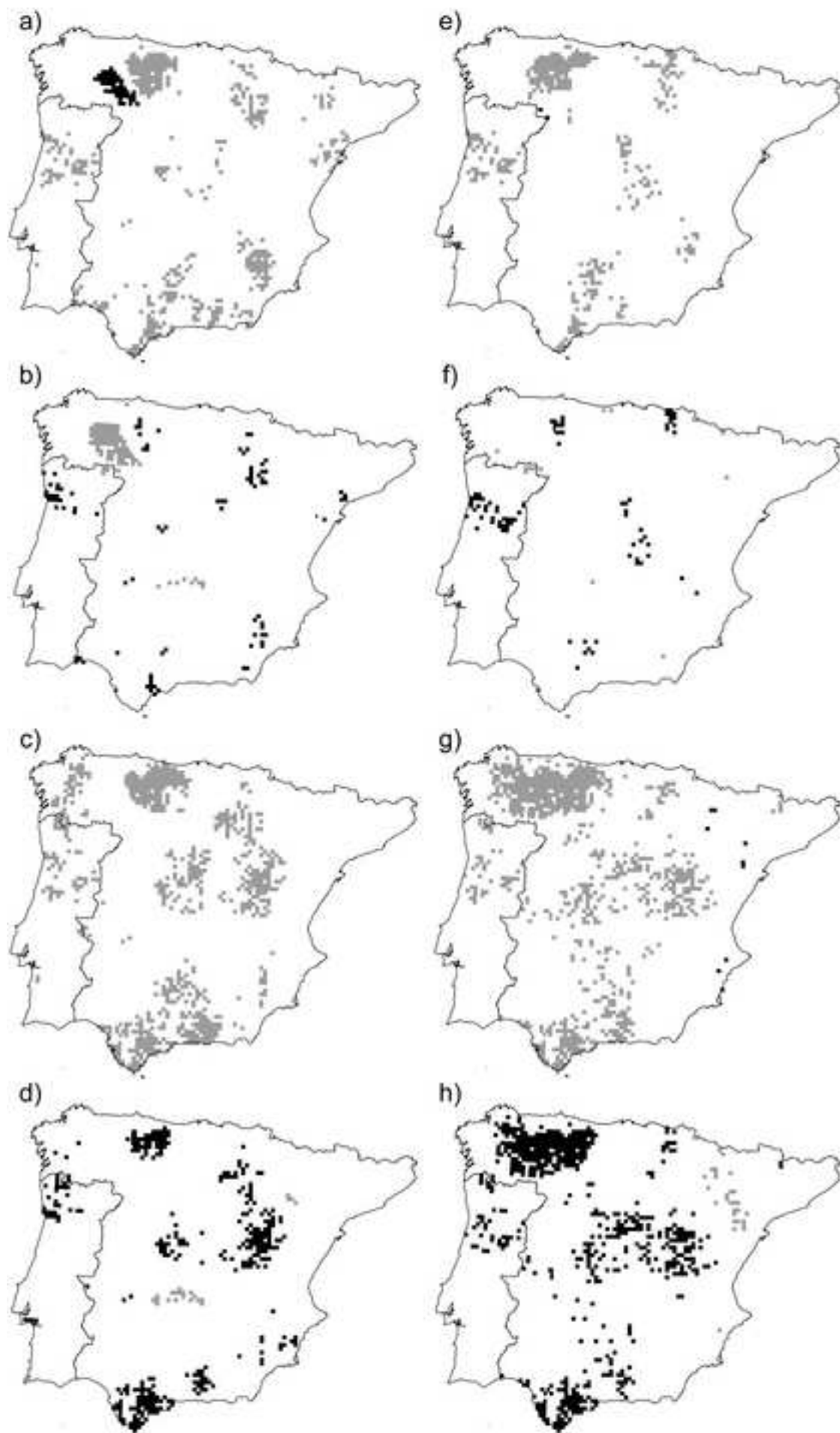**Figure3**
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Supplementary Data