



UNIVERSIDAD DE MURCIA

FACULTAD DE BIOLOGÍA

Challenges for the Conservation of Aquatic
Macroinvertebrates and their Habitats in the Iberian
Peninsula

Retos para la Conservación de los Macroinvertebrados
Acuáticos y sus Hábitats en la Península Ibérica

D. Simone Guareschi

2015



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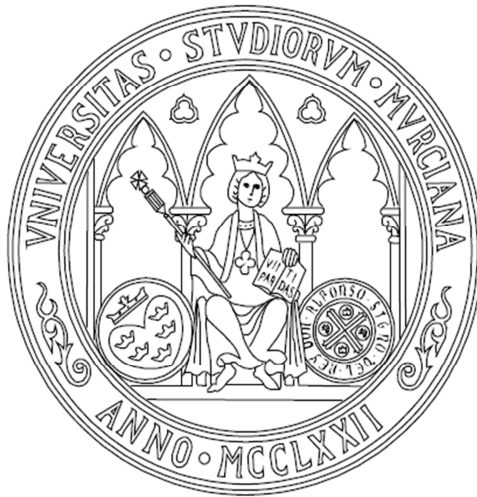
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**Faculty of Biology
Department of Ecology and Hydrology**

Doctoral programme "Biodiversity and Environmental Management"

Challenges for the conservation of aquatic macroinvertebrates and their habitats in the Iberian Peninsula

Dissertation submitted by

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to obtain the PhD degree with the International Mention
by the University of Murcia

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BIOGRAPHICAL SKETCH

I was born 6th August 1983 in Parma (Emilia-Romagna, Italy).

Since I was a child I have been interested in freshwaters, their quality and the life inside these amazing ecosystems. At the same time I was always fascinated by river flows, from little Apennine streams to the giant of my home region: the Po River.

From the University of Parma I hold the Master's degree in Environmental Sciences (2009) and presented the project titled *Analysis of the benthic and interstitial invertebrate community in the headwater of the Parma River (Northern Apennines) with special reference to the impacts caused by hydropower*.

Lessons of Prof. Ireneo Ferrari (Ecology) were very important for my formation, as was my final project to improve my skills in freshwater ecosystem assessment.

During 2009-2010 I collaborated, as the responsible scientist for macroinvertebrate sampling and analysis, in the project "Definition of the minimum vital flow for the Oglio River (Northern Italy)" thanks to Dr. Marco Bartoli, and took my first steps in aquatic ecology research. The result of this collaboration was an article published in *Ecohydrology* 7, 366-377 (2014).

I arrived in Murcia (Spain) in 2010 thanks to Prof. Andrés Millán and funded by the international grant "Spinner2013". During 2011 I achieved an M.Sc. in Biodiversity management in Mediterranean ecosystems and started the Doctorate Program "Biodiversity and Environmental Management" that led to the present thesis.

During these years at the University of Murcia (Aquatic Ecology Group) I enjoyed several collaboration grants focusing on aquatic macroinvertebrate, hydrology and protected areas, and have participated in several sampling campaigns throughout Spain, in different aquatic ecosystems (Pyrenees, Ramsar wetlands, Segura River Basin, Mediterranean saline streams, etc.). I have also collaborated with numerous researchers from different Institutes: Miguel Hernandez Elche University, Estación Biológica de Doñana (EBD-CSIC), Parma University, University of Piemonte Orientale and Plymouth University (UK).

I have attended International Congresses on freshwater ecosystems (AIL 2010, SEFS 2011) and invasive species (NeoBiota2012) and in 2012 I passed the exam of the course *Introduction to the Analysis of the Community of benthic macroinvertebrates in river ecosystems* (Bologna, Italy) for the implementation of the STAR_ICM index in Italy.

At the beginning of 2014 I visited Plymouth University (School of Biological Sciences, Marine Biology & Ecology Research Centre), where I attended seminars with internationally recognized speakers in the field of Ecology. Here, I developed an important chapter of this thesis thank to my directors and the collaboration of Dr. Bilton and formed several ideas for future publications.

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Resumen

Esta tesis aborda diferentes retos relacionados con la conservación de la biodiversidad acuática en la península ibérica utilizando los macroinvertebrados acuáticos como sistema modelo. Esta información pretende contribuir a un mejor conocimiento de los factores que determinan y amenazan la biodiversidad de macroinvertebrados acuáticos así como proporcionar herramientas útiles para su conservación. Los Capítulos 1 y 2 se centran en la búsqueda y evaluación de posibles sustitutos o indicadores de biodiversidad en ecosistemas acuáticos, mientras que el capítulo 3 está dedicado a testar la eficacia de las redes de áreas protegidas en la representación de la biodiversidad de macroinvertebrados. En el capítulo 4, a partir de nuevos registros de un insecto acuático invasor detectado a lo largo de la península ibérica, se proporcionan mapas globales de distribución potencial considerando que la prevención de invasiones biológicas es la estrategia más efectiva para evitar problemas de conservación y nuevas expansiones.

El Capítulo 1 revela que los parques nacionales de montaña en España contienen un porcentaje importante de la biodiversidad ibérica con respecto a las familias de macroinvertebrados. La riqueza de familias de Coleoptera muestra la correlación más alta con los otros grupos taxonómicos y puede ser propuesta como un sustituto/indicador de la biodiversidad de macroinvertebrados en las zonas montañosas bien conservadas. Tal indicador taxonómico podría complementarse con el uso de la riqueza de familias de Odonata en ambientes estancados.

El Capítulo 2 presenta una evaluación del funcionamiento de un grupo carismático (aves acuáticas) como sustituto de la biodiversidad de macroinvertebrados en humedales. Los resultados muestran una concordancia limitada entre la composición de la comunidad de aves acuáticas y macroinvertebrados, así como correlación no significativa o negativa entre las métricas de riqueza taxonómica. Ambos grupos muestran diferentes respuestas a gradientes ambientales, y por lo tanto las aves acuáticas se pueden considerar malos indicadores de la biodiversidad acuática en estos ecosistemas.

El Capítulo 3 proporciona el primer intento de evaluar la efectividad de las redes de áreas protegidas en la representación de los componentes alfa, beta y gamma de la diversidad tanto taxonómica como funcional de macroinvertebrados

a diferentes escalas espaciales. Los resultados muestran un funcionamiento de las áreas protegidas marcadamente diferente en el mantenimiento de la diversidad taxonómica y funcional de macroinvertebrados, y apuntan a un sesgo en la representación de determinados hábitats acuáticos dentro de las redes de reservas. Tal desajuste llama a la prudencia en cuanto al uso de cualquier componente de una diversidad como un sustituto para los demás, y hace hincapié en la importancia de adoptar un enfoque integral para la conservación de la biodiversidad en los ecosistemas acuáticos.

El último capítulo se centra en *Trichocorixa verticalis verticalis* (Corixidae, Hemiptera), una de las pocas especies de insectos acuáticos consideradas como exóticas, y para la que se han detectado nuevos registros de poblaciones importantes en numerosos humedales Ramsar en Andalucía (suroeste de España). Los mapas predictivos de distribución potencial obtenidos sugieren que este corixido puede extenderse mucho más allá de su área de distribución actual y encontrar condiciones habitables en áreas templadas a lo largo de una amplia gama de latitudes. Además, al considerar un escenario climático futuro, el área de idoneidad muestra cambios limitados en comparación con la distribución potencial actual. Los resultados permiten la detección de zonas de contacto entre áreas actualmente colonizadas y áreas potenciales de invasión, así como zonas con alto nivel de idoneidad que coinciden con áreas reconocidas como puntos calientes de biodiversidad a nivel mundial.

La combinación de estos resultados entronca con algunos de los retos claves para la conservación de la biodiversidad de macroinvertebrados acuáticos (indicadores de biodiversidad, eficacia de las áreas protegidas y potenciales amenazas a la biodiversidad) y proporciona información útil acerca de temas claves para gestores y biólogos de la conservación.

Introducción General

Ecosistemas acuáticos continentales: amenazados pero a menudo olvidados

Los ecosistemas acuáticos continentales son escasos comparado con otros ecosistemas y pueden ser considerados como islas en un mar de agua salada y ecosistemas terrestres. Sin embargo existe una estrecha relación entre las aguas dulces (p. ej., las condiciones del hábitat acuático) y las áreas adyacentes ya que muchas de sus características proceden de su cuenca vertiente y de las actividades que allí se desarrollan (Strayer, 2006).

A pesar de ocupar solo 0,8% de las superficie terrestres (Dudgeon et al., 2006) estos ecosistemas son capaces de albergar alrededor de 125.000 especies de animales de aguas dulce (Strayer & Dudgeon, 2010). Por tanto, estos ecosistemas pueden considerarse objetivamente como “puntos calientes” de biodiversidad (Strayer & Dudgeon, 2010) a pesar de estar sufriendo al mismo tiempo numerosas amenazas que los convierten en unos de los ambientes más amenazados a nivel global (Revenga et al., 2005; Strayer & Dudgeon, 2010). En estos ambientes se han detectados mayores descensos de biodiversidad comparados con otros ecosistemas terrestres (Sala et al., 2000) y todo eso se hace especialmente alarmante en el contexto de cambio global con posibles efectos e impactos a diferentes niveles de organización (Woodward et al., 2010).

Las principales amenazas que afectan globalmente a los ecosistemas acuáticos continentales pueden ser resumidas en: sobreexplotación de los recursos hídricos, contaminación, alteración de los hábitats, modificaciones hidrológicas e invasión por especies exóticas (Dudgeon et al., 2006). Por lo tanto numerosos autores han observado y destacado la urgente necesidad de mayor protección, investigación y concienciación pública para estos ecosistemas amenazados y las especies que albergan (p. ej., Kingsford & Neville, 2005; Dudgeon et al., 2006; Strayer, 2006; Suski & Cooke, 2007; Moilanen et al., 2008; Monroe et al., 2009). No obstante, y a pesar de ello, los estudios relacionados con la conservación de los ambientes acuáticos son todavía limitados en cantidad y calidad, sobre todo en comparación con otros ambientes y en términos de aplicación de programas sistemáticos de conservación (Abell, 2002). Los esfuerzos para la conservación de la biodiversidad en ambientes acuáticos parecen limitados debido a la importante

falta de información disponible de numerosas áreas geográficas, tipos de ambientes o grupos taxonómicos (Dudgeon et al., 2006; Strayer, 2006).

En este contexto, llama la atención el caso de los grupos taxonómicos no carismáticos, como los invertebrados, que a pesar de desempeñar un papel clave en los procesos ecosistémicos (Covich et al., 1999) y constituir una inmensa proporción de la biodiversidad animal (Ramos et al., 2001), son todavía poco estudiados y escasamente protegidos comparado con otros taxones más atractivos para la gente en general (Strayer, 2006; Martín-López et al., 2009; Cardoso et al., 2011). Los invertebrados dominan entre los organismos multicelular en términos de riqueza, abundancia y, a menudo, biomasa (Cardoso et al., 2011); y de forma similar los macroinvertebratos acuáticos (invertebrados de tamaño superior a 1 mm) representan uno de los componentes más importante en los medio acuáticos continentales. Agrupan a un amplio grupo de organismos de diferentes phyla: principalmente artrópodos (insectos, arañas, crustáceos), anélidos y moluscos. Entre ellos, los insectos representan el grupo más numeroso, donde Odonatos, Efemerópteros, Plecópteros, Tricópteros, Coleópteros, Dípteros, Hemípteros suelen estar entre los principales habitantes de los ambiente acuáticos continentales (Tierno de Figueroa et al., 2013). Destacan Coleópteros y Hemípteros por ser los únicos ordenes con la mayoría de los ejemplares adultos acuáticos y capaces de colonizar prácticamente cualquier ambiente dulceacuícola o salino, desde pequeñas pozas y lagunas hasta arroyos, ríos y canales artificiales (Jäch & Balke, 2008; Tierno de Figueroa et al., 2013; Millán et al., en prensa).

Además, los coleópteros acuáticos representan un elevado, y funcionalmente diverso, porcentaje de la biodiversidad acuáticas en general (Jäch & Balke, 2008) y constituyen uno de los grupos más diversos y conocidos desde el punto de vista sistemático y biogeográfico en el contexto de la península ibérica (Ribera et al., 1998; Ribera, 2000; Millán et al., en prensa). Una extensa literatura científica se ha centrado en la ecología de los macroinvertebrados acuáticos explorando especialmente su uso como indicadores biológicos para monitorear el estado de la calidad de las aguas en ambientes continentales (p. ej., Rosenberg & Resh, 1993; Bonada et al., 2006; Menetrey et al., 2011). Sin embargo, menor atención e interés han encontrado las temáticas relacionadas con la conservación de la biodiversidad de macroinvertebrados, a pesar del papel clave que

desempeñan en el funcionamiento y dinámicas de los ecosistemas acuáticos (p. ej., flujos de energía y recirculación de nutrientes, Merritt et al., 1984; Merritt & Lawson, 1992; Covich et al., 1999; Fenoglio et al., 2005) y del enorme porcentaje de biodiversidad animal que representan en términos filogenéticos, taxonómicos y funcionales en estos medios. En este contexto, se deben abordar importantes retos para llenar las lagunas aún presentes en la conservación de los ecosistemas de agua dulce y, sobre todo, de la biodiversidad de macroinvertebrados acuáticos.

La planificación sistemática de la conservación (Margules & Pressey, 2000; Groves et al., 2002) es un proceso orientado a identificar redes de áreas prioritarias que aseguren la representación y la persistencia, a largo plazo, de la biodiversidad. Este enfoque de planificación tiene varias características distintivas. Por ejemplo, requiere la elección clara de los elementos que serán utilizados como sustitutos de biodiversidad global en el proceso de planificación. También reconoce la importancia de determinar el grado en que se han cumplido los objetivos de conservación de las reservas actuales (por ejemplo mediante la revisión de las redes de áreas protegidas existentes) como paso previo para localizar y diseñar nuevas reservas para complementar las ya presentes. Además, adopta objetivos explícitos y mecanismos para el mantenimiento de las condiciones dentro de las reservas al objeto de fomentar la persistencia de los elementos naturales clave. Al mismo tiempo, una mejor comprensión de los actuales y futuros patrones de distribución de las amenazas resulta fundamental para ayudar a centrar los recursos limitados en aquellas áreas de conservación y elementos naturales bajo mayor riesgo (Margules & Pressey, 2000). Si bien la planificación sistemática de la conservación es ahora una práctica bastante común en todo el mundo en ecosistemas terrestres o marinos (Watson et al., 2011), su uso en sistemas de aguas continentales sigue siendo escasa (Moilanen et al., 2008; Hermoso et al., 2014), especialmente con relación a la biodiversidad de macroinvertebrados (ver Sánchez-Fernández et al., 2004, 2008; Abellán et al., 2005, 2007). En este sentido, investigaciones sobre indicadores eficaces de biodiversidad en ambientes acuáticos continentales, así como sobre la eficacia de las áreas protegidas existentes en la preservación de la biodiversidad acuática, junto con la evaluación de amenazas potencialmente nuevas (ej. las especies invasoras y el cambio climático) representan sin duda alguna unos de los retos más

importantes para la conservación de los macroinvertebrados acuáticos y sus hábitats.

Indicadores de biodiversidad acuática: necesidades y finalidad

La evaluación y el monitoreo de la biodiversidad es una tarea crucial para la conservación y restauración de los ecosistemas de aguas continentales. Sin embargo, la evaluación de la biodiversidad presenta dificultades asociadas con el tiempo y los recursos financieros limitados y, a menudo, requiere un alto grado de especialización, sobre todo para determinados grupos de invertebrados. Un enfoque común para resolver este problema ha sido la utilización de indicadores de biodiversidad, también conocidos como subrogados o sustitutos de biodiversidad. Entre tales sustitutos, han sido sugeridos diferentes enfoques, como la diversidad ambiental (Faith, 2003), niveles taxonómicos superiores (Balmford et al., 2000) o taxones indicadores (Pawar et al., 2007). Los taxones indicadores de biodiversidad son grupos taxonómicamente y ecológicamente bien conocidos, fácilmente detectables y presentes en diferentes ambientes que demuestran tener una fuerte relación con las medidas de biodiversidad de otros grupos taxonómicos (Rodrigues & Brooks 2007). Por lo tanto, un indicador de biodiversidad debe definirse como un grupo de taxones (especies, género o nivel superior) cuya diversidad refleja alguna medida de la diversidad de otros grupos taxonómicos en un hábitat (Caro & O'Doherty, 1999).

Mientras que los macroinvertebrados acuáticos se han utilizado ampliamente en la vigilancia biológica como indicadores ambientales o ecológicos, especialmente para ambientes lóticos (Rosenberg & Resh, 1993; Bonada et al., 2006), se ha prestado menos atención al desarrollo de taxones indicadores para la evaluación de la biodiversidad de macroinvertebrados (pero ver Bilton et al., 2006; Sánchez-Fernández et al., 2006; Heino, 2010 para una revisión). Por lo tanto, existe la necesidad de evaluar posibles indicadores de la biodiversidad de macroinvertebrados para obtener herramientas nuevas y útiles para el monitoreo rápido y económico de la biodiversidad, evaluar las reservas existentes y seleccionar nuevas áreas con alto valor de biodiversidad acuática. Puesto que la riqueza taxonómica es probablemente la variable principal que se utiliza para

describir la diversidad de una comunidad (Gaston, 1996), y la maximización de la riqueza de especies es a menudo un objetivo explícito o implícito de los estudios y los esfuerzos de conservación (May, 1988; Rodrigues et al., 2004), numerosas evaluaciones de los indicadores de biodiversidad se centran en los patrones de riqueza (p. ej., Fleishman et al., 2005; Velghe & Gregory-Aleros, 2013). Sin embargo, la composición de la comunidad representa otra medida relevante de la diversidad de especies en el contexto de las estrategias de conservación (Su et al., 2004; Bilton et al., 2006) que, sin embargo, rara vez ha sido utilizado en las evaluaciones de la congruencia en los patrones de diversidad entre diferentes taxones.

Además, resulta importante destacar que son muy raros los estudios sobre la congruencia entre patrones de biodiversidad de macroinvertebrados acuáticos y vertebrados distintos de peces. En biología de la conservación, los taxones carismáticos y atractivos para el público en general, como las aves, representan un ejemplo común de taxones utilizados como sustitutos para monitorear o medir la biodiversidad. Esto se debe principalmente a la amplia disponibilidad de datos pertinentes sobre su distribución y estado y su amplio atractivo popular (Gregory, 2003, 2006; Eglington et al., 2012; Kajtoch et al., 2014). Las aves son por tanto objeto de muchas iniciativas internacionales de conservación como la red mundial de Áreas Importantes para las Aves (IBA), y las Zonas de Especial Protección para las Aves (“Directiva Aves” 79/409/CE y 2009/147/CE) en Europa. En el caso de los ecosistemas acuáticos, las aves tienen un papel estratégico para la designación de Humedales de Importancia Internacional bajo la Convención Ramsar, un tratado intergubernamental a nivel mundial para la conservación y el uso sostenible de los humedales y sus recursos (Ramsar Bureau, 2000). A pesar de que las aves desempeñan un papel funcional clave en muchos ambientes acuáticos, con una influencia en las estructuras de las comunidades de invertebrados y macrófitos (Green & Elmberg, 2014), su fiabilidad como sustituto de la biodiversidad de macroinvertebrados sigue siendo extremadamente poco estudiada y necesita más investigación.

En definitiva, investigaciones específicas sobre los sustitutos de biodiversidad en ambientes de agua continentales representan uno de los principales retos en la conservación de estos medios (Nel et al., 2009) para lograr

una mejor comprensión de la biodiversidad de macroinvertebrados acuáticos, obtener indicadores de zonas bien conservadas, evaluar la eficacia de indicadores tradicionales (carismáticos) y explorar los patrones de biodiversidad en términos no sólo de la riqueza taxonómica, sino teniendo en cuenta también la información y congruencia en la composición de especies entre diferentes grupos taxonómicos.

Ecosistemas acuáticos en zonas protegidas: integrando diversidad biológica y conservación

Las redes de áreas protegidas representan uno de los pilares de las políticas de conservación en todo el mundo y juegan un papel clave en la protección de la biodiversidad (Chape et al., 2005). La superficie total que se beneficia de una protección jurídica ha ido en aumento en todo el mundo (Jenkins & Joppa, 2009), y entre el 10,1% y el 15,5% de la superficie terrestre se considera bajo alguna forma de protección (Soutullo, 2010). Sin embargo, las redes de reservas existentes en todo el mundo parecen contener una muestra sesgada de la biodiversidad, a menudo la de lugares remotos u otras áreas consideradas menos atractivas para las actividades comerciales (Margules & Pressey, 2000). La protección de las áreas de mayor altitud son ejemplos comunes de áreas protegidas debido a la falta de interés económico y actividades humanas en el zona (Joppa & Pfaff, 2009). Sin embargo, las redes de áreas protegidas deberían representar una red de ecosistemas de interés para la conservación en paralelo con otros intereses.

No obstante, la definición de áreas naturales protegidas es sólo el inicio de la tarea (Lovejoy, 2006) y determinar su efectividad en la representación y mantenimiento de todos los elementos de la biodiversidad es una prioridad de investigación en biología de la conservación (Bertzky et al., 2012) y la cuestión principal demandada por los gestores de áreas protegidas en todo el mundo (Parrish et al., 2003). Por lo tanto, la revisión de las áreas de conservación existentes es una de las principales etapas de la planificación sistemática de la conservación (Margules & Pressey 2000), ya que constituye la base para identificar los elementos de la biodiversidad que no están suficientemente representados en las áreas protegidas existentes y para determinar cómo los esfuerzos de conservación pueden mejorar (Groves et al., 2002).

La biota de muchas áreas protegidas y reservas naturales de todo el mundo han sido a menudo inventariada de manera escasa, en parte debido a la percepción de que estas áreas ya están "protegidas" y que los fondos del monitoreo se gastarían mejor en áreas que aún no se ha designado para la conservación (Groves et al., 2002). En este contexto, la eficacia a nivel ecológico de estas áreas, tanto en términos de la representación y como del mantenimiento de componentes y características claves de su biodiversidad permanece escasamente conocidos (Gastón et al., 2008a).

Por otra parte, las estrategias de conservación parecen tener importante sesgos hacia grupos de organismos terrestres o determinados grupos taxonómicos específicos (Martín-López et al., 2009). Ya que las áreas protegidas planeadas o propuestas específicamente para las aguas continentales son escasas (p. ej., Abell et al., 2007; Suski & Cooke, 2007), estos hábitats son protegidos a menudo sólo accidentalmente como parte de las reservas terrestres. Sin embargo, las redes de reservas terrestres podrían tener importantes problemas a la hora de representar adecuadamente la biota acuática (Suski & Cooke, 2007; Herbert et al., 2010). En este sentido, la efectividad de las reservas en general, en la representación de los diferentes elementos de la biodiversidad acuática es todavía poco conocida.

Del mismo modo, es probable que los grupos que han sido el foco de la mayoría de los esfuerzos de conservación (por ejemplo, los vertebrados y las plantas) sean pobres indicadores de los patrones de diversidad de muchos grupos de organismos acuático (ver Darwall et al., 2011), y además, se conoce poco acerca la idoneidad de las áreas protegidas en la representación de taxones que no suelen ser centro de medidas específicas de conservación, como los macroinvertebrados acuáticos. Resulta importante explorar este vacío para obtener un mejor entendimiento de la eficacia de las redes de áreas protegidas. Al mismo tiempo, investigaciones multidisciplinarias y la necesidad de integrar ecología y biología de la conservación constituyen una prioridad para el mantenimiento y el mejor conocimiento de la biodiversidad acuática (Strayer & Dudgeon, 2010; Geist et al., 2011).

Además, mientras que los esfuerzos de conservación se han centrado tradicionalmente en la protección de áreas que garanticen una representación adecuada de la diversidad taxonómica, en términos de riqueza en especies, en la

actualidad se reconoce ampliamente la necesidad de que las áreas protegidas preserven todos los componentes de la biodiversidad, incluyendo los procesos ecológicos y evolutivos que generan y mantienen la biodiversidad, así como y los bienes y servicios que los humanos obtienen de la naturaleza (Mulongoy & Chape, 2004). La diversidad funcional, que refleja la diversidad de rasgos biológicos, fisiológicos y ecológicos dentro de las comunidades biológicas (Petchey & Gaston, 2006), ha sido destacada como una faceta importante de la diversidad para asegurar la provisión de bienes y servicios (Díaz et al., 2006), y ha demostrado ser un factor clave de los procesos de los ecosistemas (Mokany et al., 2008), esencial en la comprensión de las relaciones entre la diversidad biológica, el funcionamiento del ecosistema y las limitaciones ambientales (Mouchet et al., 2010). En este marco, la incorporación de información funcional en las estrategias de conservación permite ir más allá de la representación del simple número de especies. Además, redes de áreas protegidas eficientes en un mundo que se enfrenta a cambios globales también deben basarse en el mantenimiento de las especies y los procesos funcionales a diferentes escalas espaciales (Gering et al., 2003; Brooks et al., 2006; Devictor et al., 2010). Teniendo en cuenta que tanto la diversidad taxonómica como funcional se pueden descomponer en diversidad local, entre-sitios y regional (llamada alfa, beta y gamma, respectivamente; Whittaker, 1972), estos componentes deberían también ser evaluados para obtener una mejor y más completa comprensión de la eficiencia de estas zonas protegidas.

Especies invasoras: una nueva amenaza para la biodiversidad de macroinvertebrados

En el contexto de la crisis de la biodiversidad, la introducción y establecimiento de especies invasoras en nuevas áreas es reconocido como uno de los impactos humanos más importantes en una amplia gama de ecosistemas (McKinney & Lockwood, 1999; Clavero & García-Berthou, 2005). Las invasiones biológicas representan una preocupación global y las áreas protegidas, a pesar de sus condiciones ambientales privilegiadas, no están exentas de este problema (Usher, 1988; Lovejoy, 2006). Por ejemplo, Lonsdale (1999) estudiando

numerosos sitios protegidos en todo el mundo encontró una relación positiva entre el número de visitantes en las reservas y el número de plantas invasoras.

Esta amenaza es un problema especialmente preocupante en los ecosistemas acuáticos (Dudgeon et al., 2006) donde las especies invasoras pueden presentar impactos diversificados sobre la biodiversidad y el funcionamiento de los ecosistemas (Scott et al., 2012; Gallardo et al., 2013). Aquí, las especies invasoras acuáticas son de creciente preocupación para los conservacionistas y gestores ambientales, debido a sus altos costos de erradicación, lo que exige políticas de gestión eficaces y específicas (Gallardo et al., 2013). En estos ecosistemas amenazados, la necesidad de comprender mejor, prevenir e incluso predecir futuras invasiones (también en el contexto del cambio climático) parece ser decisivo y representa un tema de investigación innovador, especialmente en el caso de los insectos acuáticos. Las especies invasoras representan un subconjunto no aleatorio de la biota acuática y, aunque los insectos dominan los ecosistemas de aguas continentales a nivel mundial, estos aparecen muy poco representados en las listas de especies invasoras (Statzner et al., 2008; Karataev et al., 2009; Strayer, 2010). Debido a esta rareza, es muy escaso el conocimiento científico sobre los insectos acuáticos invasores, sus efectos sobre la biodiversidad y su potencial de distribución. Esto es todavía más cierto para la mayoría de especies de invertebrados de menor importancia económica y social (Kenis et al., 2009).

Teniendo en cuenta que la prevención de las invasiones biológicas ha resultado ser la manera más efectiva, en términos de gastos económicos, para evitar la pérdida de biodiversidad y problemas en conservación de la naturaleza (Bax et al., 2001), uno de los retos en la biología de la conservación es comprender los límites del nicho fundamental de las especies invasoras, ya que esta información permite mapear el conjunto de los lugares donde las especies pueden habitar (es decir, su distribución potencial). La identificación de áreas con condiciones ambientales adecuadas para las especies invasoras puede ofrecer importantes oportunidades para prevenir o frenar las invasiones (Guisan & Thuiller, 2005; Jeschke & Strayer, 2008).

Recientemente, un hemípteros invasor (*Trichocorixa verticalis verticalis*, Corixidae) se detectó en diversos ecosistemas acuáticos (inclusos humedales protegidos) a lo largo de Marruecos, Portugal y España, convirtiendo esta especie

en una de las prácticamente únicas especies de insectos exclusivamente acuáticos (es decir, con todas sus etapas del ciclo de vida acuáticas) que puede ser considerado como especie invasora. El término invasor es aplicable en este caso porque la especie se ha movido fuera de su área de distribución natural y ha conseguido establecerse y dispersarse en la nueva región (Rabitsch, 2008; Strayer, 2010). Por otra parte, este corixido eurihalino representa el hemíptero dominante en muchos de los sitios invadidos donde se encontró y, cuando consigue reproducirse, compite agresivamente con las otras especies de corixidos nativas (Rodríguez-Pérez et al., 2009), presentando un carácter invasivo actualmente bajo investigación, especialmente a lo largo de la península ibérica (Carbonell et al., 2012; Coccia et al., 2013).

Además, los invertebrados invasores pueden superar algunas de las estrategias más comunes para limitar la propagación de especies (por ejemplo, los controles fronterizos) gracias a numerosas formas naturales o artificial de difusión (a escala local e incluso a nivel global), a lo que hay que añadir, además, que las especies con amplia tolerancia a la salinidad pueden presentar importantes ventajas (Ricciardi, 2006). Teniendo en cuenta que Europa occidental ha sido destacada como zona sensible a las invasiones biológicas de invertebrados (Devin et al., 2005; Devin & Beisel, 2008), los registros recientes de *Trichocorixa verticalis verticalis* a lo largo de la península ibérica deben tomarse con la debida consideración por los gestores ambientales y la comunidad científica. En este contexto, los programas de control de especies invasoras deberían centrarse en las zonas de mayor biodiversidad y riesgo de invasiones (Saunders et al., 2002). Por lo tanto, las investigaciones sobre la distribución potencial de estas especies representan una herramienta de vanguardia para entender mejor las invasiones en medios acuáticos y hacer posible el logro de importantes recomendaciones para la prevención de futuras propagación al detectar posibles zonas de contacto entre las áreas actualmente colonizadas y áreas potenciales con alto nivel de idoneidad para la invasión.

El marco espacial: los ecosistemas de aguas continentales y las redes de áreas protegidas en la península ibérica

La pérdida de biodiversidad acuática preocupa especialmente en la cuenca Mediterránea, área considerada como uno de los puntos calientes de biodiversidad en la Tierra para las especies animales y vegetales en general (Myers et al., 2000; Cuttelod et al., 2008), y particularmente para los organismos de agua dulce (Tierno de Figueroa et al., 2013). Sin embargo, debido a la fuerte influencia antropogénica durante siglos (Blondel & Aronson, 1999) y al actual proceso de cambio global, la biodiversidad acuática mediterránea se encuentra sometida a fuertes presiones (Filipe et al., 2012; Bruno et al., 2014).

La península ibérica, principalmente constituida por los territorios continentales de Portugal y España, representa una de las regiones europeas más ricas en términos de especies (Williams et al., 2000). Situada en la parte occidental del “hotspot” mediterráneo, su extensión roza los 600.000km², y se caracteriza por una gran variedad de ambientes, relieves, climas y tipos de suelo que han dado lugar a una amplia gama de ecosistemas acuáticos, algunos de ellos extremadamente raros en un contexto europeo (Millán et al., 2011). Esta gran diversidad de ambientes abarca desde los ecosistemas acuáticos de montaña (sean lóticos, lénticos o mixtos) a los humedales de llanura o costero, con una amplia variedad de conductividad del agua (desde agua dulce hasta humedales salinos litorales) y de usos del suelo en las cuencas vertientes. Aquí los ecosistemas acuáticos no están exentos de importantes amenazas que van de la alteración del hábitat a la presencia de especies invasoras (Prenda et al., 2006).

En la península ibérica la conservación de la naturaleza comienza a principios del siglo pasado. Sin embargo, a pesar de que la red de parques nacionales españoles se inició en 1918 con el objetivo general de preservar la naturaleza, es solo al final del siglo pasado cuando las áreas protegidas alcanzan un mayor nivel en términos de valores naturales y extensión (Morillo & Gómez-Campo, 2000). En Portugal, la estrategia de conservación comenzó bastante tarde, básicamente durante la década de los años 70 con la definición de las primeras áreas protegidas y una ulterior intensificación en la creación de reservas durante la última parte del siglo pasado.

Las áreas protegidas designadas a nivel nacional (es decir, las incluidas en la legislación propia española y portuguesa) representan el núcleo de las políticas nacionales y regionales de conservación, e incluyen Parques, Reservas Naturales, Monumentos Naturales, Áreas Protegidas Marinas, Paisajes Protegidos, así como diferentes tipos de espacios protegidos locales. Sin embargo, además de las áreas protegidas nacionales, el número y la extensión de los espacios protegidos en la península ha crecido en las últimas décadas como resultado de la aplicación de la Red Natura 2000. Esta red representa una herramienta clave para la conservación de la biodiversidad a escala europea y tiene por objeto garantizar la supervivencia a largo plazo de las especies y hábitats más valiosos y amenazados de Europa. La Red Natura 2000 incluye zonas especiales de conservación (LIC) designadas en virtud de la Directiva Hábitats (92/43/CEE), y Zonas de Especial Protección para las Aves (ZEPA) que se designan bajo la Directiva Aves (79/409/CEE). Como resultado de esta actuación, la Unión Europea (UE) es una de las regiones del mundo con mayor número de zonas protegidas (Araújo et al., 2011; Pyšek et al., 2013). Las áreas protegidas en la UE cubren el 15,3% de la superficie total (661.692 km²), o incluso el 25% (1.081.195 km²) teniendo en cuenta los sitios implementados como parte la red Natura 2000 (Programa de Redes Natura 2000, 2007; Gastón et al., 2008b; Pyšek et al., 2013). En el caso de la península ibérica, un porcentaje importante de su territorio (hasta el 28% en el caso de España y el 22% para Portugal) se puede considerar actualmente bajo algún nivel de protección (regionales, nacionales o europeos; Europarc-España, 2010). Sin embargo, la efectividad tanto del sistema nacional de áreas protegidas, como de la red Natura2000 en la representación de la biodiversidad acuática continental Ibérica se ha evaluado en muy pocos estudios y de forma incompleta (por ejemplo, Abellán et al., 2007; Sánchez-Fernández et al., 2008; Abellán et al., 2013). Como resultado, la eficacia de las diferentes redes (tanto nacional como europea) en el contexto de la conservación de los diferentes componentes de la biodiversidad acuática y de taxones no carismáticos en general, sigue siendo poco clara y necesita ser investigada.

Objetivos y estructura de la tesis

El objetivo principal de esta tesis es abordar diferentes retos relacionados con la conservación de la biodiversidad acuática en la península ibérica utilizando los macroinvertebrados acuáticos como sistema modelo. Esta información tiene como objeto contribuir a un mejor conocimiento de los factores determinantes que afectan y amenazan la biodiversidad de macroinvertebrados acuáticos y sus hábitats así como proporcionar información útil para su gestión y conservación. Más concretamente, esta tesis tiene como objetivos:

- Evaluar y testar distintos grupos taxonómicos como indicadores de la biodiversidad de macroinvertebrados acuáticos en diferentes ambientes de áreas protegidas (*Capítulo 1*);
- Investigar cuáles son las variables ambientales asociadas con la composición y riqueza de macroinvertebrados en las áreas protegidas de montaña (*Capítulo 1*).
- Evaluar el papel de un grupo carismático (aves acuáticas) como posible indicador para la predicción de la biodiversidad de macroinvertebrados acuáticos en humedales (*Capítulo 2*).
- Determinar qué variables ambientales están asociadas con los patrones de biodiversidad de aves acuáticas y macroinvertebrados, con el propósito de identificar factores clave que expliquen la potencial discordancia en estos patrones (*Capítulo 2*).
- Evaluar la eficacia de las redes de áreas protegidas no designadas específicamente para los ecosistemas acuáticos en la representación de la biodiversidad acuática utilizando los coleópteros acuáticos como indicadores (*Capítulo 3*).

- Explorar el comportamiento de medidas de diversidad taxonómica y funcional a escala local (alfa diversidad), regional (gamma diversidad) y entre sitios (beta diversidad), considerando diferentes escalas espaciales, en la evaluación del funcionamiento de las áreas protegidas (*Capítulo 3*).
- Estimar la distribución potencial global de *Trichocorixa verticalis verticalis* (Hemiptera: Corixidae), uno de los pocos insectos acuáticos invasores conocidos en el todo el mundo, teniendo en cuenta las condiciones climáticas actuales y futuras (*Capítulo 4*).
- Detectar posibles nuevas áreas de invasión y averiguar zonas de contacto entre las áreas actualmente colonizadas y las que tienen un elevado potencial de invasión (*Capítulo 4*).

Esta tesis se estructura en cuatro capítulos, que corresponden a cuatro artículos científicos. Los capítulos 1, 2 y 4 ya se han publicado en revistas internacionales indexadas en el SCI, mientras que el capítulo 3 se ha enviado también a una revista del SCI y se encuentra en revisión. Los cuatro artículos en los que se basan esta tesis son:

- Capítulo 1** Guareschi S., Gutiérrez-Canovas C., Picazo F., Sánchez-Fernández D., Abellán P., Velasco J., Millán A. (2012). Aquatic macroinvertebrate biodiversity: patterns and surrogates in mountainous Spanish national parks. *Aquatic Conservation: Marine and Freshwater Ecosystems* 22: 598-615.
- Capítulo 2** Guareschi S., Abellán P., Laini A., Green A.J., Sánchez-Zapata J.A., Velasco J., Millán A. (2014). Cross-taxon congruence in wetlands: assessing the role of waterbirds as surrogates of macroinvertebrate biodiversity in Mediterranean Ramsar sites. *Ecological indicators* 49: 204–215.

Capítulo 3 Guareschi S., Bilton D., Velasco J., Millán A., Abellán P. How well do protected area networks support taxonomic and functional diversity in non-target taxa? The case of Iberian freshwaters. *Biological Conservation*, en revision.

Capítulo 4 Guareschi S., Coccia C., Sánchez-Fernández D., Carbonell J.A., Velasco J., Boyero L., Green A.J., Millán A. (2013). How far could the alien boatman *Trichocorixa verticalis verticalis* spread? Worldwide estimation of its current and future potential distribution. *PLoS ONE* 8(3): e59757.

Resúmenes de los Capítulos

Capítulo 1. Biodiversidad de macroinvertebrados acuáticos: patrones e indicadores en los Parques Nacionales de montaña españoles

En España, los Parques Nacionales representan el pilar de las políticas de conservación y tratan de proteger los ecosistemas naturales más representativos. Sin embargo, los estudios sobre la ecología y la conservación de la biodiversidad acuática en las áreas protegidas son todavía escasos. Este estudio tuvo como objetivo elaborar un inventario de las familias de macroinvertebrados que habitan en los ecosistemas acuáticos de cada Parque Nacional español montañoso (Sierra Nevada, Cabañeros, Ordesa, Picos de Europa, Aigüestortes y Monfragüe). Los resultados se utilizaron para responder a dos preguntas: (i) ¿Qué variables ambientales están relacionados con la composición y riqueza de macroinvertebrados en estos ecosistemas protegidos? (ii) ¿Qué taxón o grupo de taxones podría actuar como indicador de biodiversidad? El muestreo se llevó a cabo en 81 estaciones a lo largo de los seis Parques Nacionales durante los veranos de 2008 y 2010.

Picos de Europa y Cabañeros resultaron los Parques Nacionales con la mayor riqueza taxonómica. En conjunto, los seis parques incorporan al 66,2% de los taxones representados en la península ibérica. Análisis multivariantes mostraron que la altitud máxima y la presencia de hábitats lóticos fueron las variables más importantes relacionadas con la composición de la comunidad. El mejor modelo de riqueza contó con la presencia de hábitat lótico, junto con el porcentaje de cuenca vertiente ocupada por agricultura de secano y una litología silíceo.

La selección de cuerpos de agua lóticos y lénticos a diferentes altitudes parece ofrece la mejor forma de representar la diversidad de macroinvertebrados en estos ambientes protegidos. La riqueza de familias de Coleoptera se puede utilizar como indicador de la biodiversidad de macroinvertebrados en áreas protegidas montañosas ibéricas ya que mostraron la correlación más alta con los otros grupos taxonómicos y los valores de riqueza restantes. Dicho indicador

podría complementarse con el uso de la riqueza de familias del orden Odonata en el caso de ambientes lenticos.

La eficacia de Coleoptera y Odonata como indicadores de biodiversidad necesita más estudios y debería testarse también a una escala geográfica más amplia, así como se debería integrar con otros conceptos (p. ej., la composición de la comunidad) para evaluar el papel de esta red en la protección de especies con interés de conservación.

Capítulo 2. Congruencia entre taxones en humedales: evaluando el papel de las aves acuáticas como indicadoras de la biodiversidad de macroinvertebrados en humedales Ramsar mediterráneos

Los humedales son uno de los hábitats más amenazados a nivel mundial y las especies que albergan se encuentran entre los taxones con mayor peligro de extinción. El seguimiento de la biodiversidad de los humedales es vital para la conservación, la restauración y la gestión, y con frecuencia se basa en el uso de indicadores. Las aves acuáticas son comúnmente utilizadas como especies bandera y objeto de las principales iniciativas de conservación. Por lo tanto, es importante evaluar el grado en que las aves acuáticas representan la biodiversidad de los humedales en general y su eficacia como taxones indicadores.

Se exploró la relación entre la composición de la comunidad y la riqueza de especies de aves y macroinvertebrados acuáticos en 36 humedales Ramsar en el sur de España para evaluar si las aves acuáticas pueden ser buenos indicadores de otros grupos taxonómicos. En concreto, el estudio tuvo como objetivo: i) testar la congruencia de los patrones de composición y riqueza entre las aves acuáticas y los macroinvertebrados acuáticos; y ii) investigar las variables ambientales asociadas con los patrones de biodiversidad de aves acuáticas y macroinvertebrados, con el propósito de identificar los factores clave capaces de explicar la potencial discordancia en estos patrones.

Los resultados demostraron una concordancia limitada entre los patrones de diversidad de ambos grupos taxonómicos que pueden estar relacionados con su respuesta diferente a los gradientes ambientales. La composición de la comunidad de aves acuáticas parece estar más afectada por las variables climáticas y la extensión de la superficie del agua, mientras que la conductividad fue el factor más importante en las comunidades de macroinvertebrados. Además, se encontró una relación inversa o falta de relación en sus patrones de riqueza, de manera que los humedales con una mayor riqueza de aves acuáticas mostraron significativamente menor riqueza en especies de hemípteros y familias de macroinvertebrados, y ninguna relación con los patrones de coleópteros. Además, los modelos GLM mostraron que, en general, diferentes variables ambientales están relacionadas con los patrones de riqueza de los distintos grupos taxonómicos.

Dada la importancia de la Convención Ramsar para la conservación de una red internacional de humedales, los resultados ponen de relieve el potencial limitado de las aves acuáticas como indicadores de la biodiversidad acuática en los humedales mediterráneos, y la necesidad de cautela al utilizar las aves acuáticas como especies bandera. Un análisis integrador de las diferentes comunidades biológicas, utilizando conjuntos de datos de diferentes grupos taxonómicos, parece representar el requisito necesario para el éxito de las políticas de conservación y monitoreo en estos ambientes. Los resultados ilustran la necesidad de crear una red diversificada y completa de sitios protegidos capaces de conservar los múltiples componentes de la biodiversidad de los humedales.

Capítulo 3. ¿Cómo de bien representan las redes de áreas protegidas la diversidad taxonómica y funcional en taxones no objetivo? El caso de las aguas continentales ibéricas

Las redes de áreas protegidas representan uno de los pilares de las políticas de conservación a nivel mundial y son por lo tanto esenciales actualmente para mantener la biodiversidad. Sin embargo, una limitación importante de la mayoría de las estrategias de conservación es su sesgo hacia determinados grupos taxonómicos y ecosistemas, lo que significa que muchos taxones y hábitats son a menudo sólo casualmente protegidos como un subproducto de su inclusión dentro de las reservas. En este trabajo se investigó la eficacia de las redes de áreas protegidas, no designadas específicamente para los medios acuáticos, en preservar la biodiversidad acuática de la península ibérica (España y Portugal), a partir de datos de coleópteros acuáticos, excelentes indicadores de la diversidad acuática. Se exploró el comportamiento de diferentes componentes (alfa, beta y gamma) de la diversidad taxonómica y funcional a diferentes escalas espaciales. En general, los resultados ponen de relieve el contraste en la eficacia de las redes de reservas en la representación de las dos formas de diversidad estudiada (taxonómica y funcional), así como la importancia de la escala espacial. Las áreas protegidas ibéricas funcionan relativamente bien representando la diversidad taxonómica de los coleópteros acuáticos a escala peninsular, pero las mismas áreas protegidas representan escasamente la diversidad funcional. Esta falta de coincidencia advierte contra el uso de cualquier componente de la diversidad como un sustituto para otros componentes de la misma, y hace hincapié en la importancia de adoptar un enfoque integral para la conservación de la biodiversidad en los ecosistemas acuáticos. Por otra parte, los resultados muestran a menudo patrones contradictorios a menor escala espacial, destacando la necesidad de considerar la influencia de la escala en la evaluación de la eficacia de las redes de áreas protegidas.

Capítulo 4. ¿Hasta dónde podría establecerse el corixido invasor *Trichocorixa verticalis verticalis*? Estimación mundial de su distribución potencial actual y futura

La invasión de especies exóticas se encuentra entre los impactos humanos menos reversibles, con efectos múltiples y diversificados en los ecosistemas acuáticos. Teniendo en cuenta que la prevención es la manera más efectiva para evitar problemas de pérdida de la biodiversidad, uno de los retos en la investigación ecológica es entender los límites del nicho fundamental de las especies con el fin de estimar hasta qué punto las especies invasoras podrían propagarse. *Trichocorixa verticalis verticalis* (Tvv) es una corixido (Hemiptera) originalmente distribuido en América del Norte, que se ha citado como una especie invasora en tres continentes. Su impacto en las comunidades nativas está en estudio, pero ya se destaca como la especie dominante en varios humedales salinos y representa uno de los pocos casos de un insecto acuático invasor. Este estudio tiene como objetivos principales: i) estimar las áreas con condiciones ambientales adecuadas para Tvv a escala global, identificando así las nuevas zonas potenciales de invasión; y ii) testar los posibles cambios en esta distribución potencial global bajo un escenario de cambio climático. Las distribuciones potenciales se calcularon mediante la aplicación de modelos de envoltura climática multidimensional basados en datos climáticos obtenidos a partir de los datos de presencia y en datos fisiológicos de tolerancia térmica. Los resultados obtenidos sugieren que Tvv puede ampliar su distribución mucho más allá de su área de distribución actual y encontrar condiciones habitables en áreas templadas a lo largo de un amplio rango de latitudes, con especial énfasis en las zonas costeras de Europa, África del Norte, Argentina, Uruguay, Australia, Nueva Zelanda, Myanmar, India, el límite occidental entre EE.UU. y Canadá, y zonas de la península arábiga. Considerando un escenario climático futuro (CCM3 para el año 2100) el área de idoneidad de Tvv mostró sólo cambios limitados en comparación con la actual distribución potencial. Estos resultados permiten la identificación de zonas de contacto entre áreas actualmente colonizadas y áreas con elevado potencial de invasión. También se identificaron zonas con un alto nivel de idoneidad que se superponen con áreas reconocidas como puntos calientes globales de biodiversidad. Finalmente, se presentan

hipótesis sobre los posibles medios de difusión, centrándose en diferentes escalas geográficas.

Conclusiones generales

Capítulo 1

1. Los parques nacionales de montaña en España contienen un porcentaje importante (casi el 70%) de la biodiversidad ibérica de macroinvertebrados acuáticos a nivel taxonómico de familia. Los parques nacionales con la mayor riqueza fueron "Picos de Europa" y "Cabañeros".

2. La altitud máxima y el tipo de hábitat (presencia de hábitats lóticos) fueron las variables más importantes relacionadas con diferentes composiciones de las comunidades. Mientras tanto, la litología (sustrato silíceo), uso del suelo (porcentaje de la cuenca vertiente con agricultura de secano) y, en particular, el tipo de hábitat (presencia de sistemas lóticos) parecen ser los factores más importantes para predecir la riqueza de la familia en el conjunto de los parques nacionales estudiados.

3. La selección de diversos cuerpos de agua tanto lóticos como lénticos a diferentes altitud parece ser esencial en la representación de la más amplia gama de diversidad de macroinvertebrados. La riqueza de familias de coleópteros se podría utilizar como un indicador de biodiversidad de macroinvertebrados en áreas protegidas montañosas en cuanto muestra la correlación más alta con los otros grupos taxonómicos y los valores de riqueza restantes. Tal indicador taxonómico podría complementarse con el uso de la riqueza de familias de Odonata en caso de ambientes de aguas estancas.

Capítulo 2

4. Los resultados pusieron de relieve una concordancia limitada entre los patrones de diversidad de aves acuáticas y macroinvertebrados, lo que puede estar relacionado con sus diferentes respuestas a gradientes ambientales. Las variables climáticas relacionadas con la temperatura parecen afectar a las aves acuáticas más que las comunidades de macroinvertebrados, mientras que los factores directamente relacionados con los ecosistemas acuáticos, como las características

químicas del medio, la precipitación o el hidroperíodo, afectan en mayor medida a los diferentes componentes de la comunidad de macroinvertebrados.

5. Los análisis destacaron una relación inversa o nula en los patrones de riqueza, los humedales con mayor riqueza de aves acuáticas mostraron significativamente menor riqueza de especies de hemípteros y familias de macroinvertebrados, y ninguna relación con la riqueza de Coleópteros. Los resultados de los modelos de riqueza de especies sugieren que diferentes procesos, o los mismos procesos operando en diferentes direcciones, pueden ser la base de los patrones observados de riqueza de aves y macroinvertebrados acuáticos.

6. Estos resultados subrayan el potencial limitado de las aves acuáticas como indicadores de biodiversidad acuática en los humedales mediterráneos, y la necesidad de precaución al utilizarlos como especies bandera. Por lo tanto, la gestión de las áreas protegidas centrada sólo en diversidad de las aves acuáticas es probable que no sea suficiente para garantizar la conservación de la biodiversidad de macroinvertebrados acuáticos. Integrar la información de diferentes grupos biológicos, utilizando conjuntos de datos de diferentes grupos taxonómicos, constituye un etapa importante para mejorar el éxito de las políticas de conservación.

Capítulo 3

7. A escala ibérica, las redes de áreas protegidas tienden a incluir las zonas de mayor diversidad (tanto taxonómica y funcional) de Coleópteros acuáticos, de acuerdo con la evaluación de la diversidad alfa entre áreas protegidas y no protegidas. Sin embargo, con relación a la diversidad gamma, se encontraron resultados contradictorios para la diversidad taxonómica y funcional: mientras que las reservas funcionan relativamente bien en la representación de la diversidad taxonómica, dada su área, no recogen más diversidad funcional de lo esperado por azar. Además, estos patrones no fueron congruentes a menor escala espacial en el caso de la diversidad taxonómica, con un porcentaje considerable de ventanas de 100 km de radio que no muestran diferencias significativas en cuanto a diversidad

alfa entre las áreas protegidas y no protegidas, y la mayoría sin diferencias significativas en la representación total de especies (diversidad gamma).

8. La beta diversidad (tanto taxonómica como funcional) fue principalmente el resultado de la sustitución de las especies/rasgos entre los sitios, y siempre fue significativamente inferior a lo esperado por el azar a escala ibérica. Sin embargo, cuando separamos la diversidad beta en reemplazamiento y anidamiento, de nuevo, se encuentran resultados contradictorios para la diversidad taxonómica y funcional: mientras que las redes de áreas protegidas mostraron significativamente menos reemplazamiento y más anidamiento que lo esperado por azar para la diversidad funcional, se encontró generalmente el patrón opuesto en el caso de la diversidad taxonómica, lo que sugiere que los procesos que subyacen a estos valores de diversidad beta son diferentes. Aunque los resultados a una escala espacial menor fueron más ambiguos, por lo general, apuntan a la misma pauta.

9. No se encontraron importantes diferencias cualitativas entre las dos redes de áreas protegidas estudiadas. Sin embargo, la red Natura2000 permite la representación de la mayoría de las especies de interés de conservación.

10. En general, estos resultados ponen de relieve el rendimiento contradictorio de las redes de espacios protegidos en el mantenimiento de la diversidad acuática taxonómica y funcional, apuntando a un sesgo en la representación de determinados hábitats en la redes de áreas protegidas. Resulta importante destacar que la falta de coincidencia invita a la precaución en el uso de cualquier componente de la diversidad como sustituto para otros, y hace hincapié en la importancia de adoptar un enfoque integral para la conservación de la biodiversidad en los ecosistemas acuáticos. Por último, estos resultados ponen de manifiesto también la importancia de considerar la influencia de la escala espacial a la hora de evaluar la eficacia de los sistemas de áreas protegidas.

Capítulo 4

11. Recientes actividades de muestreo detectaron nuevos registros de importantes poblaciones del Hemiptera invasor *Trichocorixa verticalis verticalis* (Tvv) en numerosos humedales designados bajo la Convención de Ramsar en Andalucía (sur de España).

12. Los mapas de predicción de distribución potencial actual sugieren que Tvv puede expandirse más allá de su rango actual y encontrar condiciones habitables en las zonas templadas a lo largo de una amplia gama de latitudes. Al considerar un escenario climático futuro, el área de idoneidad mostró cambios limitados en comparación con la actual distribución potencial. Esto es probablemente debido a su amplia tolerancia térmica.

13. Los resultados permiten la detección de zonas de contacto entre áreas actualmente colonizadas y áreas con elevado potenciales de invasión (por ejemplo, los humedales costeros en Francia, Italia, algunas zonas del Norte de África y numerosas islas mediterráneas). Estas zonas deben mantenerse en especial observación debido al elevado riesgo de futuras invasiones y se recomiendan esfuerzos específicos (programas de muestreos y biomonitorio, vigilancia del comercio naval) para prevenir potenciales invasiones de estas áreas.

14. Las zonas con un alto nivel de idoneidad para Tvv solaparon con áreas reconocidas como puntos calientes de biodiversidad mundial (cuenca mediterránea, Nueva Zelanda, India y Birmania Región y, en menor medida, la zona atlántica de América del Sur) y por lo tanto resultan particularmente importantes y necesitan más esfuerzos de investigaciones. Se sugirieron posibles medios de propagación, dependiendo de las diferentes escalas geográficas consideradas. Nuevas y relevantes rutas en el comercio marítimo internacional pueden representar vías adecuadas para la propagación de especies invasoras acuáticas, en particular las eurihalinas de los ecosistemas costeros y de transición, como es el caso de Tvv. La dispersión a pequeña escala parece estar relacionado a procesos

naturales tales como el transporte pasivo por el viento, los eventos climáticos extremos o las aves acuáticas migratorias.

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Challenges for the conservation of aquatic macroinvertebrates and their habitats in the Iberian Peninsula



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Abstract

This thesis addresses different challenges related to the conservation of freshwater biodiversity in the Iberian Peninsula using aquatic macroinvertebrates as a model system. This information will contribute to a better understanding of the determinants that affect and threat aquatic macroinvertebrate biodiversity and, aims to provide insights for use in nature conservation policies. Chapters 1 and 2 focus on the assessment of potential biodiversity surrogates in aquatic ecosystems, while Chapter 3 is dedicated on the effectiveness of protected areas networks in representing freshwater diversity. In Chapter 4, starting from new records of an alien aquatic insect detected in the Iberian Peninsula, global potential distribution maps for this species are produced since the prevention of biological invasions is the most cost-effective way to avoid problems related with nature conservation.

Chapter 1 reveals that mountainous national parks in Spain contain a large percentage of the overall Iberian biodiversity with respect to aquatic macroinvertebrates at family level. Coleoptera family richness displays the highest correlation with the other taxonomic groups and remaining richness values and may be used as a macroinvertebrate biodiversity surrogate in well preserved mountainous areas. Such a taxonomic indicator could be complemented by the use of Odonata family richness in case of standing waters.

Chapter 2 assesses the performance of a charismatic group (waterbirds) as surrogate of macroinvertebrates biodiversity in wetlands. The results show limited concordance between the community composition of waterbirds and macroinvertebrates, and negligible or negative correlations between the metrics of their taxonomic richness. Contrasting responses to environmental gradients were detected and waterbirds can therefore be considered poor indicators of aquatic biodiversity in these ecosystems.

Chapter 3 provides the first attempt at assessing the effectiveness of protected areas in representing alpha, beta and gamma components of taxonomic and functional macroinvertebrate diversity at different spatial scales. The main findings highlight the contrasting performance of reserve systems in the maintenance of taxonomic and functional freshwater diversity, and point to a bias in environmental representation within protected area networks. Importantly, this

mismatch means that caution should be exercised when using any one diversity component as a surrogate for others, and emphasizes the importance of adopting an integrative approach to biodiversity conservation in aquatic ecosystems.

The last chapter focuses on *Trichocorixa verticalis verticalis* (Corixidae, Hemiptera), one of the few exclusively aquatic insects that can be considered as an alien species, and for which large populations have been newly recorded in numerous Ramsar wetlands in Andalusia (south-west Spain). The predictive maps obtained of current potential distribution suggest that this corixid may expand well beyond its current range and find inhabitable conditions in temperate areas across a wide range of latitudes. When considering a future climatic scenario, the suitability area showed only limited changes compared with the current potential distribution. The results allow the detection of potential contact zones among currently colonized areas and potential areas of invasion, as well as zones with a high level of suitability overlapping areas recognized as global biodiversity hotspots.

These results, taken as a whole, point to some of the main challenges for the conservation of aquatic macroinvertebrate biodiversity (biodiversity surrogates, reserve performance and biodiversity threats) and provide useful information about important topics asked of and by protected area managers and conservationists.

General Introduction

Freshwater ecosystems: threatened but often neglected

Freshwater ecosystems are scarce compared with other habitats on the Earth and can be considered as islands in a sea of dry land and salt water. However, there is a strong link between freshwaters and adjacent areas since much of their characters derive from their drainage basins and the activities they support (Strayer, 2006). Although they cover just 0.8% of the Earth's surface area (Dudgeon et al., 2006), they hold around 125,000 species of the freshwater animals that have so far been described (Strayer & Dudgeon, 2010). Therefore, freshwater ecosystems can rightly be considered hotspots of biodiversity (Strayer & Dudgeon, 2010) despite the numerous pressures they suffer, which makes their biota one of the most threatened in the world (Revenga et al., 2005; Strayer & Dudgeon, 2010). Indeed, declines in biodiversity are far greater in freshwaters than in the most affected terrestrial ecosystems (Sala et al., 2000), which is especially alarming in the context of global change involving possible impacts on multiple levels of organization (Woodward et al., 2010).

The main threats affecting global freshwater ecosystems are generally recognized as water overexploitation, pollution, habitat alteration, flow modification and invasion by exotic species (e.g., Dudgeon et al., 2006). Thus, numerous authors have emphasized the urgent need for greater protection, research and public awareness concerning freshwater ecosystems and freshwater species (e.g., Kingsford & Neville, 2005; Dudgeon et al., 2006; Strayer, 2006; Suski & Cooke, 2007; Moilanen et al., 2008; Monroe et al., 2009). However, despite these known features, aquatic conservation science is still lagging in quality and quantity compared with terrestrial assessments of conservation value and applications of systematic conservation planning (Abell, 2002). Conservation efforts for freshwater biodiversity seem to be constrained by the paucity of complete and reliable information for a number of geographical areas, habitat types and taxonomic groups (Dudgeon et al., 2006; Strayer, 2006). In this context, it is noteworthy that non-charismatic groups, such as invertebrates, that play a key role in the ecosystem process (Covich et al., 1999) and make up the bulk of animal biodiversity (Ramos et al., 2001), are still less studied and protected than other

taxa that catch the public's eye (Strayer, 2006; Martín-López et al., 2009; Cardoso et al., 2011).

As invertebrates dominate multicellular organisms in terms of richness, abundance and, often, biomass (Cardoso et al., 2011), aquatic macroinvertebrates (i.e. invertebrates exceeding about 1 mm in length) represent one of the most important components of freshwater biota. They form a large group of organisms, which includes representatives from multiple phyla, such as arthropods (itself comprising multiple orders of insects, spiders, and crustaceans), annelids, and molluscs. Insects constitute the most numerous group, and orders such as Odonata (dragonflies and damselflies), Ephemeroptera (mayflies), Plecoptera (stoneflies), Trichoptera (caddisflies), Coleoptera (water beetles), Diptera (flies), and Hemiptera (water bugs) are the main inhabitants of freshwater bodies (Tierno de Figueroa et al., 2013). Among them, Coleoptera and Hemiptera are the only orders in which most of their adults are strictly aquatic and inhabit every kind of fresh- and brackish water habitats, from the smallest ponds to lagoons and wetlands, and from streams to irrigation ditches, large rivers and reservoirs (Jäch & Balke, 2008; Tierno de Figueroa et al., 2013; Millán et al. in press). More specifically, water beetles constitute a high and functionally diverse proportion of inland water biodiversity (Jäch & Balke, 2008) and, compared with other groups of freshwater invertebrates in the Iberian Peninsula, they are one of the most diverse and well known group in their systematic and biogeography (Ribera et al., 1998; Ribera, 2000; Millán et al., in press).

There is an extensive body of literature examining the ecology of macroinvertebrate communities and exploring their use as indicators to monitor the status of water quality in freshwater ecosystems (e.g., Rosenberg & Resh, 1993; Bonada et al., 2006; Menetrey et al., 2011). However, less attention has been paid to macroinvertebrate biodiversity conservation despite the key role that macroinvertebrates play in the functions and dynamics of aquatic ecosystems (e.g., energy flows and nutrient cycling; Merritt et al., 1984; Merritt & Lawson 1992; Covich et al., 1999; Fenoglio et al., 2005), and the large percentage of aquatic animal biodiversity that they represent in terms of phylogenetic, taxonomic and functional diversity. In this framework, crucial challenges need to be addressed to

fill the important gaps that still exist concerning freshwater ecosystem conservation and, especially, macroinvertebrate biodiversity.

Systematic conservation planning (Margules & Pressey, 2000; Groves et al., 2002) is a target-driven process that aims to identify networks of priority areas to ensure the representation and long-term persistence of biodiversity. This planning approach has several distinctive characteristics. For instance, it requires clear choices to be made about the features to be used as surrogates for overall biodiversity in the planning process. It also recognizes the extent to which conservation goals have been met in current reserves (review of existing protected areas), as a prior step to locating and designing new reserves to complement existing ones. Furthermore, the approach adopts explicit objectives and mechanisms for maintaining the conditions within reserves that are required to foster the persistence of key natural features. At the same time, a better understanding of the present and future distribution patterns of threats is crucial, as this will help focus limited conservation resources on the areas and features most at risk (Margules & Pressey, 2000). While systematic conservation planning is now commonly practised around the world in terrestrial or marine ecosystems (Watson et al., 2011), its use in freshwater systems is not so common (see Moilanen et al., 2008; Hermoso et al., 2014), especially when it comes to macroinvertebrate biodiversity (but see Sánchez-Fernández et al., 2004, 2008; Abellán et al., 2005, 2007). In this sense, research on effective freshwater biodiversity surrogates as well as on the effectiveness of existing protected areas for preserving aquatic biodiversity, coupled with an assessment of new potential threats (e.g., alien species and climate change), represent some of the most important challenges for aquatic macroinvertebrate conservation and their habitats.

Aquatic biodiversity indicators: needs and purposes

Measuring and monitoring biodiversity is a crucial task for the conservation or restoration of freshwater ecosystems. However, surveying biodiversity involves difficulties concerning the limited time and financial resources available, and often requires a large degree of expertise, particularly in case of certain invertebrate

groups. A common approach to resolve this problem has been to use indicators of biodiversity or so-called biodiversity surrogates. Among such surrogates, a wide range of approaches, such as environmental diversity (e.g., Faith, 2003), higher-taxa (e.g., Balmford et al., 2000) or indicator taxa (i.e. the cross-taxon approach; e.g., Pawar et al., 2007), are frequently used. Biodiversity indicator taxa are taxonomically and ecologically well understood groups, which are easily monitored, occur in various environmental conditions and show strong relationships with other target groups as regards their biodiversity values (see Rodrigues & Brooks 2007 for a review). Thus, a biodiversity indicator should be defined as a group of taxa (e.g., species, genus or higher level) whose diversity reflects some measure of the diversity of other taxa in a habitat (see Caro & O'Doherty, 1999).

While aquatic macroinvertebrates have been extensively used in aquatic biomonitoring as environmental or ecological indicators, especially in running waters (e.g., Rosenberg & Resh, 1993; Bonada et al., 2006), less attention has been paid to identifying indicator taxa for the assessment of macroinvertebrate biodiversity (but see Bilton et al., 2006; Sánchez-Fernandez et al., 2006; Heino, 2010 for a review). Hence, there is a need for testing possible indicators of macroinvertebrate biodiversity to obtain new and useful tools for rapid and inexpensive biodiversity monitoring, to evaluate existing reserves and to select new areas with high aquatic biodiversity values. As taxon richness is probably the main variable used to describe community diversity (Gaston, 1996) and, since maximizing species richness is often an explicit or implicit goal of conservation studies and efforts (May, 1988; Rodrigues et al., 2004), numerous assessments of surrogates have basically focused on richness patterns (e.g., Fleishman et al., 2005; Velghe & Gregory-Eaves, 2013). Nevertheless, community composition represents another relevant measurement of species diversity in the context of coarse-filter conservation strategies (Su et al., 2004; Bilton et al., 2006) and one that has been less examined in cross-taxon congruence assessments.

Unfortunately, cross-taxon congruence in biodiversity patterns between aquatic macroinvertebrates and vertebrates other than fishes has seldom been assessed. In conservation biology, charismatic and public-appealing taxa like birds represent an example of commonly used surrogates of biodiversity owing to the

wide availability of relevant data concerning their distribution and status and their broad popular appeal (Gregory, 2003, 2006; Eglington et al., 2012; Kajtoch et al., 2014). Birds are thus the object of many international nature conservation initiatives, such as the worldwide network of Important Bird Areas (IBA), and the Special Protected Areas (EU Birds Directive) in Europe. In the case of aquatic ecosystems, waterbirds usually drive the designation of Wetlands of International Importance under the Ramsar Convention, a global intergovernmental treaty for the conservation and sustainable use of wetlands and their resources (Ramsar Bureau, 2000). Even though waterbirds play a key functional role in many aquatic environments, with a structuring influence on the communities of invertebrates and macrophytes (Green & Elmberg, 2014), their reliability as surrogate of macroinvertebrate diversity remains poorly tested and needs to be investigated.

Overall, specific research on freshwater biodiversity surrogates represents one of the main challenges in freshwater conservation (Nel et al., 2009) if we are to achieve a better understanding of aquatic macroinvertebrate biodiversity, obtain indicators of well-preserved areas, assess traditional (charismatic) bioindicator effectiveness and recognize biodiversity patterns in terms not only of taxonomic richness but also considering information and congruence in species composition among different taxonomic groups.

Freshwater ecosystems in protected areas: integrating freshwater diversity and biological conservation

Protected area networks represent one of the mainstays of worldwide conservation policies and play a key role in the protection of biodiversity (Chape et al., 2005). The total area benefiting from legal protection has gradually been increasing worldwide (Jenkins & Joppa, 2009), and between 10.1% and 15.5% of land area is now under some form of protection worldwide (Soutullo, 2010). However, existing reserve networks throughout the world seem to contain a biased sample of biodiversity, usually referring to remote places and other areas that are unsuitable for commercial activities (Margules & Pressey, 2000). For instance, the protection of high-altitude environments is a common example of protected areas due to the lack of economic interest and human activities (Joppa &

Pfaff, 2009). Nevertheless, protected areas should represent a network of ecosystems of conservation concern in parallel with other interests.

However, the implementation of nature reserves is only the start of the task (Lovejoy, 2006) and determining how effective they are in representing and maintaining biodiversity is a research priority in conservation biology (e.g., Bertzky et al., 2012) and the main question asked of and by protected area managers worldwide (Parrish et al., 2003). Thus, a review of existing conservation areas is one of the main stages of systematic conservation planning (Margules & Pressey, 2000), as it constitutes the basis for identifying those elements of biodiversity not sufficiently represented in existing protected areas and for determining how conservation efforts can be improved (Groves et al., 2002).

The biota of many protected areas and nature reserves around the world have been poorly inventoried, in part because of the perception that these areas are already “protected” and that survey funds would be better spent on areas yet to be designated for conservation management (Groves et al., 2002). In this context, the ecological performance of these areas, both in terms of the representation and the maintenance of key biodiversity features, remains weakly understood (Gaston et al., 2008a). Furthermore, a major fault in conservation strategies is their bias towards primarily terrestrial and/or specific taxonomic groups (Martín-López et al., 2009). As very few protected areas have been planned or proposed specifically for freshwaters (e.g., Abell et al., 2007; Suski & Cooke, 2007), freshwater habitats are often only incidentally protected as part of terrestrial reserves. However, terrestrial reserve networks may not adequately represent aquatic biota (Suski & Cooke, 2007; Herbert et al., 2010). In this sense, the effectiveness of these reserves in representing freshwater features is still extremely poorly known.

Similarly, the groups that have been the focus of most conservation efforts (e.g., vertebrates and plants) are likely to be poor surrogates of diversity patterns for many freshwater groups (see Darwall et al., 2011) and little is known about how well protected areas support biodiversity of non-target taxa like aquatic macroinvertebrates. This gap should be explored to obtain a better understanding of reserves effectiveness. At the same time, multidisciplinary research and integrative freshwater ecology and biological conservation represent a priority for

the maintenance and better knowledge of freshwater biodiversity (Strayer & Dudgeon, 2010; Geist et al., 2011).

Besides, while conservation efforts have traditionally focused on protecting areas to ensure adequate representation of taxonomic diversity (e.g., species richness), it is now well recognized that protected areas should strive to preserve all the components of biodiversity, including the ecological and evolutionary processes that generate and maintain biodiversity, and the goods and services that humans obtain from nature (Mulongoy & Chape, 2004). Functional diversity, which reflects the diversity of biological, physiological and ecological traits within biological communities (Petchey & Gaston, 2006), has been advocated as an important facet of diversity to ensure 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) that are essential for understanding the relationships between biodiversity, ecosystem functioning and environmental constraints (Mouchet et al., 2010). In this framework, incorporating functional information into conservation strategies goes beyond simply representing the number of species present. Additionally, to be effective, protected area systems in a changing world should also rely on the maintenance of species and functional processes at different spatial scales (Gering et al., 2003; Brooks et al., 2006; Devictor et al., 2010). Both taxonomic and functional diversity can be broken down into local, inter-site and regional components (so-called alpha, beta and gamma diversities; Whittaker, 1972) which should be assessed to obtain a complete and better understanding of protected areas performance.

Alien species: a new threat for macroinvertebrate biodiversity

In the context of biodiversity crisis, the introduction and establishment of alien species in new areas is recognized as one of the most important human impacts on a wide range of ecosystems (e.g., McKinney & Lockwood, 1999; Clavero & García-Berthou, 2005). Biological invasion is of global concern and even protected areas, despite their privileged conditions in terms of habitat alteration, are not exempt (e.g., Usher 1988; Lovejoy 2006). For example, Lonsdale (1999), in a study on numerous protected sites around the world, found a positive

relationship between the number of visitors in protected areas and the number of alien plants.

This threat is a problem of particular concern in aquatic ecosystems (Dudgeon et al., 2006), where alien species can have diverse impacts on biodiversity and ecosystems functioning (Scott et al., 2012; Gallardo et al., 2013). Here, aquatic invasive species are of growing concern to conservationists and environmental managers because of their high eradication costs, necessitating effective management policies (Gallardo et al., 2013). In these threatened ecosystems, the need to better understand, prevent and even predict future invasions (also in the context of climate change) seems to be decisive and represents a precursor and innovative topic of research, especially in the case of aquatic insects.

Alien species are a non-random subset of aquatic biota and, although insects dominate the world's freshwater ecosystems, they are unrepresented in the lists of alien species (Statzner et al., 2008; Karatayev et al., 2009; Strayer, 2010). Due to this rarity, scientific knowledge on alien aquatic insects, their effects on biodiversity and potential distribution is very scarce, an observation that is particularly true for invertebrate species of low economic and general public interest (Kenis et al., 2009).

As the prevention of biological invasions is the most cost-effective way to avoid biodiversity loss and nature conservation problems (Bax et al., 2001), one challenge in biological conservation is to understand the limits of the fundamental niche of the species, since this information will allow us to map the places which the species might inhabit (i.e., the potential distribution). The identification of environmentally suitable areas for invasive species may offer important opportunities for preventing or slowing invasions (Guisan & Thuiller, 2005; Jeschke & Strayer, 2008).

Recently, an alien Hemiptera (*Trichocorixa verticalis verticalis*, Corixidae) has been detected in various aquatic ecosystems (including protected wetlands) in Morocco, Portugal and Spain, converting this species into one of the almost unique, exclusively aquatic, insects (i.e., all their life cycle stages are aquatic) that can be considered as an alien species. The term "alien" is applicable here because the species has moved outside its native range and has established itself successfully

in a new region (Rabitsch, 2008; Strayer, 2010). Furthermore, this euryhaline corixid represents the dominant hemipteran in many of the invaded sites where it has been found and, when reproduction has occurred, it outcompeted native corixids (Rodríguez-Pérez et al., 2009), presenting an invasive character that is currently under study, especially in the Iberian Peninsula (e.g., Carbonell et al., 2012; Coccia et al., 2013).

Besides, alien invertebrates may overcome some of the strategies used to limit their spread (e.g., border controls) as a result to numerous natural or human-induced ways of spreading (at local and even worldwide scales) and species with broad salinity tolerance may be particularly favoured in this respect (Ricciardi, 2006). Considering that Western Europe has already been highlighted as a recipient area sensitive to invertebrate biological invasions (e.g., Devin et al., 2005; Devin & Beisel, 2008), the recent records of this species in the Iberian Peninsula should be taken with due consideration by environmental managers and scientists. Alien species control programmes should focus on the areas of highest value for native biodiversity and those most at risk from alien invaders (Saunders et al., 2002). Thus, research on the potential distribution of such species represents a vanguard tool for better understanding aquatic invasions and could result in important recommendations for preventing future spread by detecting potential contact zones among currently colonized areas and potential areas of invasion.

Spatial framework: freshwater ecosystems and protected area networks in the Iberian Peninsula

The loss of freshwater biodiversity is of particular concern in areas of the Mediterranean Basin, which is considered one of the Earth's biodiversity hotspots for animals and plants (Myers et al., 2000; Cuttelod et al., 2008) as well as freshwater organisms (Tierno de Figueroa et al., 2013). However, due to the strong century-long anthropogenic influence (Blondel & Aronson, 1999) and ongoing process of global changes, Mediterranean aquatic biodiversity is under strong pressures (Filipe et al., 2012; Bruno et al., 2014).

The Iberian Peninsula, which is mainly composed of the mainland territories of Portugal and Spain, represents one of the richest European regions in

terms of species (Williams et al., 2000) and is located in the western part of the Mediterranean Basin. It covers nearly 600,000 km², and is characterized by a great variety of biomes, relief, climates and soil types that have originated a wide range of aquatic ecosystems, some of which are extremely rare on a European context (e.g., Millán et al., 2011). This wide diversity of environments runs from mountainous aquatic ecosystems (lotic, lentic or complex) to lowland wetlands, with a wide range of water conductivities (from freshwaters to coastal or inland saline wetlands) and land uses in the adjacent basins. However, aquatic ecosystems are not exempt from important threats, ranging from habitat alteration to invasive species (Prenda et al., 2006).

The course of nature conservation in the Iberian Peninsula starts with the beginning of the last century. However, although the Spanish national park network was set up in 1918 with the general aim of preserving nature, it was only at the end of the 20th century that protected areas reached a more representative level in terms of Spain's natural values and surface extension (Morillo & Gómez-Campo, 2000). In Portugal, nature conservation strategies started later, basically during the 1970s with the implementation of the first protected areas and subsequent intensification in the creation of reserves during the last part of the century.

The nationally designated protected areas (i.e. those included in Spanish and Portuguese legislation) represent the core of national and regional conservation policies, and include Parks, Natural Reserves, Natural Monuments, Marine Protected areas, Protected Landscapes as well as different types of local protected areas. In addition to national protected areas, the number and extension of protected areas in the Iberian Peninsula has grown rapidly in recent decades as a result of the implementation of the Natura2000 Network. This network represents a key tool for biodiversity conservation at the European scale and aims to guarantee the long-term survival of Europe's most valuable and threatened species and habitats. It includes Special Areas of Conservation (SACs) designated under the Habitats Directive (92/43/EEC), and Special Protection Areas (SPAs) which are designated under the Birds Directive (79/409/EEC). As a result, the European Union (EU) is one the regions of the world with the highest number of protected areas (Araújo et al., 2011; Pyšek et al., 2013). Protected Areas in the EU

cover 15.3% of the total surface (661,692 km²), or even 25% (1,081,195 km²) if sites implemented as part of the Natura2000 scheme are considered (Natura2000 Networking Programme 2007; Gaston et al., 2008b; Pyšek et al., 2013). In the case of the Iberian Peninsula, an important percentage of its territory (around 28% in case of Spain and 22% for Portugal) can currently be considered under some degrees of protection (Regional, National or European; Europarc-España, 2010). However, the effectiveness of both the national protected area system and the Natura2000 network in representing Iberian freshwater biodiversity has been assessed in very few studies and, even then, incompletely (e.g., Abellán et al., 2007; Sánchez-Fernández et al., 2008; Abellán et al., 2013). As a result, the effectiveness of both networks in the context of aquatic biodiversity conservation and non-target taxa still remains unclear and needs to be investigated.

Objectives and thesis structure

The main goal of this thesis is to address different challenges related to the conservation of freshwater biodiversity in the Iberian Peninsula using aquatic macroinvertebrates as a model system. This information aims to contribute to a better knowledge of the determinants that affect and threat aquatic macroinvertebrate biodiversity and to provide insights for use in nature conservation policies. More specifically, this thesis aims to:

- Evaluate and test the importance of different taxonomic groups as indicators of macroinvertebrate biodiversity in aquatic protected environments (*Chapter 1*).
- Investigate which environmental variables are associated with macroinvertebrate compositions and richness in protected areas (*Chapter 1*).
- Assess the performance of a charismatic group (waterbirds) as surrogate for predicting the biodiversity of aquatic macroinvertebrates in wetlands (*Chapter 2*).

- Determine which environmental variables are associated with the biodiversity patterns of waterbirds and macroinvertebrates, with the purpose of identifying key factors explaining potential discordance in these patterns (*Chapter 2*).
- Assess the effectiveness of protected area networks (not specifically designated to include freshwaters) in representing freshwater biodiversity using water beetles as indicators (*Chapter 3*).
- Explore the behaviour of both taxonomic and functional diversity measures of local (alpha), inter-site (beta) and regional (gamma) biodiversity at different spatial scales, in the assessment of protected area performance (*Chapter 3*).
- Estimate the worldwide potential distribution of *Trichocorixa verticalis verticalis* (Hemiptera: Corixidae), one of the first recorded aquatic alien insect worldwide, considering both current and future climatic conditions (*Chapter 4*).
- Recognize potential new zones of invasion and detect contact zones among currently colonized areas and potential areas of invasion (*Chapter 4*).

This thesis is structured in four chapters, corresponding to four scientific articles. Chapters 1, 2 and 4 have already been published in international peer-reviewed journals indexed in SCI, while chapter 3 has recently been submitted for publication and it is currently under review. The four articles on which this thesis is based are:

Chapter 1 Guareschi S., Gutiérrez-Canovas C., Picazo F., Sánchez-Fernández D., Abellán P., Velasco J., Millán A. (2012). Aquatic macroinvertebrate biodiversity: patterns and surrogates in mountainous Spanish national parks. *Aquatic Conservation: Marine and Freshwater Ecosystems* 22: 598-615.

- Chapter 2** Guareschi S., Abellán P., Laini A., Green A.J., Sánchez-Zapata J.A., Velasco J., Millán A. (2014). Cross-taxon congruence in wetlands: assessing the role of waterbirds as surrogates of macroinvertebrate biodiversity in Mediterranean Ramsar sites. *Ecological indicators* 49: 204–215.
- Chapter 3** Guareschi S., Bilton D., Velasco J., Millán A., Abellán P. How well do protected area networks support taxonomic and functional diversity in non-target taxa? The case of Iberian freshwaters. *Biological Conservation*, under review.
- Chapter 4** Guareschi S., Coccia C., Sánchez-Fernández D., Carbonell J.A., Velasco J., Boyero L., Green A.J., Millán A. (2013). How far could the alien boatman *Trichocorixa verticalis verticalis* spread? Worldwide estimation of its current and future potential distribution. *PLoS ONE* 8(3): e59757.

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Chapters



Rio Yaga (Parque Nacional de Ordesa y Monte Perdido, Aragón)

Chapter 1:

Aquatic macroinvertebrate biodiversity: patterns and surrogates in mountainous Spanish national parks



Río Bellos (Parque Nacional Ordesa y Monte Perdido, Aragón)

Guareschi, S., Gutiérrez-Canovas, C., Picazo, F., Sánchez-Fernández, D., Abellán, P., Velasco, J., Millán, A. (2012). *Aquatic Conservation: Marine and Freshwater Ecosystems* 22: 598-615.

Abstract and keywords

In Spain, national parks represent the mainstay of conservation policies and attempt to protect the most representative natural ecosystems. However, studies on the ecology and conservation of aquatic biodiversity within protected areas are still scarce. This study aimed at compiling an inventory of the macroinvertebrate families inhabiting the aquatic ecosystems of each mountainous Spanish national park (Sierra Nevada, Cabañeros, Ordesa, Picos de Europa, Aigüestortes and Monfragüe). The results were used to answer two questions: (i) Which environmental variables are related to macroinvertebrate composition and richness in these protected ecosystems? (ii) Which taxon or group of taxa could act as biodiversity surrogates? Sampling was carried out in 81 aquatic ecosystems across the six national parks during the summers of 2008–2010.

The national parks with the highest richness were Picos de Europa and Cabañeros. Overall, the six parks incorporated 66.2% of the taxa included in the Iberian checklist. Multivariate techniques showed that maximum altitude and the presence of lotic habitats were the most important variables related to different community compositions. The best richness model included the presence of a lotic habitat, together with the percentage of the catchment area with non-irrigated agriculture and siliceous geology.

Selecting several diverse lotic and lentic water bodies at different altitudes provides the best way of representing Iberian macroinvertebrate diversity. Coleoptera family richness may be used as a macroinvertebrate biodiversity surrogate in Iberian mountainous protected areas because it displayed the highest correlation with the other taxonomic groups and remaining richness values. Such an indicator could be complemented with the use of Odonata family richness for standing waters.

The adequacy of Coleoptera and Odonata as biodiversity surrogates should be tested at a wider geographic scale, and other surrogacy concepts (e.g., community composition) considered for assessing the role of this network in the protection of rare and endemic species.

Biodiversity indicators • Aquatic conservation • Macroinvertebrates • Protected areas • Spanish national parks

1. Introduction

The Iberian Peninsula, located in the western part of the Mediterranean Basin biodiversity hotspot (Myers et al., 2000), is one of the richest European regions in terms of species (Médail & Quézel, 1997; Williams et al., 2000; Reyjol et al., 2007). However, a large amount of these species are currently threatened by the growing human intensification of land use, mainly for agricultural and urban activities, resulting in unprecedented rates of biodiversity loss (Pimm et al., 1995, Fontaine et al., 2007). In aquatic habitats, this situation has become even more dramatic, given the increasing demand of freshwater resources by human activities, the intensity of diffuse pollution and other direct impacts (Allan & Flecker, 1993; Strayer, 2006; Dudgeon et al., 2006).

To prevent or mitigate biodiversity loss, the establishment of protected areas has become the mainstay of most conservation policies. However, the criteria used to design protected areas have been often based on the presence of certain charismatic plant or vertebrate species (Western, 1987; Dietz et al., 1994), while aquatic biodiversity has not generally been included among the selection criteria (Keith, 2000; Abellán et al., 2007). Aquatic conservation science is still lagging in quality and quantity compared to terrestrial assessments of conservation value and applications of systematic conservation planning (Abell, 2002). In this sense, most currently protected areas have not been delineated based on the requirements of freshwater organisms, and as a result, terrestrial reserve networks do not adequately represent aquatic ecosystems (Herbert et al., 2010). This is true despite the fact that some aquatic habitats, such as mountainous water bodies, constitute ecosystems of considerable ecological importance, and the species loss in these habitats is alarmingly high (Allan & Flecker, 1993; Saunders et al., 2002; Darwall & Vié, 2005). Furthermore, mountainous freshwater habitats are especially vulnerable ecosystems in the context of global warming (Ormerod, 2009).

As an important component of aquatic biodiversity, invertebrate fauna is a fundamental part of these ecosystems and has become a useful element for applying appropriate conservation and management measures in protected areas (Samways, 1993; Samways et al., 2010; McGeoch et al., 2011), above all in those

that display high species richness such as aquatic mountainous ecosystems. Apart from knowing the environmental factors that influence their assemblage composition and richness patterns determining their diversity should be a key task. Numerous studies have assessed the influence of environmental and anthropogenic factors on freshwater macroinvertebrate communities, reporting that both factors are crucial in determining the taxonomic composition at site scale (e.g., Tolonen et al., 2001; Bonada et al., 2005; Hinden et al., 2005). Thus, if one aims to study the true effects of environmental variables on unaltered freshwater communities, it is necessary to concentrate on areas with minimal human influence. Among these areas, national parks, especially those in mountainous areas, are undoubtedly the most important, since these protected natural spaces can be considered to be natural islands.

The Spanish National Parks Network was started in 1918 with the general aim of nature conservation and currently seems to represent most of Spanish natural values (Morillo & Gómez-Campo, 2000). However, studies on the ecology and conservation of aquatic biodiversity within protected areas are still scarce, especially within national parks. Therefore, in order to preserve freshwater biodiversity, it is necessary to improve the biodiversity inventories in these areas and design specific protection measures (Abell, 2002; Abell et al., 2007; Susky & Cooke, 2007).

However, the elaboration of exhaustive inventories that encompass different groups of organisms (i.e., algae, fungi, plants, invertebrates, vertebrates) can be prohibitive in terms of time and effort, and requires vast and heterogeneous taxonomic expertise. In this context, a common alternative is the use of biodiversity surrogates (Pearson, 1994). While aquatic macroinvertebrates have been used extensively as indicators to monitor the status of water quality in freshwater habitats (Davis et al., 1987; Wallace et al., 1996), minor attention has been paid to the development of indicator taxa for the assessment of freshwater biodiversity or conservation priorities (but see Bilton et al., 2006; Sánchez-Fernández et al., 2006; Ormerod et al., 2010).

Species level identification for all orders of aquatic invertebrates is often problematic or impossible due to the aerial stage form of most adults. For example, among insects, only the majority of Coleoptera and Hemiptera adults are strictly

aquatic. As a result, the use of higher taxonomic levels (e.g., family) has been proposed in some studies due to its high correlation with species richness (Williams & Gaston, 1994; Bournaud et al., 1996; Baldi, 2003; Sánchez-Fernández et al., 2006), which can allow easier and more economical management measures to ensure biodiversity protection (Gaston, 2000; Kerr et al., 2000; Villaseñor et al., 2004). At the same time, species richness has been demonstrated to be well correlated with rare species richness (Sánchez-Fernández et al., 2004).

This study aims to inventory macroinvertebrate families inhabiting the aquatic ecosystems within each of the six mountainous parks belonging to the Spanish National Parks network. This information was first used to calculate the percentage of Iberian aquatic invertebrate richness (i.e., the number of Iberian families) represented in the six mountainous Spanish national parks. Using this data, the study aims to answer the following questions: (i) Which environmental variables are related to macroinvertebrate composition and richness patterns in these mountainous and protected ecosystems? (ii) Which taxon or group of taxa could act as invertebrate biodiversity surrogates in these areas? The present study uses “family richness” as a proxy of overall freshwater macroinvertebrate biodiversity.

2. Methods

Study area

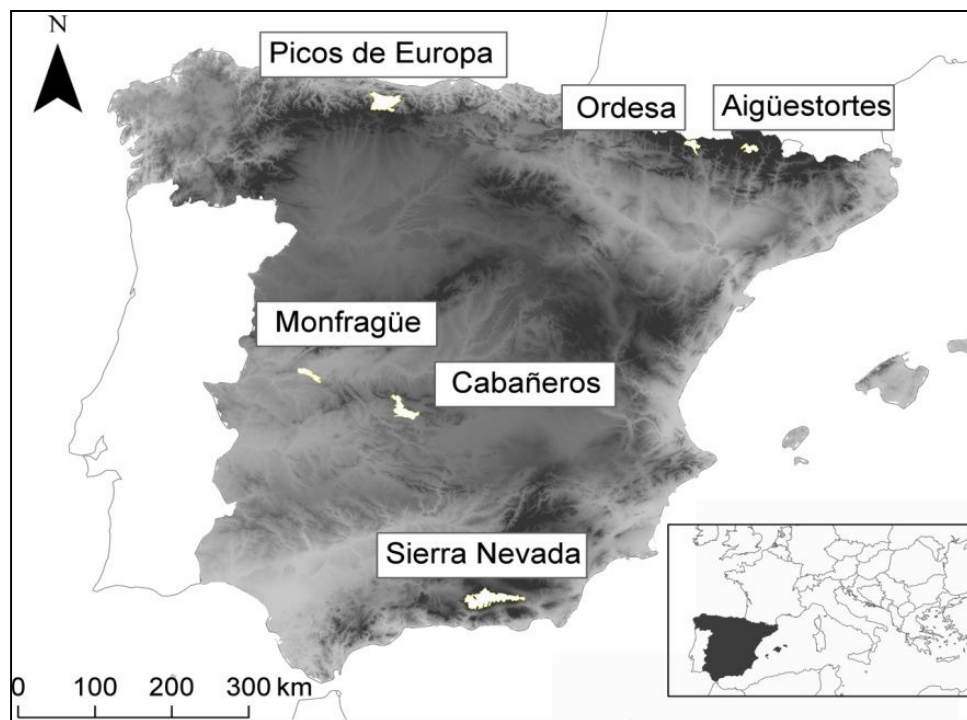
The study was conducted in the six mountainous national parks (IUCN category II) of peninsular Spain (Sierra Nevada, Cabañeros, Monfragüe, Picos de Europa, Ordesa y Monte Perdido and Aigüestortes i Estany de Sant Maurici) (Fig. 1). These parks are highly protected by national and international legislation. All of the land corresponding to the studied parks is already included in the Natura 2000 network as Special Areas of Conservation (SACs following EU Directive 92/43/ECC) and/or Special Protection Areas (SPAs according to EU Directive 79/409/EEC). Furthermore, these parks feature a high diversity of lotic, lentic and mixed aquatic habitats (e.g., streams, springs, rivers, ponds, lagoons, peat-bogs, etc.) and environmental conditions (from low to high mountains). Doñana and Tablas de Daimiel National Parks were not used in this study because they include

essentially standing waters and are located in non-forested lowlands where human pressures are stronger.

The southernmost park was Sierra Nevada (37° N), whereas the northernmost was Picos de Europa (43° N). In general, Monfragüe Park presented the lowest altitude, with an average of 250 meters above sea level, while Sierra Nevada and Aigüestortes i Estany de Sant Maurici showed a very similar average beyond 1700 m.a.s.l. (see Table 1). The sampling site located at the highest altitude was Laguna de Aguas Verdes, which is situated at 3,050 m.a.s.l. (Sierra Nevada Park). According to the European Water Framework Directive following the biogeographic classification of Illies (1978), most Iberian Parks belong to the Iberic-Macaronesian ecoregion; only Ordesa y Monte Perdido (hereafter, Ordesa) and Aigüestortes i Estany de Sant Maurici (hereafter, Aigüestortes) are located in the Pyrenees ecoregion. The Iberian Peninsula is traditionally divided into two main phytogeographical regions: the Eurosiberian Region (from north western Portugal to the Pyrenees: including Picos de Europa, Ordesa and Aigüestortes) and the Mediterranean Region (Rivas-Martínez, 1983). Aigüestortes, Ordesa, Picos de Europa and Sierra Nevada Parks presented basins covered with characteristic mountainous vegetation such as evergreen and deciduous trees, shrubs and high-altitude grasslands, while Cabañeros and Monfragüe Parks displayed typical Mediterranean oaks and scrubs (Rey Benayas & Scheiner, 2002). Siliceous lithologies were frequent in the study area, except in Ordesa Park, and a few other sites distributed among the rest of the parks. As expected, the main land uses were natural vegetation and dryland farming (non-irrigated agriculture such as pasture lands and dry crops).

Table 1. Main features of the six Spanish national parks studied. MSA: Mean Site Altitude.

National Park	Province	Area (ha)	MSA (m.a.s.l.)	Mean Lat. N	Mean Long. W
Aigüestortes i Estany de Sant Maurici	Lleida	26,773	1,746	42°34'50"	00°56'50"
Cabañeros	Ciudad Real, Toledo	40,856	696	39°22'04"	04°26'16"
Monfragüe	Cáceres	18,118	250	39°48'50"	05°56'30"
Ordesa y Monte Perdido	Huesca	15,608	1,460	42°38'50"	00°02'30"
Picos de Europa	Asturias, León, Cantabria	64,660	957	43°12'17"	4°54'23"
Sierra Nevada	Granada, Almería	86,208	1,745	37°04'48"	03°8'52"

**Figure 1.** Location of the six mountainous national parks studied.

Gathering biological data

A total of 81 aquatic ecosystems, including rivers, streams, springs, ponds and peat bogs spread throughout the six mountainous Spanish national parks were sampled once during the summers of 2008-2010 (see Appendix 1 and Table 3). This time of year generally corresponds to maximum species activity. Furthermore, it has been suggested that samples taken from Mediterranean

streams during one particular season may be representative of the average annual community (Bonada et al., 2007).

Sampling sites were selected in order to cover all of the different environmental conditions and water-body types (e.g., streams, lakes, ponds and springs) in each national park. At each sampling site, macroinvertebrate samples were collected from a representation of all occurring mesohabitat types with a kick-net of 500 μm mesh, following a multihabitat protocol (Jáimez-Cuéllar et al., 2002). Each kick-sample was examined in the field and successive samples were taken until no new families were found. Finally, the kick-sample contents were pooled into a unique site-sample. The collected material was preserved in 96% ethanol and identified to family level (in the laboratory), except for Ostracoda, Hydracarina, Aranei and Nematoda (see Appendix 2).

Finally, in order to perform further analyses, each sampling site was assigned to one of the three general macro habitat types: lotic (running waters), lentic (standing waters) or complex system (i.e., sites that include both lotic and lentic habitats).

Assessing inventory completeness

As taxon richness is probably the main variable used to describe community diversity (Gaston 1996), collector's curves (Soberón & Llorente, 1993) were performed for each national park in order to assess the completeness of their inventories at family level. These curves show the expected accumulated number of taxa occurring within a geographical area as a function of collecting efforts (Colwell & Coddington, 1994; Gotelli & Colwell, 2001). The slope of the collector's curve decreases with sampling efforts reaching a hypothetical value of 0 when all taxa are detected. The Clench function was fitted to smoothed data and the asymptotic value (i.e., the taxa richness predicted for an ideally unlimited sample size) was computed. The ratio of recorded to predicted richness (asymptotic score) was employed as a measure of completeness in the samples. All of these analyses were carried out using EstimateS 6.0 (Colwell, 2000) and Statistica 6.1 (StatSoft, 2004) software.

The performance of the national parks in representing mountain freshwater biodiversity was addressed by assessing how many families were represented in

the different parks in relation to the total number of macroinvertebrate families present in the Iberian Peninsula. The estimated richness values for each park were compared with a checklist that potentially gathered all of the aquatic families present in the Iberian Peninsula. This list was compiled based on the IBMWP checklist (Alba-Tercedor et al., 2002, Jáimez-Cuéllar et al., 2002) and completed with several families typical of Iberian lentic ecosystems (Boix & Sala, personal communication), which were not included in the IBMWP checklist. The final checklist was composed of 145 families.

Multivariate analysis

The catchment area of each sampling site was delineated using ESRI Arcview 3.2. In a few small ponds and springs, the basin was delineated assuming a 1-km-radius buffer. Then, a total of 22 basin-scale descriptors (geographic, climatic, morphologic, lithological and land use variables) were obtained for each site using digital layers. Conductivity was measured *in situ* on each sampling occasion with an ECmeter (TetraConR 325). Furthermore, two dummy variables were considered: lotic habitat (1 or 0) and Mediterranean climate (1 or 0) (Table 2). Variables that normally have significant effects on invertebrate communities like ionic composition (Ormerod and Edwards, 1987) were indirectly taken into account by considering factors such as lithology and conductivity, which are generally highly correlated with some water chemistry variables (Toro et al., 2002; Bonada et al., 2005).

In order to reduce distribution skewness and avoid distortions due to the effects of different transformations and magnitudes, variables were transformed (log-transformation for quantitative variables and the arcsine of the square root transformation of the variables expressed as percentages) and standardised to improve linear relationships among them prior to multivariate analysis. Then, the sites were ordered using a Principal Components Analysis (PCA) based on continuous environmental variables to summarise the environmental variation across sites. Sites were also ordinated using a Non-metric MultiDimensional Scaling (nMDS) based on a presence-absence macroinvertebrate family matrix to explore the faunal similarity among sites (using Bray-Curtis distance). PCA and nMDS were performed using PC-ORD 5 (McCune & Grace, 2002). Distance-based

linear models (DistLM: Legendre & Anderson, 1999; McArdle & Anderson, 2001) were performed to assess which environmental variables were related to faunal composition variability (presence-absence matrix) at all sites and for each habitat type (complex systems were not considered). DistLM analysis was carried out using the PRIMER 6.0 software package (Clarke & Gorley, 2006) and final models were selected aiming to minimise the BIC (Bayesian Information Criterion; Schwarz, 1978). Finally, Generalised Linear Models (McCullagh & Nelder, 1989; Crawley, 1993) were employed to explore which environmental variables were associated with family richness (FR) at all sites and for each habitat type (complex systems were not considered). A Gaussian error distribution was assumed for the dependent variables. The final model was constructed following a forward stepwise procedure that included only significant predictors in order to minimise the BIC value for the model. This criterion is structurally similar to AIC (Akaike Information Criterion), but includes a penalty term dependent on sample size and tends to favour simpler models with a reduced number of variables (Johnson & Omland, 2004). GLM were carried out using the *bestglm* package (Mcleod & Xu, 2010) and the statistical computing software R (R-Development core-team, 2010). Predictors that showed a significant linear correlation (Pearson $R \leq -0.60$ or $R \geq 0.60$) were removed to minimise collinearity. The set of uncorrelated predictors that explained the greatest marginal variability was retained for each of the three habitat types considered (all stations, lotic and lentic systems). The quadratic terms of each selected predictor were also taken into account in order to improve the analysis.

Table 2. List of the environmental variables measured for each sampling site.

Type	Code	Description
Geomorphological ^a	area	Basin area drained in each site (ha)
	min.alt	Minimum basin altitude (m.a.s.l.)
	max.alt	Maximum basin altitude (m.a.s.l.)
	mean.alt	Mean basin altitude (m.a.s.l.)
	sd.alt	Basin SD altitude (m.a.s.l.)
	s.slp	Site slope (°)
	b.slp	Basin slope (°)
	sd.slp	SD basin slope (°)
Lithological ^a	% sil	% Siliceous in basin area
	% cal	% Calcareous in basin area
	% eva	% Evaporitic in basin area
Land uses ^a	% nat	% Natural area in basin area
	% dry	% Non-irrigated agriculture in basin area
	% urb	% Urban area in basin area
Climatic ^a	b.temp	Mean basin annual temperature (°C)
	jan.temp	Mean basin January temperature (°C)
	jul.temp	Mean basin July temperature (°C)
	b.prec	Mean basin annual precipitation (mm)
	jul.prec	Mean basin July precipitation (mm)
	% jul	% July precipitation
	oct.prec	Mean basin October precipitation (mm)
	% oct	% October precipitation
Site ^b	Cond	Site water conductivity (µS/cm)
Dummy variable	Lotic=1	Lotic habitat
	Med=1	Mediterranean climate

^a Variables measured using GIS^b Variables measured in field sampling

Code corresponds to the codes used in Figures 2 and 3.

“SD”=Standard Deviation

Richness pattern congruence

Surrogate taxa have been used in several ways to monitor or solve conservation problems (Caro & O'Doherty, 1999; Ormerod et al., 2010). Here, the indicator value of each taxonomic group was investigated by examining the degree to which their family richness patterns correlated with the richness patterns of other groups. Specifically, the term “biodiversity surrogate” has been used in reference to taxonomic groups for which patterns of family richness are indicative of similar patterns for other taxa in the region (*sensu* Pearson, 1994). For this purpose, Coleoptera, Hemiptera, Plecoptera, Trichoptera, Ephemeroptera,

Mollusca, Odonata orders and EPT metric (family richness of Ephemeroptera, Trichoptera and Plecoptera combined) were used because they displayed the most accurate taxonomic information. Spearman correlation values were applied between the family richness values of these different groups and the remaining richness (RR), i.e., overall richness minus that of the studied group, both globally (using all sampling sites) and separately for lotic and lentic sites to refine the results. To choose potential richness surrogates, only the significant correlations were retained ($p < 0.05$). Spearman correlations were used because data were not normally distributed and they were carried out using the Statistica 6.1 software.

3. Results

Representation of aquatic macroinvertebrates in mountainous Spanish national parks

A total of 93 macroinvertebrate families were recorded in 81 sites sampled from the six national parks. With 73 families recorded, Cabañeros and Picos de Europa were the richest parks (Table 3 and Appendix 2). In contrast, the park with the lowest richness was Aigüestortes, with only 44 families recorded.

Collector's curves showed that at least 75% of the total families estimated for each park had already been recorded in the samples (Table 3). In this sense, the inventories of Sierra Nevada and Picos de Europa reached completeness values above 90%, whereas the inventory of Aigüestortes represented just 75% of the total number of families estimated. The 6 parks combined accounted for 66.2% of the families included in the proposed checklist according to the estimated value obtained by the collector's curves. Cabañeros and Picos de Europa Parks presented the highest representativeness values, containing 60.7% and 55.2% of families registered in the total Iberian checklist, respectively. Although the same number of families has been recorded for both parks, the number of families estimated for Cabañeros was higher (see Table 3), which explains the varying degrees of representativeness.

Table 3. Number of sites sampled (Sites), number of observed (S obs) and estimated taxa (S exp) for each national park (obtained by Collector's curves). For each park, the completeness degree (% Compl) and percentage of taxonomic representation in relation to the Spanish macroinvertebrate checklist (n=145) are also displayed (using estimated values).

National Park	Sites	S obs	S exp	% Compl	% of Spanish list
Aigüestortes	8	44	59	74.6	40.7
Cabañeros	13	73	88	83.0	60.7
Ordesa	12	58	71	81.7	49.0
Picos de Europa	21	73	80	90.9	55.2
Sierra Nevada	15	55	59	93.2	40.7
Monfragüe	12	52	64	81.3	44.1
Total	81	93	96	96.9	66.2

Environmental variables shaping freshwater communities

The first PCA axis explained 46.1% of the environmental variable variance representing a climatic gradient (Fig. 2). This axis was positively correlated with temperature variables and negatively correlated with precipitation variables. Regarding the first axis, sites belonging to Aigüestortes, Picos de Europa and Ordesa were placed on the left of the figure, as the climate is wetter in the northern Iberian Peninsula. In contrast, Cabañeros, Monfragüe and Sierra Nevada were placed on the right, because they are subjected to the Mediterranean climate, which exhibits higher temperatures and less precipitation. The second axis accounted for 14.9% of the variance, likely due to a mixed gradient (land use and geological variables: %Natural and %Dryland farming in basin area; lithology with: %Siliceous and %Calcareous).

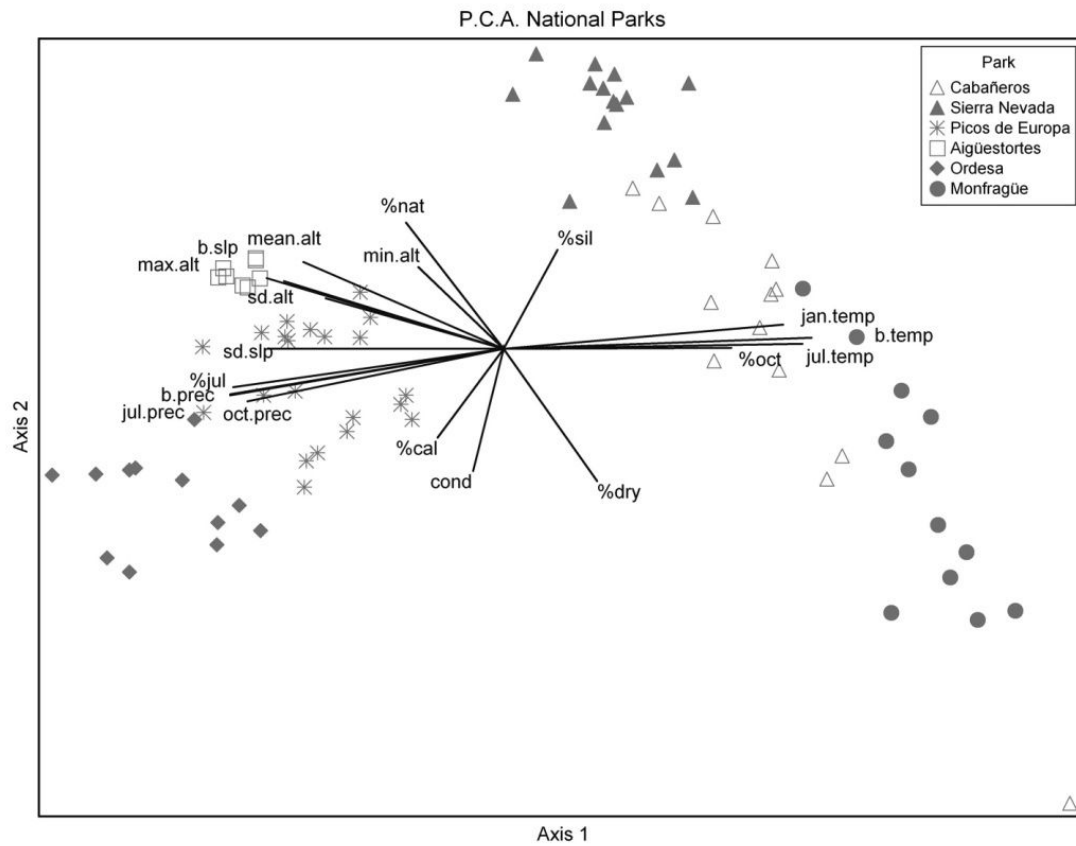


Figure 2. PCA ordination plot based on environmental variables. See Table 2 for the variable codes.

The nMDS plot established two distinct groups that consisted of lotic and lentic ecosystems (Fig. 3). Sites classified as complex systems appeared dispersed and often interspersed between lotic and lentic sites. Moreover, lotic sites were placed on the left of the plot and were better clustered in comparison to the lentic habitats (right-part). The best two-dimensional solution ordination had a stress value of 0.18.

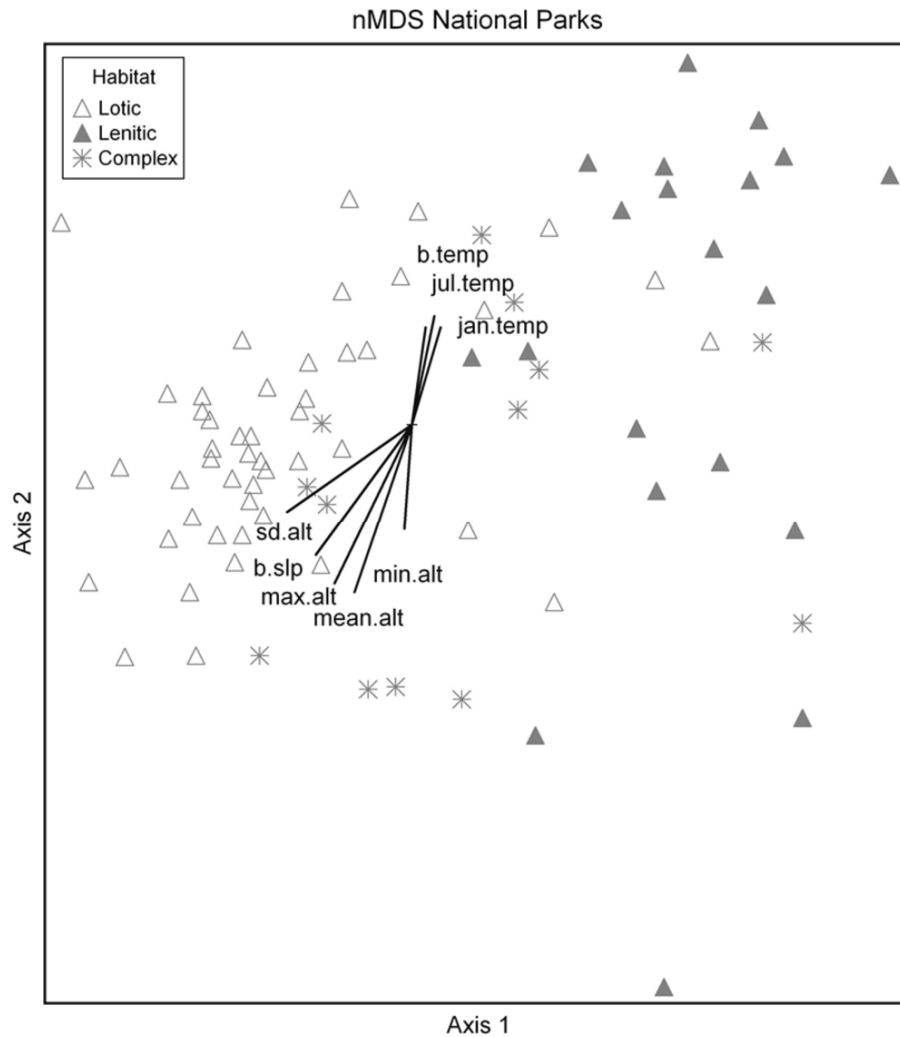


Figure 3. n-MDS plot based on the presence-absence taxonomic matrix. Sites are labelled in relation to macro habitat type (see Table 2 for variable codes). Stress=0.18.

The final DistLM model was constructed using maximum altitude and habitat type (lotic habitat) as predictors; this explained 33% of variance for the composition of the whole macroinvertebrate community. In lotic ecosystems, a model including basin slope and mean July precipitation explained 32.4% of total variability. When only lentic habitats were used, the final model included only maximum altitude and explained 26.1% of community composition variability (Table 4).

Table 4. Results of DistLM relating macroinvertebrate community structure and environmental factors for all sites, lotic and lentic systems. *Pseudo-F*: test statistic; % *Cum. Variance*: cumulative percentage of explained variance after entering this variable; *BIC*: Bayesian Information Criterion. See Table 2 for the variable codes.

All sites				
Variable	<i>Pseudo-F</i>	<i>P</i>	% <i>Cum. Variance</i>	<i>BIC</i>
max.alt	18.903	0.001	19.3	610.9
Lotic	16.012	0.001	33.1	600.3
Lotic systems				
Variable	<i>Pseudo-F</i>	<i>P</i>	% <i>Cum. Variance</i>	<i>BIC</i>
b.slp	15.392	0.001	25.1	336.9
jul.prec.	4.873	0.001	32.4	335.9
Lentic systems				
Variable	<i>Pseudo-F</i>	<i>P</i>	% <i>Cum. Variance</i>	<i>BIC</i>
max.alt	6.36	0.001	26.1	152.2

GLM explained 46% of family richness variance for all sites, using habitat type, the quadratic term of dryland farming percentage and the continuous variable percentage of siliceous soil ($FR = 0.75 \text{ Lotic} - 0.05 \%dry^2 + 0.12 \%sil + 2.52$) as predictors (Table 5). For lotic habitats, the quadratic dryland farming percentage term accounted for 21.5% of family richness variability ($FR = -0.07 \%dry^2 + 3.29$), while the percentage of calcareous rocks and minimum altitude explained 72.1% of family richness variability in lentic sites ($FR = -0.18 \text{ min.alt} - 0.34 \%cal + 2.36$).

Table 5. Results of GLM relating taxon richness and environmental variables for all sites, lotic and lentic systems. % Cum. Dev.: accumulated percentage of explained deviance; BIC: Bayesian Information Criterion. See Table 2 for the variable codes.

All sites				
Variable	Coefficient	p-value	% Cum. Dev.	BIC
Intercept	2.52	<0.0001	/	-78.46
Lotic	0.75	<0.0001	36.7	-111.05
% dry ²	-0.05	<0.01	42.4	-114.41
% sil	0.12	<0.05	46.0	-115.22
Lotic systems				
Variable	Coefficient	p-value	% Cum. Dev.	BIC
Intercept	3.29	<0.0001	/	-90.91
% dry ²	-0.07	<0.001	21.5	-98.69
Lentic systems				
Variable	Coefficient	p-value	% Cum. Dev.	BIC
Intercept	2.36	<0.0001	/	-26.95
% cal	-0.34	<0.001	62.1	-43.40
min.alt	-0.18	<0.05	72.2	-46.49

Potential macroinvertebrate richness surrogates

Considering all of the sites, the number of Coleoptera, Trichoptera, Plecoptera, Ephemeroptera families and the EPT (Ephemeroptera, Plecoptera and Trichoptera) metric were significantly correlated with the total number of families, as well as their respective remaining richness values (Appendix 3). Among them, Coleoptera family richness showed the highest correlation coefficient with total family richness ($r=0.860$; $p<0.001$) and the remaining richness value (0.784; $p<0.001$, Fig.4). Coleoptera was the order that reached the highest correlation scores with the different taxonomic groups, as it was significantly correlated with all of them except for Mollusca (Appendix 3).

When sites were grouped by habitat type in lotic ecosystems, the family richness of Coleoptera (0.715), EPT (0.513), Ephemeroptera (0.526) and Trichoptera (0.552) displayed significant correlations ($p<0.001$) with their RR values (Fig. 4 and Appendix 3). Odonata (0.410) and Plecoptera (0.308) were also

significantly correlated with their RR, albeit with lower significance levels. In lentic habitats (Fig. 4 and Appendix 3), the family richness of Odonata (0.623; $p < 0.01$), Coleoptera and Hemiptera (0.531 and 0.519; $p < 0.05$) were the only groups that significantly correlated with their RR.

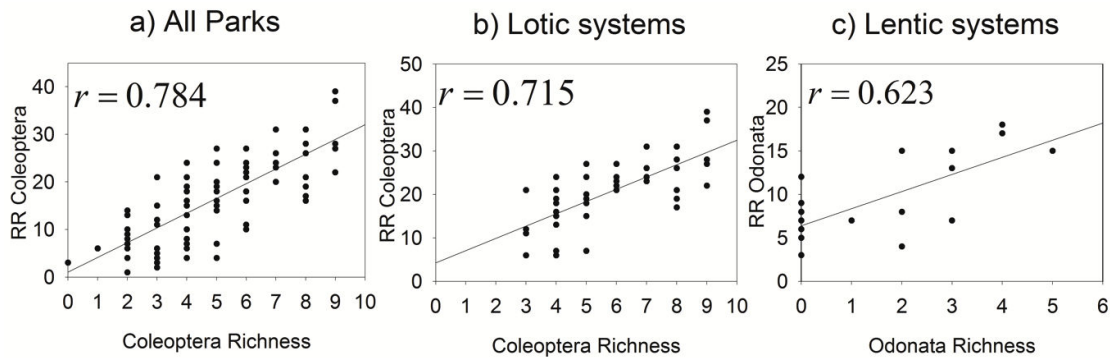


Figure 4. Relationship between proposed richness surrogates and the remaining richness (RR), i.e., overall richness minus that of the studied group. Spearman correlation values (r) were applied both globally (fig. 4a; $p < 0.001$) and separately for lotic (fig. 4b; $p < 0.001$) and lentic sites (fig. 4c; $p < 0.01$).

4. Discussion

The results of this study demonstrate that mountainous national Spanish parks contain an important percentage of the overall Iberian biodiversity concerning aquatic macroinvertebrates at the family level (almost 70%), since many of the unrepresented macroinvertebrate families would inhabit environments not included in the studied parks, such as aquatic lowland ecosystems and saline habitats (Boix et al., 2007).

Results showed that macroinvertebrate inventories compiled for the mountainous Spanish national parks (as a whole) can be considered reasonably complete as more than 95% of the expected families (predicted by collector's curves) have already been found. Although most of the parks have relatively complete inventories at the family level (generally over 75%), further sampling efforts are recommended in Aigüestortes in order to reach higher completeness values (Jiménez-Valverde & Hortal, 2003; Sánchez-Fernandez et al., 2008a).

Within each family some species may be widely distributed while others are restricted and rare, so by using higher taxonomic levels a greater part of a species' biogeographical and evolutionary history can be overlooked (Ribera, 2000; Bonada et al., 2009). Nevertheless, with a reasonable sampling and processing effort this taxonomic level allows one to work with almost the entire invertebrate community.

Cabañeros National Park should be highlighted among those with the highest estimated richness values, and consequently, the highest representative values of Iberian aquatic macroinvertebrate biodiversity (Table 3). Such high richness is probably the result of the wide environmental and topographic heterogeneity that exists in this park (Verdú et al., 2011) together with less extreme climatic conditions in comparison to the remaining parks (except for Monfragüe). It is characterised by Mediterranean mountainous and forested areas of medium altitude alternating with vast expanses of flat pastureland (Vaquero de la Cruz, 1997). This spatial configuration allows a high diversity of aquatic ecosystems (ranging from mountain streams and rivers to ponds, peat-bogs, etc.) resulting in a higher possibility of colonisation by a greater diversity of aquatic invertebrates. Although it would be interesting to conduct studies at the species

level to corroborate this result, the results of the present study are in agreement with several former studies of different taxonomic groups that pointed out the interest of this park (e.g., Rey Benayas & De la Montaña, 2003; Numa et al., 2009).

Variables related to altitude and habitat type seem to be the most important factors associated with macroinvertebrate community composition. Meanwhile, lithology, land use and, in particular, habitat type (presence of lotic systems) seem to be the most important factors in predicting family richness in the national parks as a whole. The differences between lotic and lentic systems in terms of heterogeneity, stability and other physical constraints could explain the distinctive faunal compositions and richness found (Bonada et al., 2005; Millán et al., 2006; Ribera, 2008). Lotic sites such as streams are often more diverse in habitat composition than lentic sites, including not only pool-riffle sequences along the course (Vannote et al., 1980; Allan & Castillo, 2007), but also different micro-habitats at reach scale (Allan et al., 1997). This fact may allow the presence of a higher number of taxa in comparison to pools or lakes, where the more uniform environment and lower availability of meso and micro-habitats could restrict the occurrence of some taxa.

In the present study, the most significant factor associated with community composition within lentic ecosystems was maximum basin altitude, while richness patterns were mainly affected by calcareous lithology (% of basin drained in each site) and basin altitude. Hence, the richest lentic sites were generally those located at lower altitudes with low percentages of calcareous rocks. This result is in agreement with other studies, thereby showing that altitude is one of the most important factors in determining macroinvertebrate community composition and structure in lentic habitats (Oertli et al., 2000; Füreder et al., 2006; Bagella et al., 2010). Furthermore, extreme altitude may affect aquatic community composition through a lack of resources, energy and extreme climatic conditions (Füreder et al. 2006, Mendoza & Catalan, 2010). Ponds also play an important role in conserving aquatic biodiversity (Biggs et al., 2005; Picazo et al., 2010) mainly in terms of rare or endemics taxa at high altitudes (Millán et al., in press).

On the other hand, greater dissimilarities were found in aquatic communities inhabiting lotic environments in sites with large variations in basin slope and minimum precipitations. However, it is likely that these different

communities harbour a similar number of families. In lotic environments, only 21.5% of richness variability could be explained by the model obtained. Thus, although it is difficult to find useful variables to accurately discriminate between rich and poor lotic sites, the percentage of dryland farming seems to be pertinent in predicting richness in lotic sites.

As expected, macroinvertebrate richness was related to land use (Harding et al., 1998; Bis et al., 2000) for both models constructed using all sampling sites as well as just lotic sites. The presence of the negative quadratic term in the percentage of dryland farming apparently matched the intermediate disturbance hypothesis (Connell, 1978), showing that the moderate presence of non-irrigated crop surface in the basin area is accompanied by higher macroinvertebrate richness at site-scale. However, this result should be considered carefully, because extending non-irrigated agricultural areas in national parks could lead to the extinction of local or regional populations of sensitive rare species and the replacement of more tolerant taxa. In this sense, the authors wish to emphasise the importance of complementing this study with further research at a finer taxonomic resolution in order to address the role of these protected areas in the context of freshwater biodiversity conservation, especially concerning rare and endemic species.

Surrogates of aquatic macroinvertebrate biodiversity in mountainous Spanish national parks

Coleoptera family richness seemed to be the best surrogate in the present study. Sites where a high number of water beetle families occurred were also characterised by high family counts of other taxa. This insect group exhibited the strongest correlation with the remaining family richness when overall and only lotic sites were considered. Coleoptera met most of the features surrogates need to be considered as good biodiversity surrogates (Caro & O'Doherty, 1999). Furthermore, this group covers a reasonably wide geographic range, occurs in a broad spectrum of habitat types, and appeared in practically all of the studied sites. Water beetles have already been proposed as aquatic biodiversity indicators for the Segura River basin, in the Mediterranean region (Sánchez-Fernández et al., 2006) and also in ponds in the southern UK (Bilton et al., 2006). In addition, in

terms of biodiversity conservation, water beetles have been frequently used to identify priority conservation areas (Foster et al., 1990; Sánchez-Fernández et al., 2004; Abellán et al., 2005, 2007). As other authors have pointed out, Odonata could be used as the best indicator of a pond's diversity, not only for macroinvertebrates (Briers & Biggs, 2003) but also for aquatic plants (Sahlén & Ekestubbe, 2001). Thus, in accordance with these results, both groups could be selected as aquatic biodiversity indicators in the ecosystems of well-preserved, mountainous areas in the Iberian Peninsula and could also be complementarily used for rapid and inexpensive biodiversity monitoring to select future areas with great aquatic biodiversity value. Because there is a high taxonomic composition similarity at the family level between the different Mediterranean climate zones, such as the Mediterranean Basin, California or South Africa (Bonada et al., 2008), further research could be focussed on testing the applicability of Coleoptera and Odonata as richness surrogates at a broader geographic scale.

Other macroinvertebrate groups, such as EPT taxa, that have proven useful as indicators of freshwater system health (Wallace et al., 1996), seem to perform worse than Coleoptera as indicators of overall macroinvertebrate biodiversity and very poorly as biodiversity surrogates for lentic water bodies. This is not surprising, since taxa belonging to EPT are generally scarce or even absent in lentic habitats, as well as in many natural ecosystems such as temporary streams, saline streams, lakes, ponds or wetlands (e.g., Feminella, 1996; Boix et al., 2007; Millán et al., 2011).

Further studies on conservation surrogates could have a more powerful impact by focussing on how the composition of each group (as well as its richness) acted as surrogate.

Conservation implications

A number of authors have noted that the coverage of biodiversity in existing protected areas is inadequate in several regions, both worldwide and at various geographic scales (e.g., Powell et al., 2000; Hopkinson et al., 2000; Bruner et al., 2001; Scott et al., 2001; Rodrigues et al., 2004; Abellán et al., 2007). The inadequacy of conservation strategies to protect aquatic invertebrate biodiversity was emphasised in Mediterranean wetlands (Gascón et al., 2009) and also for

endemic water beetles of the Iberian Peninsula and Balearic Islands (Sánchez-Fernández et al., 2008b) and the Segura River basin (Abellán et al., 2007).

Although most parks were not designed with freshwater conservation in mind, these findings show that the Spanish National Park Network performs relatively well in representing the diversity of macroinvertebrate families in Iberian freshwaters. However, one should consider representative and diverse aquatic ecosystems in order to gather the greatest range of taxa for the conservation of aquatic invertebrate biodiversity. According to the results of the present study, selecting several diverse lotic and lentic water-bodies at different altitudes seemed to be essential in representing the widest range of Iberian freshwater diversity. The most fundamental difference between terrestrial and freshwater conservation planning is the required spatial configuration of potential protected areas (Linke et al., 2008). Since the protection of extreme high-altitude environments should be easier due to the lack of economic interest and human activities in these areas, the main challenge is to get adequate protection for medium and low-altitude areas.

In this sense, maintenance within protected areas of some controlled areas with traditional agricultural activities, such as cereal crops or controlled grazing, could result in a variegated landscape that promotes habitat diversity, and therefore, increases biodiversity (Verdú et al., 2000; Rey Benayas et al., 2007). However, although for macroinvertebrates the number of families and species highly correlates (Sánchez-Fernández et al., 2006) these results do not allow direct conclusions to be made concerning the protection of rare and endemic species. Therefore, to achieve an effective preservation of biodiversity, it is crucial that these practices do not negatively affect the occurrence of rare and endemic taxa, which generally have specific environmental requirements scarcely considered in protection policies (Sánchez-Fernández et al., 2008b). Thus, managing the entire catchment area appears to be the core strategy for freshwater biodiversity conservation (Abellán et al., 2007; Nel et al., 2009), since the occurrence of aquatic species within a protected area is not a guarantee of long-term survival, as freshwater ecosystems can be affected by activities within the catchment area but outside park boundaries.

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Supplementary material

Appendix 1: Site name, Park and Habitat.

id_code	Site	Park	Habitat
771	Río Estena en Rocigalgo (puente)	Cabañeros	Lotic
1000	Manantial del estrecho del labradillo	Cabañeros	Complex
1001	Laguna de los cuatro cerros	Cabañeros	Lentic
1002	Turbera 1 en el arroyo Brezoso (aguas abajo)	Cabañeros	Lentic
1003	Turbera 2 en el arroyo Brezoso (aguas arriba)	Cabañeros	Lentic
1011	Barranco del Chorro	Cabañeros	Lotic
1012	Fuente de las chinás. Aguas arriba Boquerón del Estena	Cabañeros	Lotic
1013	Arroyo de los pescados	Cabañeros	Complex
1014	Arroyo del Brezoso	Cabañeros	Lotic
1015	Río Estena en La Gargantilla	Cabañeros	Lotic
1025	Fuente del rostro	Cabañeros	Complex
1026	Arroyo de los Reales	Cabañeros	Lotic
1027	Río Estena antes del Boquerón del Estena	Cabañeros	Lotic
1041	Arroyo de Ubeire	Sierra Nevada	Lotic
1042	Arroyo de la fuente encañada	Sierra Nevada	Lotic
1043	Río Isfalada	Sierra Nevada	Lotic
1044	Surgencia en la cara sur del Chullo	Sierra Nevada	Complex
1045	Arroyo en cara norte puerto de la Ragua	Sierra Nevada	Lotic
1046	Arroyo del Palancón	Sierra Nevada	Lotic
1047	Barranco de Horcajo	Sierra Nevada	Lotic
1048	Barranco de Ohanes	Sierra Nevada	Lotic
1049	Río Bermejo	Sierra Nevada	Lotic
1050	Poza y fuente en el Pinar de la Loma	Sierra Nevada	Complex
1051	Río Chico	Sierra Nevada	Lotic
1052	Río Dúrcal	Sierra Nevada	Lotic
1053	Laguna de Aguas Verdes	Sierra Nevada	Lentic
1054	Rio Genil (Confluencia Bco. San Juan-Rio Vadillos)	Sierra Nevada	Lotic
1055	Barranco de la Venta	Sierra Nevada	Lotic
1084	Hoyos de Lloroza	Picos de Europa	Lentic
1085	Turbera en las Llamas	Picos de Europa	Lentic
1086	Confluencia río Cares y Arroyo de las Brañas	Picos de Europa	Lotic
1087	Río de los Reguerones	Picos de Europa	Complex
1088	Riega en los prados de Urúy	Picos de Europa	Lotic
1089	Río Dujé en Llosa la Cal	Picos de Europa	Complex
1090	Lago Ercina	Picos de Europa	Lentic
1091	Fuente de los lobos (camino de Sotres a Bejes)	Picos de Europa	Lentic
1092	Fuente en las Vegas del Toro	Picos de Europa	Lentic
1093	Canal del Valle	Picos de Europa	Lotic
1094	Río Sella después del puente de Angoyo	Picos de Europa	Lotic
1095	Río de Bulnes (antes de su desembocadura en el Cares)	Picos de Europa	Lotic
1096	Río Cares en el puente de la Jaya	Picos de Europa	Lotic
1097	Arroyo del Lago Enol	Picos de Europa	Lotic
1098	Charca en el collado Llomba Cangas	Picos de Europa	Lentic
1099	Río Urdón antes de su confluencia con el Deva	Picos de Europa	Lotic
1100	Río Nevandi en Las Llavias	Picos de Europa	Lotic
1101	Río Dobra antes de su confluencia con el Sella	Picos de Europa	Lotic

1102	Río Zalambra en la central hidroeléctrica de Pío	Picos de Europa	Lotic
1103	Arroyo y charca en la fuente de la salud	Picos de Europa	Complex
1104	Riega El Bañe (tributario del arroyo de Urdías)	Picos de Europa	Lotic
1105	Estany de Llebre	Aigüestortes	Lentic
1106	Riu de Sant Nicolau entrada Estany de Llebre	Aigüestortes	Lotic
1107	Riu de Sant Nicolau (arriba)	Aigüestortes	Complex
1108	Font del Forn de la Pega	Aigüestortes	Complex
1109	Riu de Sant Nicolau salida Estany Llong	Aigüestortes	Complex
1110	Riu Noguera de Tor	Aigüestortes	Lotic
1111	Riu Escrita (Estany de Sant Maurici)	Aigüestortes	Lotic
1112	Confluencia Bco. de les Agudes y Riu Escrita	Aigüestortes	Lotic
1113	Barranco Forcallos	Ordesa	Lotic
1114	Barranco Forca Martín	Ordesa	Lotic
1115	Río Bellós en La Barona	Ordesa	Lotic
1116	Río Guampe en Buisán	Ordesa	Lotic
1117	Río Arazas en el Puente del Fresno	Ordesa	Lotic
1118	Fons d'Olibán	Ordesa	Complex
1119	Fuen Roya	Ordesa	Lotic
1120	Barranco Cotatuero	Ordesa	Lotic
1121	Manantial junto a Camping de Bujaruelo	Ordesa	Complex
1122	Charca en pared rezumante junto a la pista del Camping de Bujaruelo	Ordesa	Lentic
1123	Ibón de Marboré (Balcón de Pineta)	Ordesa	Lentic
1124	Charca pequeña en Balcón de Pineta	Ordesa	Lentic
1126	Charca en Villarreal de San Carlos	Monfragüe	Lentic
1127	Abrevadero en Villarreal de San Carlos	Monfragüe	Lentic
1128	Arroyo de Malvecino	Monfragüe	Lotic
1129	Charca junto a la carretera Villarreal-Embalse de Torrejón	Monfragüe	Lentic
1131	Arroyo de las Cansinas	Monfragüe	Lotic
1132	Charca entre Serradilla y la Garganta del Fraile	Monfragüe	Lentic
1133	Arroyo de Trasierra (Garganta del Fraile)	Monfragüe	Lotic
1134	Arroyo de Barbaón	Monfragüe	Lotic
1135	Charca camino de Villarreal a Serradilla, antes del Ayo. de Barbaón	Monfragüe	Lentic
1156	Arroyo gargantilla en cola embalse Torrejón	Monfragüe	Lotic
1157	Charca abrevadero en cauce arroyo de las cansinas	Monfragüe	Lentic
1158	Arroyo de la vid, bajo puente carretera Villarreal-Torrejón	Monfragüe	Lotic

Appendix 2: Taxa list showing their occurrence in the six national parks.

Taxa	Parks					
	Cabañeros	Sierra Nevada	Picos de Europa	Aigüestortes	Ordesa	Monfragüe
Aeschnidae	1	0	1	1	1	1
Ancylidae	1	0	1	0	0	1
Aphelocheiridae	1	0	0	0	0	0
Aranei	1	1	1	0	1	0
Athericidae	1	0	1	1	1	0
Baetidae	1	1	1	1	1	1
Beraeidae	1	1	0	0	0	0
Blephariceridae	0	1	1	0	1	0
Brachycentridae	0	1	1	0	1	0
Caenidae	1	0	1	0	1	1
Calopterygidae	1	0	0	0	0	0
Ceratopogonidae	1	1	1	1	1	1
Chironomidae	1	1	1	1	1	1
Chloroperlidae	0	0	1	1	1	0
Coenagrionidae	1	0	1	1	0	1
Cordulegasteridae	1	1	1	0	1	1
Corixidae	1	1	1	0	1	1
Culicidae	1	1	1	0	0	1
Dixidae	1	1	1	1	1	1
Dryopidae	1	1	1	0	1	1
Dytiscidae	1	1	1	1	1	1
Elmidae	1	1	1	1	1	1
Ephemerellidae	1	1	1	1	1	0
Ephemeridae	1	1	1	0	1	0
Erpobdellidae	1	1	1	1	0	0
Gammaridae	0	0	1	0	0	1

Taxa	Cabañeros	Sierra Nevada	Picos de Europa	Aigüestortes	Ordesa	Monfragüe
Gerridae	1	1	1	1	1	1
Glossiphoniidae	1	1	1	0	0	1
Glossosomatidae	1	0	0	0	0	0
Goeridae	0	0	0	1	0	0
Gomphidae	1	0	0	0	0	1
Gordiidae	0	0	1	0	0	0
Gyrinidae	1	0	1	0	1	1
Haliplidae	1	1	1	0	1	1
Hebridae	1	1	1	0	1	0
Helophoridae	1	1	1	0	1	1
Heptageniidae	1	1	1	1	1	0
Hydracarina	1	0	1	1	1	0
Hydraenidae	1	1	1	1	1	1
Hydrobiidae	0	0	1	1	0	0
Hydrochidae	1	1	1	0	0	1
Hydrometridae	1	1	1	0	1	1
Hydrophilidae	1	1	1	1	1	1
Hydropsychidae	1	1	1	1	1	1
Hygrobiiidae	0	0	0	0	0	1
Lepidostomatidae	1	1	0	1	0	0
Leptoceridae	1	0	0	0	0	0
Leptophlebiidae	1	0	1	1	1	1
Lestidae	1	0	1	0	0	1
Leuctridae	1	1	1	1	1	1
Libellulidae	1	0	1	1	0	1
Limnephilidae	1	1	1	1	1	1
Limoniidae	1	1	1	1	1	1
Lumbricidae	1	1	1	1	1	0
Lymnaeidae	0	0	1	1	1	0
Mesoveliidae	0	0	0	0	0	1

Taxa	Cabañeros	Sierra Nevada	Picos de Europa	Aigüestortes	Ordesa	Monfragüe
Naucoridae	1	0	0	0	0	1
Nematoda	0	1	0	0	0	0
Nemouridae	1	1	1	1	1	0
Nepidae	1	1	1	0	1	1
Noteridae	1	0	0	0	0	1
Notonectidae	1	1	1	0	1	1
Odontoceridae	0	0	1	1	1	0
Oligochaeta	0	0	1	0	0	1
Ostracoda	1	0	1	0	1	1
Perlidae	1	1	1	1	1	0
Perlodidae	0	1	1	1	1	0
Philopotamidae	1	1	1	1	1	1
Physidae	1	0	0	0	0	1
Planariidae	1	1	1	1	1	1
Planorbidae	1	0	0	0	0	0
Platycnemididae	1	0	0	0	0	0
Pleidae	1	0	1	0	0	1
Polycentropodidae	1	1	1	1	1	0
Potamanthidae	1	0	0	0	0	0
Psychodidae	1	1	1	0	1	0
Psychomyiidae	1	0	1	0	1	0
Ptychopteridae	0	1	1	0	0	0
Rhagionidae	0	0	1	0	1	0
Rhyacophilidae	1	1	1	1	1	1
Saldidae	0	1	0	0	0	0
Sciomyzidae	0	0	1	0	0	0
Scirtidae	1	1	1	1	1	1
Sericostomatidae	1	1	1	1	1	0
Sialidae	1	0	1	1	1	1

Taxa	Cabañeros	Sierra Nevada	Picos de Europa	Aigüestortes	Ordesa	Monfragüe
Simuliidae	1	1	1	1	1	1
Sphaeriidae	1	1	1	1	1	1
Stratiomyidae	1	1	1	0	1	0
Syrphidae	0	1	0	0	0	0
Tabanidae	1	1	1	0	1	1
Tipulidae	1	1	1	1	1	1
Valvatidae	0	0	0	1	0	0
Veliidae	1	1	1	1	1	1
Total	73	55	73	44	58	52

C) Results of pairwise Spearman correlation coefficients for the family richness of the groups of taxa studied only in lentic systems (20 sites).

EPT: Ephemeroptera, Plecoptera, Trichoptera. TFR: Total Family Richness; RR: Remaining richness. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

[illegible]

Chapter 2:

Cross-taxon congruence in wetlands: assessing the role of waterbirds as surrogates of macroinvertebrate biodiversity in Mediterranean Ramsar sites



Laguna del Chinche (Jaén)

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Abstract and keywords

Wetlands are among the most threatened habitats and the species they support among the most endangered taxa. Measuring and monitoring wetland biodiversity is vital for conservation, restoration and management, and often relies on the use of surrogate taxa. Waterbirds are commonly used as flagships of biodiversity and are the subject of major conservation initiatives. Therefore, it is important to assess the extent to which waterbirds indicate the general biodiversity of wetlands and serve as surrogates.

We explore the relationships between community composition and species richness of waterbirds and aquatic macroinvertebrates in 36 Ramsar wetlands in southern Spain to assess if waterbirds are good surrogates for other taxonomic groups. Specifically, we aimed to i) test the congruence of patterns of species composition and richness among waterbirds and aquatic macroinvertebrates; and ii) investigate which environmental variables are associated with the biodiversity patterns of waterbirds and macroinvertebrates, with the purpose of identifying key factors explaining potential discordance in these patterns.

We found a limited concordance between assemblage patterns of both taxonomic groups that may be related to their contrasting responses to environmental gradients. Assemblages of waterbirds appear to be more affected by climate variables and water surface area, whereas conductivity was the most important factor influencing macroinvertebrate communities. Furthermore, we found a negligible or inverse relationship in their patterns of richness, with wetlands with higher waterbird species richness showing significantly lower richness of Hemiptera and macroinvertebrate families, and no significance relationship with Coleoptera. In addition, GLM models showed that, in general, different environmental variables are related with the richness patterns of the different taxonomic groups.

Given the importance of the Ramsar convention for the conservation of an international network of wetlands, our findings underline the limited potential of waterbirds as aquatic biodiversity indicators in Mediterranean wetlands, and the need for caution when using waterbirds as flagships. An integrative analysis of different biological communities, using datasets from different taxonomic groups,

is a necessary precursor for successful conservation policies and monitoring. Our results illustrate the need to create a diversified and complete network of protected sites able to conserve multiple components of wetland biodiversity.

Aquatic ecosystems • Ramsar wetlands • Diversity patterns • Waterbirds •
Macroinvertebrates

1. Introduction

Wetlands are among the most threatened habitats and the species they support among the most endangered taxa (Millennium Ecosystem Assessment, 2005). These aquatic ecosystems are considered one of the most important to protect, due to the ecosystem services they provide and the threats they face (Costanza et al., 1997; Junk et al., 2013). Wetlands located in Southern Europe are of special interest due to the biodiversity hotspot in the Mediterranean Basin (Myers et al., 2000) and the strong anthropogenic pressures they suffer (e.g., Ortega et al., 2004). Furthermore, they are expected to suffer acutely from reduced water supply due to global change (Cížková et al., 2013).

Despite the threats affecting freshwater ecosystems, conservation efforts for freshwater biodiversity are constrained by the lack of complete and reliable information for a number of geographic areas, habitat types and taxonomic groups (Dudgeon et al., 2006). Hence, measuring and monitoring biodiversity is a crucial task for conservation or restoration of inland waters in general, and wetlands in particular. Surveying biodiversity presents difficulties associated with limited time and financial resources and often requires a large degree of expertise. Broad-scale assessments of biodiversity often rely on the use of surrogate taxa which show strong relationships with the biodiversity of other target groups, are taxonomically and ecologically well-understood, easily monitored and occur in a range of habitat types (see Rodrigues & Brooks, 2007 for a review). Therefore, the extent to which a particular taxonomic group represents the biodiversity content of a particular ecosystem needs to be assessed as a prerequisite for its use as a surrogate. While the reliability of surrogate or indicator taxa in freshwater systems has been tested in several previous studies for some taxonomic groups (e.g., Bilton et al., 2006; Sánchez-Fernández et al., 2006; see Heino, 2010 for a review), cross-taxon congruence in biodiversity patterns among aquatic invertebrates and vertebrates other than fishes has seldom been assessed.

As taxon richness is probably the main variable used to describe community diversity (Gaston, 1996) most assessments of surrogates basically focus on this aspect (e.g., Velghe & Gregory-Eaves, 2013), while cross-taxon congruence of community structure has received less attention, despite the fact that it can be a

useful indicator of how broad conservation strategies can conserve species diversity (Bilton et al., 2006; Su et al., 2004). Hence, further research is necessary to better understand whether patterns of species richness and composition are congruent between taxonomic groups in aquatic ecosystems.

Birds are commonly used as surrogates of biodiversity owing to the wide availability of relevant data on their distribution and status and their broad popular appeal (e.g., Gregory et al., 2003, Gregory, 2006; Eglington et al., 2012). They are the object of many international nature conservation initiatives, such as the worldwide network of Important Bird Areas, and the Special Protected Areas (EU Birds Directive) in Europe. In the case of inland waters, waterbirds usually drive the designation of wetlands of international importance under the Ramsar Convention, a global intergovernmental treaty for the conservation and sustainable use of wetlands and their resources (Ramsar Bureau, 2000). This Convention was adopted in 1971 and was initially focussed exclusively on waterbirds (particularly wildfowl, F. Anatidae) as a manner of promoting conservation of migratory bird species and identifying key sites for them (e.g., Kleijn et al., 2014). Although the parties to the convention have since listed many criteria for identifying and designating wetlands of international importance which depend on other aquatic organisms and biodiversity in general (<http://www.ramsar.org>, last accessed 7 March 2014) the historical emphasis on waterbirds has been very influential, notably in Europe.

Even though waterbirds play a key functional role in many aquatic ecosystems, with a structuring influence on the communities of invertebrates and macrophytes in wetlands (Green & Elmberg, 2014), their reliability as surrogate taxa in these habitats remains to be tested. Some previous studies have focused on the relationship between communities of waterbirds and plants (Green et al., 2002), zooplankton (Green et al., 2005) or fishes (Paszkowski & Tonn, 2000). Nevertheless, very few studies are available on the congruence in the diversity patterns of waterbirds and macroinvertebrates (but see Rooney & Bayley, 2012).

As important components of wetland biodiversity, aquatic macroinvertebrates and waterbirds are related to each other through trophic webs (e.g., Tománková et al., 2014) and dispersal interactions (Green & Figuerola, 2005), and both of them are widely subjected to various ecological, biomonitoring and

conservation studies. Waterbirds have been tested as indicators of aquatic ecosystem conditions (e.g., Kingsford, 1999), while aquatic macroinvertebrates have been used extensively as indicators for wetland conservation (e.g., Boix et al., 2005) and increasingly as tools for the assessment of freshwater biodiversity and conservation priorities (Bilton et al., 2006; Ormerod et al., 2010).

In the present study we examine the concordance in the patterns of community composition and species richness across waterbirds and aquatic macroinvertebrates in Ramsar wetlands of southern Spain, in order to assess if waterbirds can be a potential surrogate for predicting diversity of other taxonomic groups in wetlands. Ramsar wetlands are good candidates to investigate the cross-taxa congruence in biodiversity patterns because of their relatively good conservation status. Furthermore, they include all the most important wetlands for waterbirds in southern Spain. In this framework we aimed to: i) test the congruence of patterns of species composition and richness among waterbirds and aquatic macroinvertebrates; and ii) investigate the environmental variables associated with the biodiversity patterns of waterbirds and macroinvertebrates, with the purpose of identifying key factors explaining potential discordance in these patterns.

2. Methods

Study area

In Spain, 74 wetlands are designated as Ramsar sites, covering a total of 303,090 ha (as of June 2014). Andalusia represents the region of Spain with the largest Ramsar protected area and the highest number of Ramsar sites (25), including a mosaic of different wetland types ranging from coastal lagoons to riverine and floodplain systems, and permanent or temporal inland lakes and marshes.

The present study was conducted in 36 wetlands included within the 25 Ramsar sites of Andalusia (SW Spain) (Fig. 1, Appendix A). All the studied Ramsar wetlands are also protected areas under regional, national and/or other European legislation (Directive 92/43/ECC and Directive 79/409/EEC) and three of these

wetlands (Doñana, Odiel marshes and Cabo de Gata) are also MAB protected areas (UNESCO Biosphere Reserves).

The size of studied Ramsar site ranges from 35 to 15,246 ha while the mean altitude of wetlands ranges from the sea level to 798 m.a.s.l. According to the freshwater ecoregions of the world proposed by Abell et al. (2008), all the Andalusian wetlands belong to the Southern Iberia region. Climate is conditioned by westerly winds from the Atlantic Ocean and the Mediterranean influence, while rain distribution throughout the year is determined by the Azores High behavior (Rodrigo et al., 1999). Due to its strategic geographical position, this region represents an important bridge between Europe and Africa and a large number of migratory waterbirds move through SW Spain and Morocco (Rendón et al., 2008). One of the sites, Doñana, is one of the two most important wintering sites in Europe for waterbirds (Rendón et al., 2008). The importance of this region is also reflected by how the conservation of waterbirds in Spain can have positive consequences for the conservation of the entire European avifauna (Marfil-Daza et al., 2012; Santoro et al., 2013).

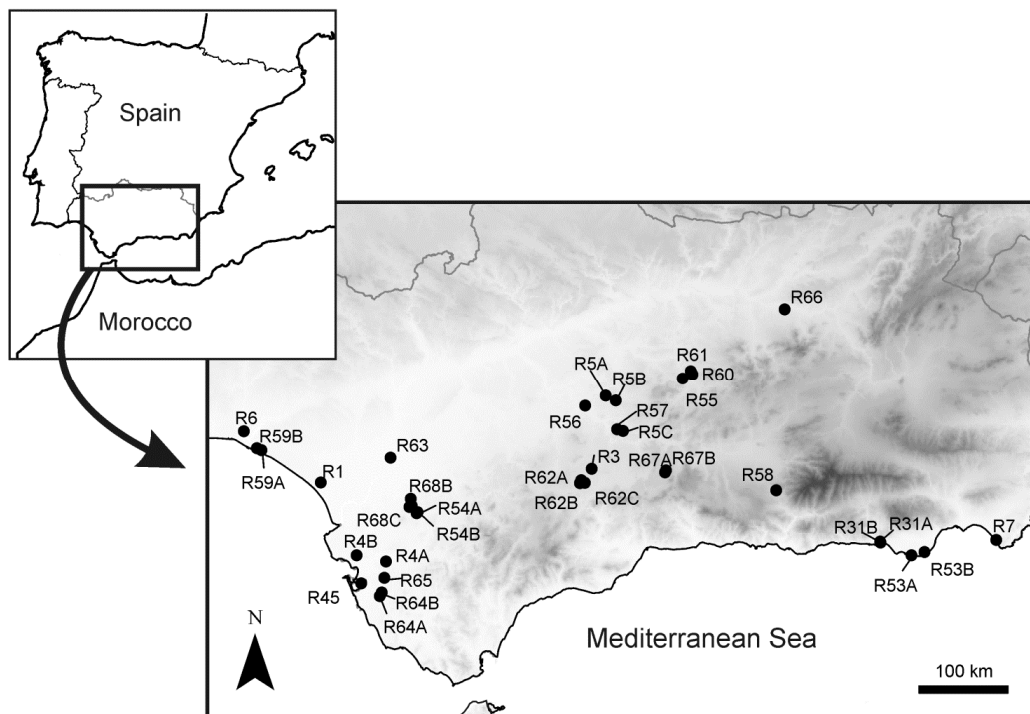


Figure 1. Location of the 36 studied wetlands. Site codes as in Table S1. Topography is given as grey shading, with darker grey indicating higher altitude.

Waterbird and macroinvertebrate data

Waterbird data were obtained from monthly surveys as part of an official monitoring program carried out by the Regional Government of Andalusia which provides a long-term dataset at the species level. For each wetland, we obtained waterbird information for the same year in which macroinvertebrates were collected (see below). Waterbird data were then separated between the winter community (hereafter WW) considering data from November to February, and the spring-summer community (hereafter SW) considering the months from April to August, in order to have a thorough assessment of waterbird biodiversity (Sebastián-González et al., 2010). We also obtained the mean and maximum monthly density of WW and SW communities (expressed as number of birds per hectare of water surface) to test its possible relationship with the macroinvertebrate community (see below). Bird species recorded as vagrants or not dependent on wetlands were excluded from the database prior to analysis.

Macroinvertebrate data were mostly gathered from field surveys at least once between the end of April and June of 2011 (31 out of 36 sites). Additionally, macroinvertebrate data were obtained from Ortega (2001) and Ortega et al. (2004) for “Albufera de Adra” and “Punta Entinas-Salobral”, and from Millán et al. (2005) and the monitoring program of Doñana Biological station (<http://www.ebd.ebd.csic.es/Seguimiento/seguimiento.htm>, last accessed 7 March 2014) for “Doñana”. Finally, macroinvertebrate data for “Salinas de Cabo de Gata” were collected by sampling activities during the summer of 2004 (A. Millán, unpublished data). Late spring and summer generally corresponds to maximum species activity, especially for aquatic insects. Furthermore, samples taken from Mediterranean ecosystems during one particular season may be representative of the pooled annual macroinvertebrate community (Bonada et al., 2007).

Macroinvertebrate samples were collected from a representation of all microhabitat types occurring in each studied wetland with a kick-net of 500 μm mesh, with sampling effort proportional to each habitat occurrence across the littoral zone. Each kick-sample was examined in the field and sampling sites were always consistently surveyed until no further taxa (morphotypes) were found (Jáimez-Cuéllar et al., 2002). Finally, the kick-sample contents were pooled into a unique site-sample and preserved in 96% ethanol. All the macroinvertebrate taxa

were identified in the laboratory to family level (except for Aranei, Ostracoda, Oligochaeta), while Coleoptera and Hemiptera were identified to species level. Thus, for each studied wetland we obtained three values of macroinvertebrate diversity: macroinvertebrate family richness, water beetle species richness and water bug species richness.

The use of higher taxonomic levels (e.g., family) allows analysis for the whole macroinvertebrate community and this metric has been used in numerous macroinvertebrate studies owing to a high correlation with species richness (e.g., Baldi, 2003; Sánchez-Fernandez et al., 2006). Moreover, macroinvertebrate family richness is generally considered among the main biological metrics assessing wetland condition (Mereta et al., 2013).

Among adult insects, only the majority of Coleoptera and Hemiptera are strictly aquatic and they generally represent the most frequently recorded taxonomic groups in wetlands (e.g., Nicolet et al., 2004; Picazo et al., 2012). Furthermore, Coleoptera is one of the most diverse and well known groups of aquatic invertebrates in the Iberian Peninsula (Ribera, 2000) and they have been shown to be sensitive to environmental factors (Menetrey et al., 2011), a good indicator of macroinvertebrate biodiversity (Bilton et al. 2006; Guareschi et al., 2012; Sánchez-Fernández et al., 2006), and useful tools for the identification of priority conservation areas for macroinvertebrates (Foster et al., 1990; Sánchez-Fernández et al., 2004). Besides, both Coleoptera and Hemiptera are key components of waterbird diet in the study area (e.g., Green & Sánchez, 2003).

Environmental variables

Wetlands were characterised using 39 environmental variables describing morphology, hydroperiod, land uses, lithology, climate, connectivity and water chemistry (Table 1) at either site or landscape scales. The water surface of each lagoon, total protected area of the Ramsar site and the distance to the coast were measured using georeferenced aerial photographs (ArcGIS9.3, ESRI, Redlands, CA, USA). Conductivity and pH were measured in situ during macroinvertebrate sampling with an EC meter (TetraConR 325). Mean values of ammonium (NH_4^+) and chlorophyll a (Chl-a) were obtained from the monitoring program “Physico-chemical characterization and hydrology of wetlands in Andalusia, 1997-2010”

carried out by the Regional Government of Andalusia and considering mean values for the last 5 years before data collection or sampling. Additionally, to characterize the trophic state of the wetland a dummy variable (eutrophic, 1 or 0) was used considering the Chl-a limits proposed by OECD (1982). The hydroperiod was also used as a dummy variable (perennial wetland, 1 or 0). For those wetlands sampled during 2011, the ECELS Index (Sala et al., 2004) was also calculated. This Index was specifically developed for Mediterranean wetlands (Sala et al., 2004) and provides a habitat condition value that takes into account littoral morphology, human activity, water appearance and vegetation.

As climatic predictors, we considered the 19 bioclimatic variables from the WorldClim dataset at a spatial resolution of 1km (<http://www.worldclim.org/>; Hijmans *et al.*, 2005). Furthermore, several landscape-scale descriptors were obtained within a 2.5 km radius of each wetland using digital maps in ArcGIS9.3. We considered this radius an appropriate average spatial scale at which waterbirds can interact with the landscape and at which land use influences water quality (Taft and Haig, 2006; Monteagudo et al., 2012). As landscape-scale descriptors can be related to biodiversity (Morelli et al., 2013), we included three geological variables (percentage of siliceous, calcareous and evaporitic substrates, respectively) and four land-use variables (percentage of natural, irrigated agricultural, non-irrigated agricultural and urban land). Digitized maps were obtained from the Regional Government of Andalusia (Lithologic Map of Andalusia, scale 1:400,000, 2004) and the European Environment Agency ("Corine Land Cover 2006"). Finally, as an estimate of the degree of connectivity of each wetland, we calculated its distance to other Ramsar sites (mean distance to the 5 nearest Ramsar sites) and its distance to other wetlands (mean distance to the 10 nearest sites). Wetland distribution in Andalusia was obtained from the Catalogue of Andalusian Wetlands (Regional Government of Andalusia).

Table 1. List of the environmental and biological variables measured for each Ramsar site.

Type	Code	Description
Geography	water_area	* Mean surface area of water (ha)
	R_area	Ramsar protected area (ha)
	Alt	Site altitude (m.a.s.l.)
	dist_coast	Distance to the sea coast
Hydroperiod	Perenn	* Perennial habitat
Connectivity	dist_5R	Mean distance to the next 5 Ramsar sites
	dist_10W	Mean distance to the next 10 wetlands
Water chemistry	Cond	* Site water conductivity ($\mu\text{S}/\text{cm}$)
	pH	* pH data
	chl_a	* Chlorophyll mean value (mg/m^3)
	NH_4^+	* Ammonium mean value (mg/L)
	Eutr=1	* Eutrophic state
Habitat condition	Ecels	ECELS Index
Lithology	% sil	% Siliceous in buffer area
	% cal	* % Calcareous in buffer area
	% eva	% Evaporitic in buffer area
Land use	% nat	* % Natural land in buffer area
	% irr	% Irrigated land in buffer area
	% dry	% Non-irrigated agriculture in buffer area
	% urb	* % Urban land in buffer area
Climate	bio01	Annual Mean Temperature
	bio02	Mean Diurnal Range (Mean of monthly (max temp - min temp))
	bio03	Isothermality (bio02/bio07)
	bio04	Temperature Seasonality (Standard Deviation)
	bio05	Max Temperature of Warmest Month
	bio06	* Min Temperature of Coldest Month
	bio07	Temperature Annual Range (bio05-bio06)
	bio08	Mean Temperature of Wettest Quarter
	bio09	* Mean Temperature of Driest Quarter
	bio10	Mean Temperature of Warmest Quarter
	bio11	Mean Temperature of Coldest Quarter
	bio12	* Annual Precipitation
	bio13	Precipitation of Wettest Month
	bio14	Precipitation of Driest Month
	bio15	Precipitation Seasonality (Coefficient of Variation)
	bio16	Precipitation of Wettest Quarter
	bio17	Precipitation of Driest Quarter
	bio18	* Precipitation of Warmest Quarter
	bio19	Precipitation of Coldest Quarter
Biological data	wint_birds	* Number of waterbird species in winter
	sum_birds	Number of waterbird species in summer
	dens_max_w	* Maximum monthly density of waterbirds (in winter)
	dens_max_s	Maximum monthly density of waterbirds (in summer)

dens_mean_w	Mean monthly density of waterbirds (in winter)
dens_mean_s	Mean monthly density of waterbirds (in summer)
MI_fam	* Number of families of macroinvertebrates
C_sp	* Number of species of Coleoptera
H_sp	* Number of species of Hemiptera

Code corresponds to the codes used in Tables 2-3 and Fig. 2.

A Quarter is a period of three months (1/4 of the year).

* Subset of variables used (not intercorrelated) only for GLM analysis.

Statistical analysis

Analyses were performed using R 3.0.1 software of the R statistical environment (R Development Core Team, 2010). The completeness of taxa inventories generated (for each taxonomic group considered) was assessed using a nonparametric estimator (chao2, function “specpool” of the R package ‘Vegan’; Oksanen, 2011) as suggested by Walther & Moore (2005) and recently tested in Iberian aquatic ecosystems (Martínez-Sanz et al., 2010).

To reduce distribution skewness and avoid distortions, environmental variables were transformed (log-transformation for quantitative variables and logit transformation: $\log(Y/[1-Y])$ for variables expressed as percentages) as recommended by Warton & Hui (2011). Moreover, all explanatory variables were z-standardized (mean = 0, SD = 1).

We used non-metric multidimensional scaling (NMDS) to assess the main patterns in assemblage structure of waterbirds and aquatic macroinvertebrates. We repeated the NMDS using WW data, SW data, aquatic macroinvertebrates (at family level), water beetles (at species level) and aquatic hemipteran (at species level) data. In order to find the optimal ordination solution, we applied the ‘metaMDS’ function implemented in the ‘Vegan’ community ecology package. The analyses were performed on a biological matrix based on presence-absence data and using the Jaccard index between wetland samples to reveal patterns in waterbird and macroinvertebrate assemblages. Linear fittings, using the vegan function ‘envfit’, were performed between the environmental variables and the output of NMDS ordinations in order to identify the environmental factors driving the composition of different biotic communities. The significance of the fitted vectors was assessed using a permutation procedure (9999 permutations).

A Procrustean analysis was also applied to evaluate the degree and significance of community concordance among the NMDS ordinations of the different taxonomic groups. Procrustean rotation analysis is regarded as a robust method for concordance analysis (Peres-Neto & Jackson, 2001) and is frequently used to study aquatic communities (e.g., Virtanen et al., 2009). Three-dimensional NMDS ordinations were compared with the function 'protest' in the vegan package (Oksanen, 2011), a procrustean rotation analysis accompanied by a permutation test.

Spearman correlation values were calculated between the richness values of winter waterbird species, summer waterbird species, families of aquatic macroinvertebrates, Coleoptera species and Hemiptera species to evaluate if those wetlands with high waterbird species richness were also sites with a high level of macroinvertebrate richness (at different taxonomic levels). Furthermore, this method was used to check possible correlations between winter and summer bird species richness. Spearman correlations were applied because the data were not normally distributed.

Generalized Linear Models (Crawley, 1993) were applied to investigate which environmental variables were associated with the richness pattern of each taxonomic group (waterbird species, macroinvertebrate families, water beetle species and hemipteran species) in Ramsar wetlands. GLM analyses were carried out using the *bestglm* R package (McLeod & Xu, 2010). Only a single variable from sets of highly correlated variables (Pearson $R \leq -0.6$ or $R \geq 0.6$) was used in the modeling to minimize collinearity, and a Poisson error distribution was assumed for the dependent variables. Final models were selected to minimize the BIC (Bayesian information criterion) and were constructed including only significant predictors. The BIC criterion is structurally similar to AIC (Akaike information criterion), but includes a penalty term dependent on sample size and tends to favor simpler models with a reduced number of variables (Johnson & Omland, 2004). Finally, outliers and spatial independence of residuals were assessed following Fox & Weisberg (2011) and Zuur et al. (2009) respectively. As patterns of species richness for winter and summer waterbird communities were highly correlated (see results), GLM models were performed considering just the wintering community, which is more diverse (e.g., Rendón et al., 2008).

3. Results

A total of 59 macroinvertebrate higher taxa (56 families plus Aranei, Ostacoda and Oligochaeta) were found in the network of studied wetlands (mean $\pm$ SD for each wetland = 17 ± 6), and 27 (6 ± 3) and 98 (13 ± 8) species of Hemiptera and Coleoptera, respectively. For waterbirds, 90 (23 ± 15) species were considered to belong to the winter community and 88 (24 ± 15) species to the spring-summer community. All species are listed in Supplementary Materials (Appendix B and C). The nonparametric estimator of species richness (chao2) suggested that at least 74% of the true total number of taxa estimated for each taxonomic group were recorded in the samples (mean value of completeness was 86%). Results showed that the datasets compiled for the Andalusian Ramsar network (as a whole) can be considered reasonably complete following the recommendations of numerous authors (e.g., Jiménez-Valverde & Hortal, 2003).

Congruence in community composition and environmental factors

NMDS ordinations of waterbird communities presented a final stress value of 0.09 and 0.10 for the three-dimensional ordination, using WW and SW data respectively (Fig. 2; only first two dimensions displayed). According to the results of the 'envfit' analysis, WW presented a greater number of significant and important variables related to their community composition than SW (Table 2).

The WW community was most strongly related with altitude and water surface area ($r^2=0.69$ and 0.66 respectively, $p=0.0001$, Table 2), as well as with the distance to the coast, lithology (evaporites), land use (particularly percentage of dryland), ECELS index, conductivity, macroinvertebrate and hemipteran richness and numerous climate predictors, among which the mean temperature of the wettest period (bio08) was the most important. On the other hand, SW species composition was mainly related with water surface area and water conductivity ($r^2=0.64$ and 0.61 respectively, $p=0.0001$). Size of the protected Ramsar area, percentage of siliceous lithology, altitude and all the macroinvertebrate richness metrics were also highly related ($p<0.001$). The SW community presented fewer significant climatic predictors than WW, the annual mean temperature (bio01) being the most important.

Table 2. Correlations (r^2) of environmental variables with the NMDS ordinations of WW (Winter waterbird community) and SW (Spring-Summer waterbird community) and the significance of the correlation based on the *envfit* function (9999 permutations). The goodness of fit statistic is the squared correlation coefficient (r^2). Only variables significant for at least one group are displayed. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. See Table 1 for details of the variable codes.

Variable	Winter bird community			Spring-Summer bird community		
	r^2	p -value		r^2	p -value	
water_area	0.66	0.0001	***	0.64	0.0001	***
R_area	0.38	0.0011	**	0.52	0.0004	***
dist_coast	0.56	0.0002	***	0.36	0.0038	**
dist_10W	0.26	0.0261	*	0.14	0.1660	
dist_5R	0.24	0.0266	*	0.03	0.8304	
%sil	0.35	0.0035	**	0.48	0.0004	***
%cal	0.10	0.3184		0.16	0.1340	
%evap	0.56	0.0001	***	0.26	0.0247	*
%urb	0.30	0.0094	**	0.14	0.1788	
%irr	0.49	0.0004	***	0.26	0.0247	*
%dry	0.57	0.0001	***	0.16	0.1307	
%nat	0.27	0.0180	*	0.15	0.1526	
bio01	0.46	0.0003	***	0.42	0.0001	***
bio03	0.25	0.0230	*	0.14	0.2020	
bio04	0.49	0.0001	***	0.30	0.0140	*
bio06	0.50	0.0002	***	0.39	0.0018	**
bio08	0.56	0.0001	***	0.34	0.0054	**
bio12	0.48	0.0001	***	0.37	0.0019	**
bio15	0.38	0.0020	**	0.14	0.1755	
bio18	0.33	0.0051	**	0.38	0.0344	*
Alt	0.69	0.0001	***	0.45	0.0004	***
Cond	0.43	0.0007	***	0.61	0.0001	***
pH	0.04	0.7572		0.35	0.0030	**
MI_fam	0.42	0.0004	***	0.43	0.0007	***
C_sp	0.07	0.4800		0.42	0.0004	***
H_sp	0.60	0.0002	***	0.52	0.0001	***
Ecels	0.49	0.0002	***	0.25	0.0465	*
Perenn	0.16	0.0052	**	0.09	0.0532	

For macroinvertebrate assemblages, the ordination space of the first three axes of the NMDS (Fig. 2) presented a final stress value of 0.11 for coleopterans and 0.13 for macroinvertebrates and hemipterans. Macroinvertebrate composition

(at the family level) was affected principally by water conductivity, percentage of irrigated land use, annual precipitation and the width of the water area (Table 3). Coleoptera species composition was mainly affected by water conductivity, siliceous lithology and annual precipitation. Hemipteran species composition was similarly related to variables important for the previous groups (water surface area, conductivity) but also showed an important relationship with waterbird species richness, especially with WW.

Table 3. Correlations (r^2) of environmental variables with the NMDS ordinations of macroinvertebrates (at family level), Coleoptera and Hemiptera and the significance of the correlation based on the *envfit* function (9999 permutations). The goodness of fit statistic is the squared correlation coefficient (r^2). Only variables significant for at least one group are displayed. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. See Table 1 for details of the variable codes.

Variable	Macroinvertebrate families			Coleoptera species		Hemiptera species		
	r^2	p -value		r^2	p -value	r^2	p -value	
water_area	0.50	0.0001	***	0.20	0.0677	0.57	0.0001	***
R_area	0.29	0.0104	*	0.07	0.4882	0.34	0.0033	**
dist_coast	0.40	0.0015	**	0.26	0.0205	0.36	0.0021	**
%sil	0.40	0.0013	**	0.50	0.0002	0.39	0.0013	**
%cal	0.23	0.0360	*	0.23	0.0373	0.18	0.0972	
%evap	0.38	0.0012	**	0.08	0.4261	0.38	0.0014	**
%urb	0.30	0.0080	**	0.06	0.6047	0.22	0.0437	*
%irr	0.43	0.0008	***	0.13	0.2136	0.19	0.0768	
%dry	0.40	0.0012	**	0.25	0.0238	0.21	0.0530	
bio03	0.10	0.3399		0.01	0.9570	0.29	0.0096	**
bio04	0.27	0.0167	*	0.32	0.0050	0.24	0.0366	*
bio08	0.22	0.0435	*	0.15	0.1518	0.25	0.0247	*
bio12	0.55	0.0007	***	0.52	0.0002	0.22	0.0391	*
bio18	0.31	0.0074	**	0.35	0.0036	0.11	0.2877	
Alt	0.36	0.0025	**	0.35	0.0039	0.35	0.0038	**
Cond	0.66	0.0001	***	0.79	0.0001	0.57	0.0001	***
Ecels	0.29	0.0161	*	0.04	0.7520	0.39	0.0035	**
Perenn	0.14	0.0017	**	0.03	0.3241	0.14	0.0023	**
wint_birds	0.34	0.0028	**	0.25	0.0225	0.48	0.0002	***
sum_birds	0.32	0.0060	**	0.23	0.0402	0.40	0.0011	**
dens_mean_w	0.06	0.6014		0.06	0.5753	0.26	0.0209	*
dens_mean_s	0.23	0.0417	*	0.09	0.4123	0.31	0.0085	**
dens_max_w	0.02	0.9190		0.06	0.5753	0.27	0.0180	*
dens_max_s	0.20	0.0782		0.07	0.5301	0.33	0.0061	**

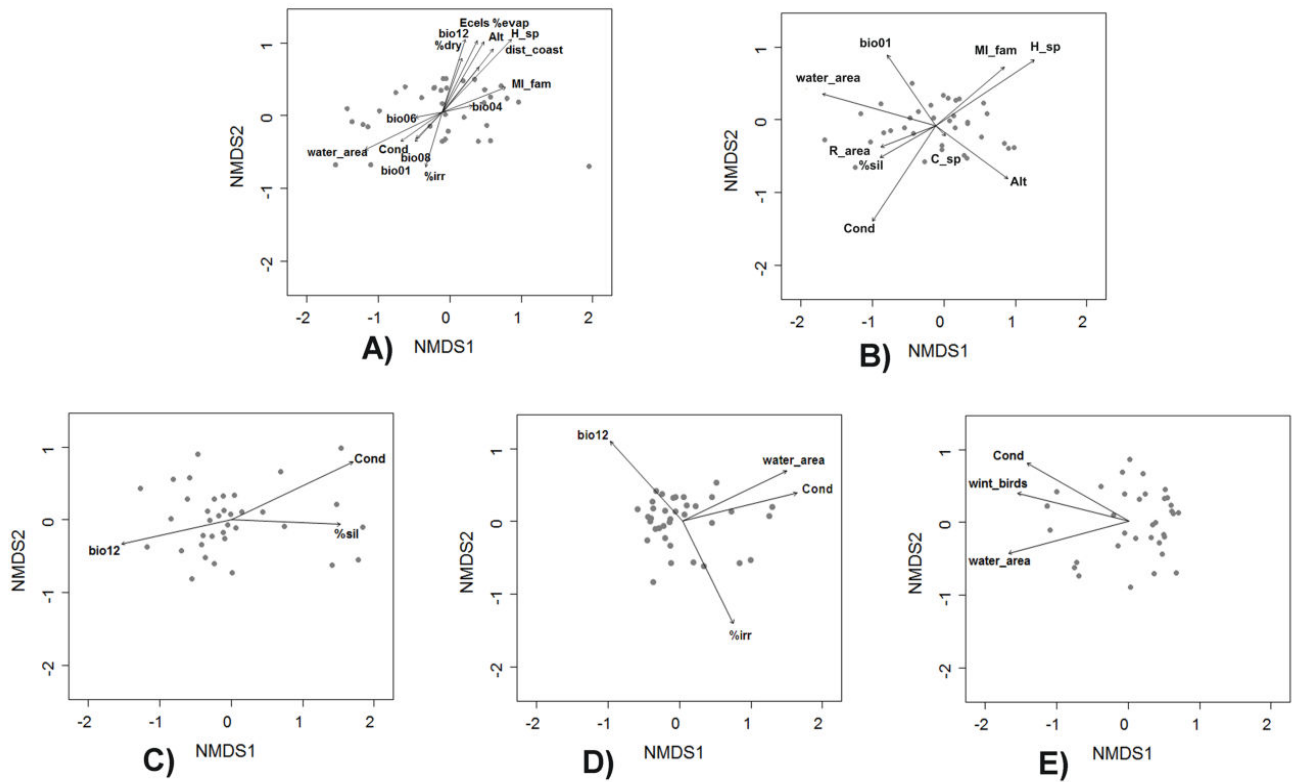


Figure 2. NMDS plots (first two dimensions displayed) based on the presence-absence taxonomic matrix. Variables significant at $p < 0.001$ were displayed. (A) Winter waterbird community; (B) Spring-Summer waterbird community; (C) Coleoptera species; (D) Macroinvertebrate families; (E) Hemiptera species (See Table 1 for details of variable codes).

According to protest analysis, the community variation was, in all cases, significantly concordant across taxa (Table 4). However, the concordance between WW and SW communities was higher (r -value= 0.77) than their concordance with macroinvertebrates (at the family level) and coleopteran or hemipteran (at the species level). Moreover, the WW and SW compositions showed similar concordance with the various invertebrate groups (macroinvertebrates, coleopteran, hemipteran), ranging from $r = 0.44$ to $r = 0.58$. Concordances between coleopteran and macroinvertebrates or hemipteran and macroinvertebrates were also significant and of a similar magnitude (r -values= 0.58–0.61). Apart from the relationship between waterbird groups, the second strongest relationship was between Coleoptera species composition and macroinvertebrate family composition ($r = 0.61$) while the weakest one was between Coleoptera and Hemiptera composition ($r = 0.42$).

Table 4. Concordance among WW, SW, macroinvertebrate, Coleoptera and Hemiptera assemblages based on Protest (NMDS for community data; shown are the Procrustean correlation and the associated m^2 statistic). Significances of the Procrustean statistic were calculated from randomisation tests (9999 permutations).

WW=Winter waterbird community; SW= Spring-Summer waterbird community.

	Protest		
	m^2	r	p -value
WW vs. SW	0.41	0.77	0.0001
WW vs. Macroinvertebrate families	0.74	0.51	0.0001
WW vs. Coleoptera species	0.81	0.44	0.0019
WW vs. Hemiptera species	0.66	0.58	0.0001
SW vs. Macroinvertebrate families	0.67	0.57	0.0001
SW vs. Coleoptera species	0.78	0.47	0.0008
SW vs. Hemiptera species	0.72	0.53	0.0001
Coleoptera species vs. Macroinvertebrate families	0.63	0.61	0.0001
Coleoptera species vs. Hemiptera species	0.83	0.42	0.0023
Macroinvertebrate families vs. Hemiptera species	0.66	0.58	0.0001

Congruence in richness patterns and environmental factors

A strong and significant relationship was detected between WW and SW richness, and between WW and SW densities, although there was no significant correlation between bird species richness and bird density whatever the season considered. Comparing waterbird and macroinvertebrate richness patterns (Table 5), both WW and SW species richness were significantly and negatively correlated with macroinvertebrate family and hemiptera species richness, while no significant relationships were found between waterbirds and Coleoptera (see also Fig. 3). On the other hand, no significant relationship was found between macroinvertebrate richness metrics (at the different taxonomic levels) and the measures of waterbird density. Furthermore, invertebrate family richness was significantly and positively correlated with both Coleoptera and Hemiptera species richness, while there was no significant correlation between these two latter groups.

Table 5. Results of pairwise Spearman's rank correlation tests applied across different measures of waterbird and invertebrate diversity in the 36 wetlands studied. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Due to the high correlation among mean and maximum measures of bird densities (Spearman r coefficient 0.96 - 0.97, $p < 0.001$), only the mean values were displayed. WW=Winter waterbird community; SW= Spring-Summer waterbird community).

	WW richness	SW richness	Macroinvertebrate family richness	Coleoptera species richness	Hemiptera species richness	WW mean density
SW richness	0.930***					
Macroinvertebrate family richness	-0.522**	-0.403*				
Coleoptera species richness	-0.043	-0.125	0.512**			
Hemiptera species richness	-0.657***	-0.541***	0.684***	0.299		
WW mean density	0.176	0.084	-0.07	0.134	0.023	
SW mean density	0.023	0.104	0.021	0.188	0.195	0.805***

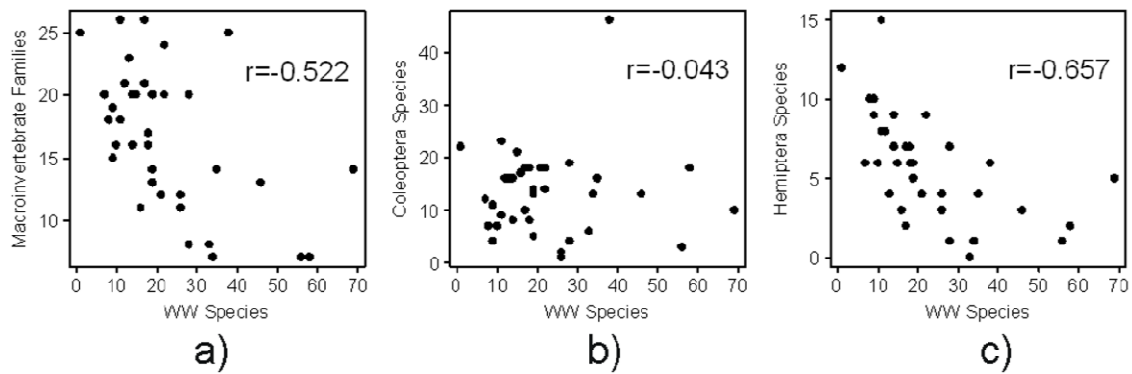


Figure 3. Scatter plots showing the relationships between the richness of the aquatic invertebrate groups (macroinvertebrate families, Coleoptera species, Hemiptera species) and Winter waterbird species (WW) showing Spearman correlation values (r). (a) $p < 0.01$; (b) not significant; (c) $p < 0.001$.

The best GLM model (Table 6) for WW richness included the following predictor variables: water surface area, minimum temperature of the coldest month and the pH value. The model as a whole explained 85% of the deviance. The best GLM model for macroinvertebrate family richness explained 54% of the deviance, and included water conductivity, hydroperiod and the mean value of NH_4^+ as predictors, in order of importance (Table 6). For Coleoptera species richness the best model included annual precipitation, pH, water area and hydroperiod, in order of importance. This model explained > 65% of the deviance. Finally, for Hemiptera species richness the best model explained around 60% of the deviance and included water area and annual precipitation as the most important predictor variables, accompanied by temperature of the driest period and percentage of natural land use (Table 6).

Table 6. Results of GLM relating taxon richness and environmental variables. *BIC*: Bayesian Information Criterion value of the selected model; *BIC_F*: BIC of the full model; *Coef*: Coefficient; % *Rel. Imp*: % Relative importance; % *Cum. Dev*: Total deviance explained. As patterns of species richness for WW and SW data were highly correlated (see Results), GLM models were performed only for WW (Winter waterbird community). See Table 1 for details of the variable codes.

BestModel	Coef.	p-value	%Rel.Imp	% Cum. Dev	BIC	BIC_F
Winter waterbirds				85.4	209.8	267.6
(Intercept)	2.97	< 0.001	/			
water_area	0.43	< 0.001	75.6			
bio06	0.18	<0.001	22.2			
pH	0.10	<0.01	2.2			
Macroinvertebrates				53.9	208.7	242.2
(Intercept)	2.88	< 0.001	/			
Cond	-0.25	< 0.001	72.0			
Perenn	-0.20	<0.05	20.2			
NH ₄ ⁺	0.09	<0.05	7.8			
Coleoptera				65.9	223.5	249.2
(Intercept)	2.65	< 0.001	/			
bio12	0.43	<0.001	41.9			
pH	-0.25	<0.001	32.9			
water_area	0.23	< 0.001	12.2			
Perenn	-0.39	<0.01	12.9			
Hemiptera				60.4	165.5	199.2
(Intercept)	1.65	< 0.001	/			
water_area	-0.33	< 0.001	43.6			
bio12	0.46	< 0.001	37.9			
bio09	0.24	<0.01	12.5			
%nat	0.24	<0.05	6.0			

4. Discussion

Congruence in community composition

We observed assemblage patterns among the studied taxonomic groups that are concordant and significant, but their value can be considered weak according to previous studies (e.g., Heino, 2010), which suggest that strong concordance between multiple organism groups is indicated by r values >0.7 . In our work, this only occurs between WW and SW communities, confirming a congruence that was quite predictable. However, the r values we obtained (0.44 - 0.58) when comparing macroinvertebrate and waterbird assemblages are similar to those obtained by Dolph et al. (2011) studying concordance between fish and macroinvertebrate communities in different North American basins. The only previous study assessing community congruence among aquatic birds and invertebrates (Rooney & Bayley, 2012), which focused on different kinds of Canadian wetlands, found also a weak relationship (0.24 Mantel r value).

The most likely reason behind the observed lack of strong community congruence between birds and macroinvertebrates is their contrasting responses to environmental gradients (see also Bilton et al., 2006), as indicated by the different variables related to their assemblage compositions. It has been hypothesized that organisms of lentic systems with disparate body size may show weaker congruence in assemblage composition than species more similar in size, as they perceive their environment at different scales and have different life-history traits which dictate different biodiversity responses to environmental gradients (Allen et al., 1999; Bilton et al., 2006; Heino 2010; Velghe & Gregory-Eaves, 2013). Thus, large-sized organisms tend to respond more strongly to large-scale environmental variation (e.g., land use, climate) than small-sized organisms that may perceive environmental gradients at smaller scales (e.g., water chemistry, habitat heterogeneity) (Heino, 2010).

In agreement with that hypothesis, our results showed that assemblages of waterbirds (especially WW) appear to be mainly affected by landscape-scale factors such as climate, lithology and land-use, while water chemistry such as conductivity appeared to be the most important influencing the community variation of macroinvertebrates at different taxonomic resolutions (although

conductivity was also important for SW). Conductivity is a well-known stressor on macroinvertebrate communities (e.g., Millán et al., 2011), causing reduction in species richness and turnover in species composition (Gutiérrez-Cánovas et al., 2013). In contrast, waterbirds are not strongly dependent on water chemistry, because they are not strictly aquatic organisms, being less affected by osmotic stress than macroinvertebrates. For this reason, in general, they are able to exploit hypersaline wetlands where few invertebrates can survive, such that avian diversity can be very high in habitats where invertebrate diversity is particularly low (e.g., Sánchez et al., 2006).

The fact that conductivity appears as an important factor for SW communities is probably because some birds such as ducks or coots avoid high salinity wetlands for breeding, and their chicks cannot osmoregulate at high salinities (Moorman et al., 1991). Interestingly, the water surface area appears as an important factor for both waterbird and macroinvertebrate communities, as predicted by island biogeography theory (McArthur & Wilson 1967), but probably affecting assemblages in a different way.

Finally, diversity patterns of waterbirds were significantly correlated with the community composition of macroinvertebrates, which reflect the importance of biotic interactions in shaping distributions and realised assemblages of species (Wisz et al., 2013) between these groups. Different macroinvertebrates are important in the diet of different waterbird species (e.g., Green & Sánchez, 2003; Macías et al., 2004). Waterbirds have been shown through enclosure experiments to reduce macroinvertebrate abundance and fine-scale diversity (Rodríguez-Pérez and Green, 2012), partly through the removal of submerged vegetation. However, these relationships are complex and waterbirds can also promote invertebrate diversity under some conditions, e.g. by reducing fish densities (Green & Elmberg, 2014). Moreover, waterbirds have been shown to disperse invertebrates (Laux & Kölsch, 2014), and corixid eggs (Hemiptera) can be abundant in their faeces in our study area (Figuerola et al., 2003). Thus, the richness and density of waterbirds appeared as an important factor for macroinvertebrate composition, especially for Hemiptera species, possibly through selective predation (e.g., Green & Sánchez, 2003). Many adult and predaceous macroinvertebrates, such as hemipterans, make frequent trips to the water's surface to respire, increasing their availability to

waterbirds (Hornung & Foote, 2006) that feed at the surface. Further research focused on trophic relationships between birds and macroinvertebrates is required to better understand the ecological relationships between hemipterans and waterbirds.

Congruence in richness patterns

Correlations between richness of waterbirds and invertebrates were either non-significant (for Coleoptera) or negative (macroinvertebrate families and Hemiptera species). Thus, in general, results show an inverse pattern in richness for both groups, i.e., wetlands with high species richness for waterbirds showed low richness of macroinvertebrates. The inverse relationship between the richness patterns of both groups would suggest that either (i) each taxonomic group has a unique response to environmental gradients or (ii) the taxonomic diversity of waterbirds has negative consequences for macroinvertebrate richness (e.g. predation; see above). While this latter hypothesis is more difficult to assess and probably needs specific research, the results of GLM models suggest that different processes, or the same processes operating in different directions, may underlie the observed species richness patterns of waterbirds and aquatic macroinvertebrates.

Thus, while wetland size was the main variable in the richness models for waterbirds, in agreement with results of previous studies on aquatic birds in different Spanish wetlands (Sánchez-Zapata et al., 2005; Sebastián-González & Green, 2014) and elsewhere in the world (Bidwell et al., 2014), its role seems to be negligible for macroinvertebrate families. However, in the case of Hemiptera species, water area had a negative effect, showing that smaller ponds hold higher species richness for this group, probably due to the lower predation pressure by fish and waterbirds. The high dispersal capacity of hemipterans and their resistance to a wide range of conditions (Velasco and Millán, 1998), allow this group to reach high richness even in small water bodies (Bruno et al., 2012). In contrast, the water surface area had a significant positive effect for Coleoptera richness, although of secondary importance, due probably to the higher number of species and functional diversity of this group. Thus, our results for macroinvertebrates (except Hemiptera species) are consistent with the weak

positive relationship found by Oertli et al. (2002) between several macroinvertebrate richness metrics and pond size.

Another relevant variable explaining waterbird richness was the minimum temperature of the coldest period, with pH showing a secondary role. On the contrary, for macroinvertebrate richness patterns at the family level, as for community composition, water conductivity was the most important factor, highlighting its strong effect on macroinvertebrate diversity patterns, as seen also for diversity of submerged plants and zooplankton (Green et al., 2002; Frisch et al., 2006). The hydroperiod was also a relevant variable for macroinvertebrate family richness (with greater richness in temporary wetlands), probably due to greater fish abundance and the artificial origin of some of the permanent wetlands in our study area, which are flow-fed by channels. When increasing the taxonomic resolution for some aquatic taxa (Coleoptera and Hemiptera), the selected variables were different, with annual precipitation being a significant factor that represents the importance of this variable in promoting different kinds of ponds in terms of size, hydroperiod and microhabitat availability. These results agree with those from Pérez-Bilbao et al. (2014) which showed mean precipitation to have a major influence on the Coleoptera community in similar areas of the Iberian Peninsula. It is clear that precipitation is of crucial concern to most macroinvertebrate species and its repartition through the year strongly influences water permanence and community structure (Florencio et al., 2009).

Management implications for Mediterranean wetlands

Our study represents the first investigation of the relationship between the biodiversity patterns of aquatic macroinvertebrates and waterbirds in Mediterranean wetlands and is one of the most comprehensive studies of cross taxon congruence in wetlands. Previous studies, mainly focused on macroinvertebrates, macrophytes and fishes, have shown that cross-taxon congruence in species richness and assemblage composition patterns of aquatic organisms is typically weak (Heino 2010), although there are some examples of high correlation in diversity patterns between some macroinvertebrate groups (e.g., Bilton et al., 2006; Sánchez-Fernández et al., 2006). Our results showed a weak concordance in the assemblage composition patterns of macroinvertebrates

and waterbirds, and an inverse or negligible relationship in their patterns of taxonomic richness. Similarly, other studies bring into question the role of waterbirds as effective bioindicators, especially in Mediterranean systems (Green and Elmberg, 2014). For instance, generalist waterbird species have increased in abundance in many Mediterranean wetlands since 1970, despite habitat degradation that has caused declines in amphibians, reptiles, mammals and fish (MWO, 2012). Some of these species, particularly gulls (F. Laridae) and herons (F. Ardeidae), may have benefited from global change drivers such as human related food subsidies and the introduction of exotic species such as the American crayfish (*Procambarus clarkii*) (Tablado et al., 2010) which is detrimental for many other taxa such as macroinvertebrates, amphibians, macrophytes and also waterfowl (F. Anatidae) (e.g., Rodríguez et al., 2005).

Our results show how some climatic variables related with temperature seem to affect waterbird more than macroinvertebrate assemblages, while factors directly related with the aquatic ecosystems like water chemistry, precipitation or hydroperiod may affect mainly different components of the macroinvertebrate community. Thermoregulation for endotherms such as birds involves a high metabolic cost, and seeking microhabitats with even a slight change in temperature can provide important benefits. On the other hand, we cannot rule out the possibility that these temperature effects are the result of confounding spatial variables and the preference of waterbirds for some aspect of the landscape. Our results also stress the importance of the water surface area of the wetland for richness patterns (alpha biodiversity measures) of the different studied groups, sometimes in opposing directions. Large surface area is a key variable for promoting waterbird richness, while different sizes and a great variety of aquatic ecosystems seem more important for macroinvertebrate representation, which could be relevant in the context of the design of future protected wetlands.

All in all, our findings underline the need for caution when using waterbirds as flagship species for the conservation of aquatic ecosystems (see also Amat & Green, 2010). Thus, protected area management focused only in waterbirds is not likely to be enough to ensure conservation of aquatic macroinvertebrate biodiversity. An integrative analysis of different biological communities, using datasets from different taxonomic groups, is desirable to improve conservation

policies and assessment methods, as pointed out by Larsen et al. (2012) for terrestrial ecosystems and other geographic regions. According to Heino (2010), it should be emphasised, however, that simple correlations between taxonomic groups are not the only option in assessing the utility of cross-taxon congruence in the conservation context. Complementary cross-taxon surrogacy, i.e. the extent to which conservation planning based on complementary representation of species surrogates effectively represents target species, could be another useful approach (e.g., Sánchez-Fernández et al., 2006). Moreover, complementary research on functional and phylogenetic aspects of wetland biodiversity is crucial for an integral understanding and to improve conservation strategies (Devictor et al., 2010). Apart from waterbirds and macroinvertebrates, wetlands are important for other numerous and diverse taxa (include many that are not strictly aquatic) which are sensitive to the conservation status of the wetlands (e.g., Gibbs 1993; Osiejuk et al., 1999; Robledano et al., 2010). Given the importance of the Ramsar Convention as the main international agreement for the conservation of wetlands, our results identify the need for caution when assessing the value of the Ramsar network for the conservation of aquatic biodiversity in general. The inadequacy of some conservation policies to protect aquatic invertebrate biodiversity has been stressed in other Mediterranean wetlands (Gascón et al., 2008), and the design of specific protection measures for aquatic ecosystems is recommended (e.g., Susky & Cooke, 2007). In this context there remains a need, in countries such as Spain, to declare additional protected wetlands on the basis of invertebrates, plants and other strictly aquatic communities, in order to obtain a diversified and complete network able to preserve multiple components of wetland biodiversity.

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Supplementary material

Appendix A. List of the Ramsar sites studied. Data from Ramsar site “Reservoir of Cordobilla and Malpasillo” were excluded during the analysis because of its artificial morphology and the difficulty of obtaining a complete invertebrate sample. Data of “Charroao” were excluded because it was completely dry during the waterbird counts.

RAMSAR_code	RAMSAR_name	Site code	Wetlands	N	O
1	Doñana	R1	Lagunas Peridunares	36°58'46"	6°29'07"
3	Laguna de Fuentedepiedra	R3	Fuente de Piedra	37°06'34"	4°45'48"
4	Lagunas de Cádiz	R4A	Medina	36°36'51"	6°03'03"
		R4B	Salada	36°38'35"	6°14'01"
5	Lagunas del Sur de Córdoba	R5A	Zoñar	37°28'51"	4°41'32"
		R5B	Rincón	37°27'38"	4°37'45"
		R5C	Amarga	37°18'48"	4°36'54"
6	Marismas del Odiel	R6	Odiel	37°16'02"	6°59'07"
7	Salinas del Cabo de Gata	R7	Salinas del Cabo de Gata	36°45'52"	2°13'23"
30	Embalse de Cordobilla Malpasillo	R30	Cordobilla Malpasillo	37°21'07"	4°42'00"
31	Albufera de Adra	R31A	Nueva	36°45'00"	2°57'10"
		R31B	Honda	36°45'26"	2°57'07"
45	Bahía de Cádiz	R45	Bahía de Cádiz	36°27'19"	6°09'16"
53	Paraje Natural Punta Entinas-Sabinar	R53A	Punta Entinas	36°41'11"	2°45'05"
		R53B	Salinas de Cerrillos	36°42'21"	2°40'21"
54	Reserva Natural Complejo Endorreico de Espera	R54A	Hondilla	36°52'18"	5°15'42"
		R54B	Salada de Zorrilla	36°52'07"	5°51'53"
55	Reserva Natural Laguna del Conde	R55	Del Conde	37°34'32"	4°12'15"
56	Reserva Natural Laguna de Tiscar	R56	Tiscar	37°25'53"	4°49'08"
57	Reserva Natural Laguna de los Jarales	R57	Jarales	37°18'19"	4°34'42"
58	Humedales y Turberas de Padul	R58	Padul	37°00'47"	3°36'21"
59	Paraje Natural Lagunas de Palos y las Madres	R59A	Madres	37°09'06"	6°51'52"
		R59B	Mujeres	37°09'54"	6°53'18"
60	Reserva Natural Laguna Honda	R60	Honda	37°35'60"	4°08'34"
61	Reserva Natural Laguna del Chinche	R61	Chinche	37°36'53"	4°09'12"
62	Reserva Natural Lagunas de Campillos	R62A	Cerero	37°02'22"	4°48'56"
		R62B	Dulce	37°03'03"	4°49'58"
		R62C	Salada	37°02'18"	4°50'41"
63	Paraje Natural Brazo del Este	R63	Brazo este	37°10'23"	6°02'08"
64	Reserva Natural Complejo Endorreico de Chiclana	R64A	Jeli	36°26'32"	6°04'49"
		R64B	Montellano	36°27'34"	6°04'18"
65	Reserva Natural Complejo Endorreico de Puerto Real	R65	Taraje	36°32'08"	6°03'24"
66	Paraje Natural Laguna Grande	R66	Grande	37°55'58"	3°33'36"
67	Reserva Natural Lagunas de Archidona	R67A	Chica	37°05'58"	4°18'32"
		R67B	Grande	37°06'35"	4°18'11"
68	Reserva Natural Complejo Endorreico Lebrija-Las Cabezas	R68A	Charroao	36°56'15"	5°54'30"
		R68B	Pilón	36°54'15"	5°53'58"
		R68C	Galiana	36°53'43"	5°54'46"

Appendix B. List of the waterbird species (separated between Winter and Spring-Summer period) detected in the study area.

	Winter	Spring-Summer
Accipitridae		
<i>Circus aeruginosus</i> (Linnaeus 1758)	1	1
Anatidae		
<i>Anas acuta</i> Linnaeus 1758	1	0
<i>Anas clypeata</i> Linnaeus 1758	1	1
<i>Anas crecca</i> Linnaeus 1758	1	1
<i>Anas penelope</i> Linnaeus 1758	1	0
<i>Anas platyrhynchos</i> Linnaeus 1758	1	1
<i>Anas querquedula</i> Linnaeus 1758	0	1
<i>Anas strepera</i> Linnaeus 1758	1	1
<i>Anser anser</i> Linnaeus 1758	1	0
<i>Aythya ferina</i> (Linnaeus 1758)	1	1
<i>Aythya fuligula</i> (Linnaeus 1758)	1	1
<i>Aythya nyroca</i> (Güldenstädt 1770)	1	1
<i>Cygnus olor</i> (Gmelin 1803)	1	1
<i>Marmaronetta angustirostris</i> (Ménétriés 1832)	1	1
<i>Mergus serrator</i> Linnaeus 1758	1	1
<i>Netta rufina</i> (Pallas 1773)	1	1
<i>Oxyura leucocephala</i> (Scopoli 1769)	1	1
<i>Tadorna ferruginea</i> (Pallas 1764)	0	1
<i>Tadorna tadorna</i> (Linnaeus 1758)	1	1
Ardeidae		
<i>Ardea alba</i> Linnaeus 1758	1	1
<i>Ardea cinerea</i> Linnaeus 1758	1	1
<i>Ardea purpurea</i> Linnaeus 1766	1	1
<i>Ardeola ralloides</i> (Scopoli 1769)	1	1
<i>Bubulcus ibis</i> (Linnaeus 1758)	1	1
<i>Egretta garzetta</i> (Linnaeus 1758)	1	1
<i>Egretta gularis</i> (Bosc 1792)	1	1
<i>Ixobrychus minutus</i> (Linnaeus 1766)	0	1
<i>Nycticorax nycticorax</i> (Linnaeus 1758)	1	1
Charadriidae		
<i>Charadrius alexandrinus</i> Linnaeus 1758	1	1
<i>Charadrius dubius</i> Scopoli 1786	1	1
<i>Charadrius hiaticula</i> Linnaeus 1758	1	1
<i>Pluvialis apricaria</i> (Linnaeus 1758)	1	0
<i>Pluvialis squatarola</i> (Linnaeus 1758)	1	1
<i>Vanellus vanellus</i> (Linnaeus 1758)	1	1
Ciconiidae		

<i>Ciconia ciconia</i> (Linnaeus 1758)	1	1
<i>Ciconia nigra</i> (Linnaeus 1758)	1	0
Glareolidae		
<i>Glareola pratincola</i> (Linnaeus 1766)	0	1
Gruidae		
<i>Grus grus</i> (Linnaeus 1758)	1	0
Haematopodidae		
<i>Haematopus ostralegus</i> Linnaeus 1758	1	1
Laridae		
<i>Larus argentatus</i> Pontoppidan 1763	1	0
<i>Larus audouinii</i> Payraudeau 1826	1	1
<i>Larus cachinnans</i> Pallas 1811	1	1
<i>Larus canus</i> Linnaeus 1758	1	0
<i>Larus fuscus</i> Linnaeus 1758	1	1
<i>Larus genei</i> Breme 1840	1	1
<i>Larus marinus</i> Linnaeus 1758	1	0
<i>Larus melanocephalus</i> Temminck 1820	1	1
<i>Larus michahellis</i> Naumann 1840	1	1
<i>Larus minutus</i> Pallas 1776	1	1
<i>Larus ridibundus</i> Linnaeus 1766	1	1
Sternidae		
<i>Chlidonias hybridus</i> (Pallas 1811)	1	1
<i>Chlidonias leucopterus</i> (Temminck 1815)	0	1
<i>Chlidonias niger</i> (Linnaeus 1758)	1	1
<i>Gelochelidon nilotica</i> (Gmelin 1789)	0	1
<i>Sterna albifrons</i> Pallas, 1764	0	1
<i>Sterna caspia</i> Pallas 1770	1	1
<i>Sterna hirundo</i> Linnaeus 1758	1	1
<i>Sterna sandvicensis</i> Latham 1787	1	1
Pandionidae		
<i>Pandion haliaetus</i> (Linnaeus 1758)	1	1
Phalacrocoracidae		
<i>Phalacrocorax carbo</i> (Linnaeus 1758)	1	1
Phoenicopteridae		
<i>Phoenicopus minor</i> (Geoffroy 1798)	1	1
<i>Phoenicopus roseus</i> Pallas 1811	1	1
Podicipitidae		

<i>Podiceps auritus</i> (Linnaeus 1758)	1	0
<i>Podiceps cristatus</i> (Linnaeus 1758)	1	1
<i>Podiceps nigricollis</i> Brehm 1831	1	1
<i>Tachybaptus ruficollis</i> (Pallas 1764)	1	1

Rallidae

<i>Fulica atra</i> Linnaeus 1758	1	1
<i>Fulica cristata</i> Gmelin 1789	1	1
<i>Gallinula chloropus</i> (Linnaeus 1758)	1	1
<i>Porphyrio porphyrio</i> (Linnaeus 1758)	1	1
<i>Porzana pusilla</i> (Pallas 1776)	0	1
<i>Rallus aquaticus</i> Linnaeus 1758	1	1

Recurvirostridae

<i>Himantopus himantopus</i> (Linnaeus 1758)	1	1
<i>Recurvirostra avosetta</i> Linnaeus 1758	1	1

Scolopacidae

<i>Actitis hypoleucos</i> (Linnaeus 1758)	1	1
<i>Arenaria interpres</i> (Linnaeus 1758)	1	1
<i>Calidris alba</i> (Pallas 1764)	1	1
<i>Calidris alpina</i> (Linnaeus 1758)	1	1
<i>Calidris canutus</i> (Linnaeus 1758)	1	1
<i>Calidris ferruginea</i> (Pontoppidan 1763)	1	1
<i>Calidris minuta</i> (Leisler 1812)	1	1
<i>Gallinago gallinago</i> (Linnaeus 1758)	1	1
<i>Limosa lapponica</i> (Linnaeus 1758)	1	1
<i>Limosa limosa</i> (Linnaeus 1758)	1	1
<i>Numenius arquata</i> (Linnaeus 1758)	1	1
<i>Numenius phaeopus</i> (Linnaeus 1758)	1	1
<i>Phalaropus lobatus</i> (Linnaeus 1758)	1	1
<i>Philomachus pugnax</i> (Linnaeus 1758)	1	1
<i>Tringa erythropus</i> (Pallas 1764)	1	1
<i>Tringa glareola</i> Linnaeus 1758	1	1
<i>Tringa nebularia</i> (Gunnerus 1767)	1	1
<i>Tringa ochropus</i> Linnaeus 1758	1	1
<i>Tringa stagnatilis</i> (Bechstein 1803)	1	1
<i>Tringa totanus</i> (Linnaeus 1758)	1	1

Stercorariidae

<i>Stercorarius parasiticus</i> (Linnaeus 1758)	0	1
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Strigidae

<i>Asio flammeus</i> (Pontoppidan 1763)	1	0
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Threskiornithidae

<i>Platalea leucorodia</i> Linnaeus 1758	1	1
<i>Plegadis falcinellus</i> (Linnaeus 1766)	1	1
<i>Threskiornis aethiopicus</i> (Latham 1790)	1	1
	90	88

Appendix C. List of the macroinvertebrate families, coleopteran species and hemipteran species detected in the study area.

Macroinvertebrate taxa identified to family level (except Aranei, Oligochaeta, Ostacoda)

1 Aeshnidae	30 Hydropsychidae
2 Ancyliidae	31 Hygrobiidae
3 Aranei	32 Lestidae
4 Artemiidae	33 Libellulidae
5 Asellidae	34 Limnephilidae
6 Atyidae	35 Limoniidae
7 Baetidae	36 Lumbricidae
8 Caenidae	37 Lymnaeidae
9 Cambaridae	38 Mesoveliidae
10 Ceratopogonidae	39 Naucoridae
11 Chironomidae	40 Nepidae
12 Coenagrionidae	41 Noteridae
13 Corixidae	42 Notonectidae
14 Culicidae	43 Oligochaeta
15 Dixidae	44 Ostracoda
16 Dryopidae	45 Palaemonidae
17 Dytiscidae	46 Physidae
18 Ephyridae	47 Planariidae
19 Gammaridae	48 Planorbidae
20 Gerridae	49 Pleidae
21 Gyrinidae	50 Psychodidae
22 Haliplidae	51 Scirtidae
23 Helophoridae	52 Simuliidae
24 Heteroceridae	53 Stratiomyidae
25 Hydracarina	54 Syrphidae
26 Hydraenidae	55 Tabanidae
27 Hydrobiidae	56 Tipulidae
28 Hydrometridae	57 Triopsidae
29 Hydrophilidae	58 Valvatidae
	59 Veliidae

Coleoptera**Dryopidae***Dryops algiricus* (Lucas, 1849)*Dryops luridus* (Erichson, 1847)*Dryops striatellus* (Fairmaire and Brisout de Barneville, 1859)**Dytiscidae***Agabus biguttatus* (Olivier, 1795)*Agabus bipustulatus* (Linnaeus, 1767)*Agabus conspersus* (Marsham, 1802)*Agabus nebulosus* (Forster, 1771)*Bidessus goudoti* (Laporte de Castelnau, 1835)*Colymbetes fuscus* (Linnaeus, 1758)*Colymbetes schildknechti* Dettner, 1983*Cybister lateralimarginalis* (De Geer, 1774)*Cybister tripunctatus africanus* Laporte de Castelnau, 1835*Deronectes moestus* (Fairmaire, 1858)*Graptodytes flavipes* (Olivier, 1795)*Hydaticus leander* (Rossi, 1790)*Hydroglyphus geminus* (Fabricius, 1792)*Hydroglyphus signatellus* (Klug, 1834)*Hydroporus discretus* Fairmaire and Brisout de Barneville, 1859*Hydroporus gyllenhali* Schiödte, 1841*Hydroporus limbatus* Aubé, 1836*Hydroporus lucasi* Reiche, 1866*Hydroporus marginatus* (Duftschmid, 1805)*Hydrovatus cuspidatus* (Kunze, 1818)*Hygrotus confluens* (Fabricius, 1787)*Hygrotus inaequalis* (Fabricius, 1777)*Hygrotus lagari* (Fery, 1992)*Hygrotus pallidulus* (Aubé, 1850)*Hyphydrus aubei* Ganglbauer, 1892*Ilybius montanus* (Stephens, 1828)*Laccophilus hyalinus* (De Geer, 1774)*Laccophilus minutus* (Linnaeus, 1758)*Lioporus atriceps* Sharp, 1882*Metaporus meridionalis* (Aubé, 1836)*Nebrioporus baeticus* (Schaum, 1864)*Nebrioporus ceresyi* (Aubé, 1836)*Nebrioporus clarki* (Wollaston, 1862)*Rhantus hispanicus* Sharp, 1882*Rhantus suturalis* (McLeay, 1825)*Yola bicarinata* (Latreille, 1804)**Gyrinidae***Gyrinus dejeani* Brullé, 1832

Gyrinus distinctus Aubé, 1836

Haliplidae

Haliplus andalusicus Wehncke, 1874

Haliplus lineatocollis (Marsham, 1802)

Helophoridae

Helophorus alternans Gené, 1836

Helophorus asturiensis Kuwert, 1885

Helophorus brevipalpis Bedel, 1881

Helophorus fulgidicollis Motschusky, 1860

Helophorus minutus Fabricius, 1775

Helophorus occidentalis Angus, 1983

Heteroceridae

Heterocerus sp.

Hydraenidae

Aulacohthebius exaratus Mulsant, 1844

Hydraena rugosa Mulsant, 1844

Ochthebius aeneus Stephens, 1835

Ochthebius auropallens Fairmaire, 1879

Ochthebius bifoveolatus Walzl, 1835

Ochthebius corrugatus Rosenhauer, 1856

Ochthebius cuprescens Guillebeau, 1893

Ochthebius dentifer Rey, 1885

Ochthebius dilatatus Stephens, 1829

Ochthebius meridionalis Rey, 1885

Ochthebius notabilis Rosenhauer, 1856

Ochthebius punctatus Stephens, 1829

Ochthebius quadrifossulatus Walzl, 1835

Ochthebius serratus Rosenhauer, 1856

Ochthebius subpictus Wollaston, 1857

Ochthebius tacapasensis baeticus Ferro, 1984

Ochthebius viridescens Ienistea, 1988

Ochthebius viridis fallaciosus Ganglbauer, 1901

Hydrophilidae

Anacaena limbata (Fabricius, 1792)

Anacaena lutescens (Stephens, 1829)

Berosus affinis Brullé, 1835

Berosus fulvus Kuwert, 1888

Berosus guttalis Rey, 1883

Berosus hispanicus Küster, 1847

Berosus signaticollis (Charpentier, 1825)

Chaetarthria seminulum seminulum (Herbst, 1797)/*Chaetarthria simillima* Vorst & Cuppen, 2003

Coelostoma hispanicum (Küster, 1848)
Enochrus ater (Kuwert, 1888)
Enochrus bicolor (Fabricius, 1792)
Enochrus fuscipennis (Thomson, 1884)
Enochrus halophilus (Bedel, 1878)
Enochrus natalensis (Gemminger and Harold, 1868)
Enochrus politus Küster, 1849
Enochrus salomonis (Sahlberg, 1900)
Helochares lividus (Forster, 1771)
Hydrobius fuscipes (Linnaeus, 1758)
Hydrochara flavipes (Steven, 1808)
Hydrophilus pistaceus (Laporte de Castelnau, 1840)
Laccobius atrocephalus Reitter, 1872
Laccobius ytenensis Sharp, 1910
Limnoxenus niger (Gmelin 1790)
Paracymus aeneus (Germar, 1824)
Paracymus scutellaris (Rosenhauer, 1856)

Hygrobiiidae

Hygrobia hermanni (Fabricius, 1775)

Noteridae

Noterus laevis Sturm, 1834

Scirtidae

Cyphon sp.

Elodes sp.

Hydrocyphon sp.

Hemiptera species

Corixidae

Corixa affinis Leach, 1817
Corixa panzeri Fieber, 1848
Cymatia rogenhoferi (Fieber, 1864)
Heliocorisa vermiculata (Puton, 1874)
Micronecta scholtzi (Fieber, 1860)
Paracorixa concinna (Fieber, 1848)
Sigara lateralis (Leach, 1817)
Sigara nigrolineata (Fieber, 1848)
Sigara scripta (Rambur, 1840)
Sigara selecta (Fieber, 1848)
Sigara stagnalis (Leach, 1817)
Trichocorixa verticalis (Fieber, 1851)

Gerridae

Gerris lateralis Schummel, 1832

Gerris thoracicus Schummel, 1832

Hydrometridae

Hydrometra stagnorum (Linnaeus, 1758)

Mesoveliidae

Mesovelia vittigera Horvath, 1895

Naucoridae

Naucoris maculatus Fabricius, 1798

Nepidae

Nepa cinerea Linnaeus, 1758

Notonectidae

Anisops debilis perplexus Poisson, 1929

Anisops crinitus Brooks, 1951

Anisops sardeus Herrich-Schäffer, 1849

Notonecta glauca glauca Linnaeus, 1758

Notonecta glauca meridionalis Poisson, 1926

Notonecta maculata Fabricius, 1794

Notonecta viridis viridis Delcourt, 1909

Pleidae

Plea minutissima Leach, 1817

Veliidae

Microvelia pygmaea (Dufour, 1833)

Chapter 3:

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



Laguna del Hito (Cuenca)

Submitted (under review in *Biological Conservation*)

Guareschi, S., Bilton, D.T., Velasco, J., Millán, A., Abellán, P. (2015)

Abstract and keywords

Protected area networks represent one of the mainstays of global conservation policies 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, excellent surrogates of overall 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.

Biodiversity conservation • Macroinvertebrates • Aquatic ecosystems • Reserves • Beta diversity • Functional diversity

1. Introduction

Protected area networks represent one of the mainstays of worldwide conservation policies 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 & 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 & 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 & Neville 2005; Monroe et al., 2009; Revenga et al., 2005; Strayer & 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 known. 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 & Chape, 2004). Functional diversity (FD), which reflects the range of biological,

physiological and ecological traits within natural communities (Petchey & 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 & Child, 2009), and such spatial mismatch between different aspects of diversity may result in protected area networks that do not fully represent biodiversity (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 protected area networks represent beta diversity - 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 & 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 & 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 & 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 freshwater biodiversity in the Iberian Peninsula (Spain and Portugal). 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 public appealing taxa (Strayer, 2006). Here we focus on aquatic Coleoptera, which as well as being functionally and evolutionarily diverse (Jäch & Balke, 2008) are one of the best-known groups of freshwater macroinvertebrates in the region (Ribera 2000, Millán et al. in press). In addition, aquatic beetles have been shown to be good surrogates for wider freshwater biodiversity in Iberia (Guareschi et al., 2012; Sánchez-Fernández et al., 2006) and elsewhere (Bilton et al., 2006). 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 & 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

Study area and data

This study focuses on the Iberian Peninsula, a biodiversity hotspot located in south-western Europe, which is composed by the mainland territories of Portugal and Spain (Fig. 1). The territory, which extends nearly 600 000 km², 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., in press), 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 data (10x10 km UTM cells) for 484 water beetle species. Species level was used for taxonomic diversity measures whilst genus level information was used to assess functional diversity (Dolédéc et al., 2000; Gayraud et al., 2003).

Two different protected area networks were investigated: the extant regional and national protected area network (RNAs) and the wider and incompletely implemented Natura 2000 network of protected areas (N2000) (see Fig. 1). RNAs are at the core of national and regional conservation policies, and include National and Natural Parks, Natural Reserves, Natural Monuments, Protected Landscapes, Protected Marine Areas (not included in this study) as well as different types of local protected areas (i.e. those included in Spanish and Portuguese laws). The N2000 network represents a key tool for biodiversity conservation at the European scale and aims to guarantee the long-term survival of Europe's most valuable and threatened species and habitats. It includes Special Areas of Conservation (SACs) designated under the Habitats Directive

(92/43/EEC), and Special Protection Areas (SPAs) which are designated under the Birds Directive (79/409/EEC). GIS data layers supplied by the national conservation agencies of Spain and Portugal, were edited and combined to produce single layers of Iberian RNAs and N2000 networks, respectively.

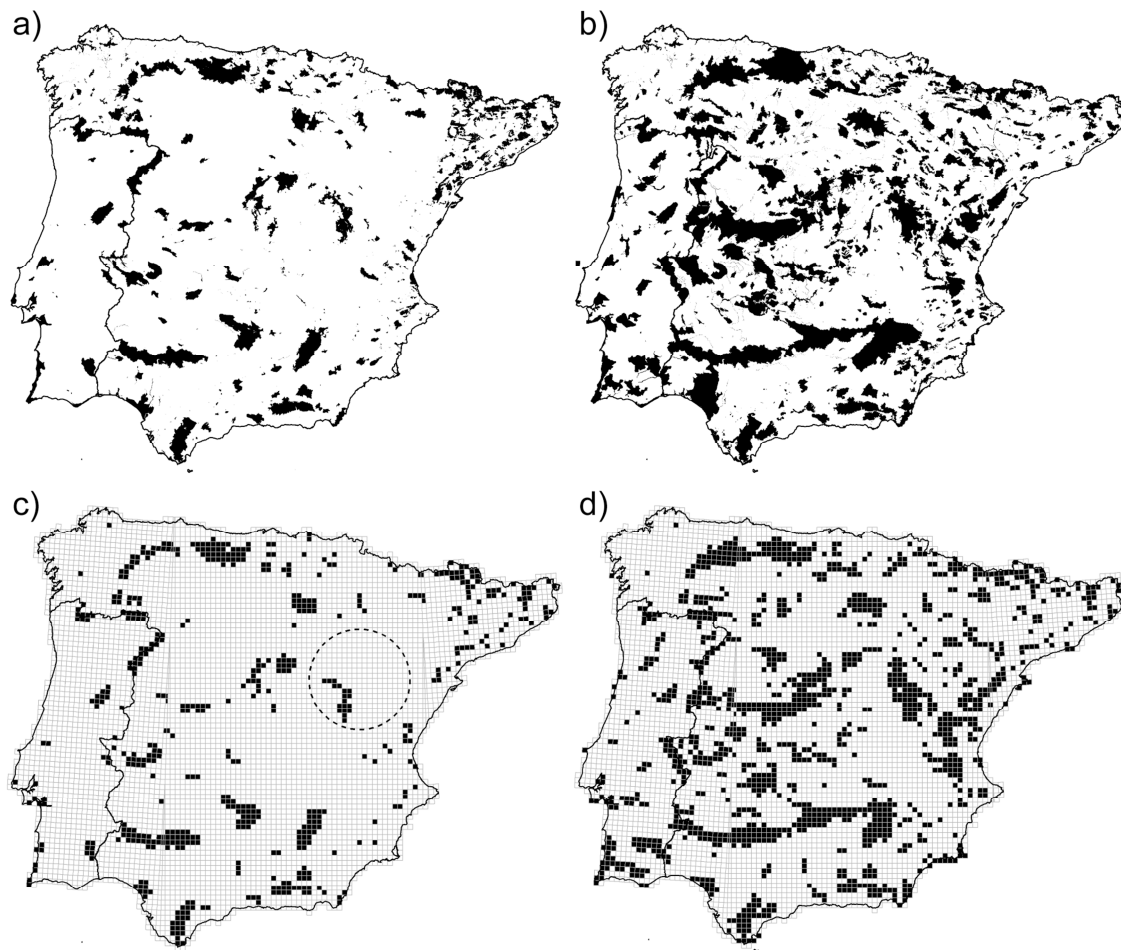


Figure 1. Study area (Iberian Peninsula) showing the two different protected area networks considered (a) regional and national protected areas (RNAs), (b) Natura 2000 (N2000) and the cells considered as protected by RNAs (c) or N2000 (d) at a threshold of 50% coverage. Dashed circle in (c) represents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

Since species distribution information is available at a resolution 10x10 km UTM cells, whereas protected areas are polygons, often smaller than these grid cells, we applied a filter to identify grid cells that can be considered protected (see Araujo et al., 2007; Sánchez-Fernandez et al., 2013 for similar approaches). We calculated the area of each 10x10 km UTM cell included within the two different

protected area scenarios and a cell was considered protected when at least 50% of its area was within RNA or N2000 sites (Fig. 1). This 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 (e.g. Araújo, 2004; D'Amen et al., 2013; Sánchez-Fernández et al., 2013). Nevertheless, to assess the sensitivity of results to this choice of threshold alternative values (1%, 25%, 75% and 90%) were also considered (see Supplementary materials).

Diversity measures

We calculated values describing the different components (α , β and γ) of water beetle TD and FD included in protected areas. Thus, for each protected area network (RNAs or N2000) we assessed the diversity (either TD or FD) within each protected cell (α diversity), the change in diversity amongst protected cells (β diversity) and the total diversity in the whole network of protected cells (γ 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). β TD was measured as both spatial turnover in species composition (β_{SIM} Simpson's dissimilarity) and variation in species composition due to nestedness (β_{NES} nestedness-driven dissimilarity), with overall β diversity (β_{SOR} , Sørensen's dissimilarity) being the sum of these components (Baselga, 2010). For a given set of grid cells, overall β diversity and its two components were calculated using multiple-site dissimilarity measures following Baselga (2010).

To characterise the functional diversity of coleopteran communities, 11 biological traits (considering 40 modalities) were considered following Tachet et al. (2010), which relate to morphology, life history, dispersal ability and trophic role. Tachet et al.'s trait database summarises expert knowledge on European freshwater invertebrates by assigning an affinity score for each taxon to each modality using a fuzzy coded approach. Selection of values was conducted using information developed for Mediterranean ecosystems by Bonada and Dolédec (2011) and Picazo et al. (2012), with some scores being modified on the basis of the authors' own fieldwork.

A matrix of trait pairwise dissimilarity among taxa was generated using Gower distance, and a functional dendrogram constructed from this distance

matrix using Ward linkage and hierarchical clustering (Petchey & Gaston, 2002 - alternative methods gave qualitatively similar results). Subsequently FD was calculated for each grid cell (α diversity) and for each protected area network (γ diversity), as the mean pairwise distance amongst species – i.e. the average of the branch lengths in the trait dendrogram joining all pairs of species in a given 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. The F_{sor} metric 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).

Assessment of protected areas performance

In order to assess the performance of protected area networks in representing 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 Mann–Whitney U tests.

We investigated the effectiveness of protected area networks in representing freshwater 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 & Orme, 2012), “picante” (Kembel et al., 2010) and “FD” (Laliberté & Legendre, 2010).

3. Results

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 (Mann–Whitney U-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).

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).

	Protected	Random	<i>p</i>
Taxonomic diversity			
RNAs	419	404.2 $\pm$ 8.4	0.04
N2000	458	442.7 $\pm$ 5.9	0.002
Functional diversity			
RNAs	0.283	0.283 $\pm$ 0.002	0.692
N2000	0.284	0.283 $\pm$ 0.001	0.131

Overall β TD of water beetles in RNAs ($\beta_{\text{SOR}} = 0.9940$) mainly results from spatial turnover ($\beta_{\text{SIM}} = 0.9866$), 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 ($\beta_{\text{SOR}} = 0.9944 \pm 0.0001$; $P = 0.002$). 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).

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 1000 random draws of an equal number of grid cells (Random).

	RNAs			N2000		
	Protected	Random	<i>p</i>	Protected	Random	<i>p</i>
Taxonomic diversity						
β_{SOR}	0.9940	0.9944	0.002	0.9969	0.997	0.002
β_{SIM}	0.9866	0.9859	0.180	0.9928	0.9925	0.038
β_{NES}	0.0074	0.0086	0.022	0.0040	0.0046	0.008
Functional diversity						
β_{SOR}	0.9890	0.9907	0.002	0.9946	0.9952	0.002
β_{SIM}	0.9671	0.9722	0.002	0.9835	0.9855	0.002
β_{NES}	0.0220	0.0186	0.001	0.0111	0.0097	0.002

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 focussed 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 $\beta_{\text{SOR}} = 0.9082 \pm 0.0528$ across windows) was mainly caused by spatial turnover ($\beta_{\text{SIM}} = 0.7939 \pm 0.1051$), with only a small contribution from nestedness ($\beta_{\text{NES}} = 0.1143 \pm 0.0698$). 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 ($\beta_{\text{SOR}} = 0.9445 \pm 0.0276$) was mainly (99.9% of windows) due to spatial turnover ($\beta_{\text{SIM}} = 0.8699 \pm 0.0673$ *versus* $\beta_{\text{NES}} = 0.0746 \pm 0.044$). 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).

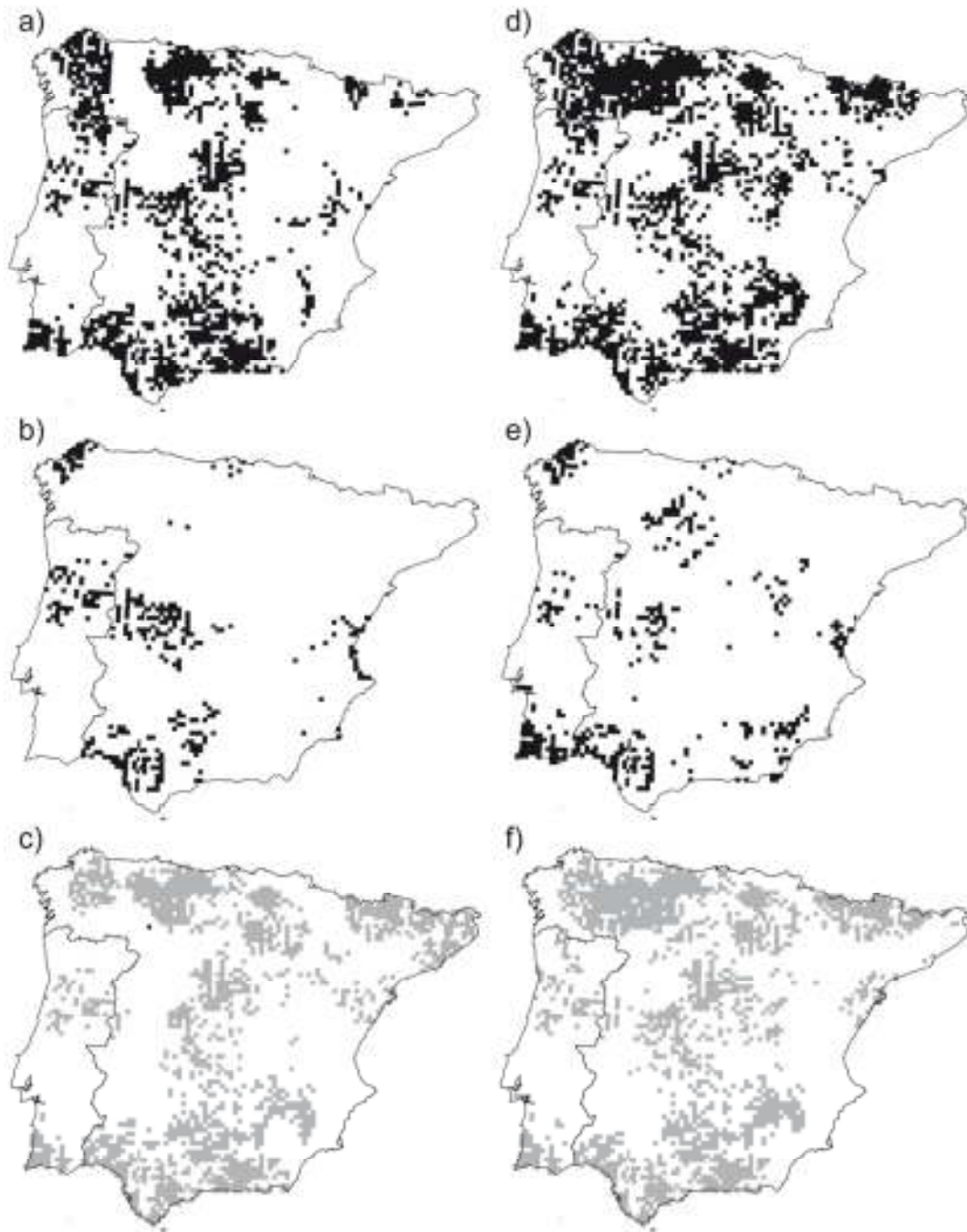


Figure 2. Performance of RNAs (a-c) and N2000 (d-f) networks in representing α , β and γ taxonomic diversity at subregional scale (100 km radius windows): a) and d) windows for which α diversity is significantly higher in protected than in unprotected cells; b) and e) windows for which γ diversity was 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.

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 (Mann–Whitney U-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 ($\beta_{\text{SOR}} = 0.8019 \pm 0.1015$) was mainly due to spatial turnover ($\beta_{\text{SIM}} = 0.5542 \pm 0.1648$), with a smaller contribution from nestedness ($\beta_{\text{NES}} = 0.2477 \pm 0.0981$). 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 $\beta_{\text{SOR}} = 0.8858 \pm 0.0674$ across windows) was mainly driven by spatial turnover (average $\beta_{\text{SIM}} = 0.7135 \pm$

0.1156 *versus* $\beta_{\text{NES}} = 0.1724 \pm 0.0638$). 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).

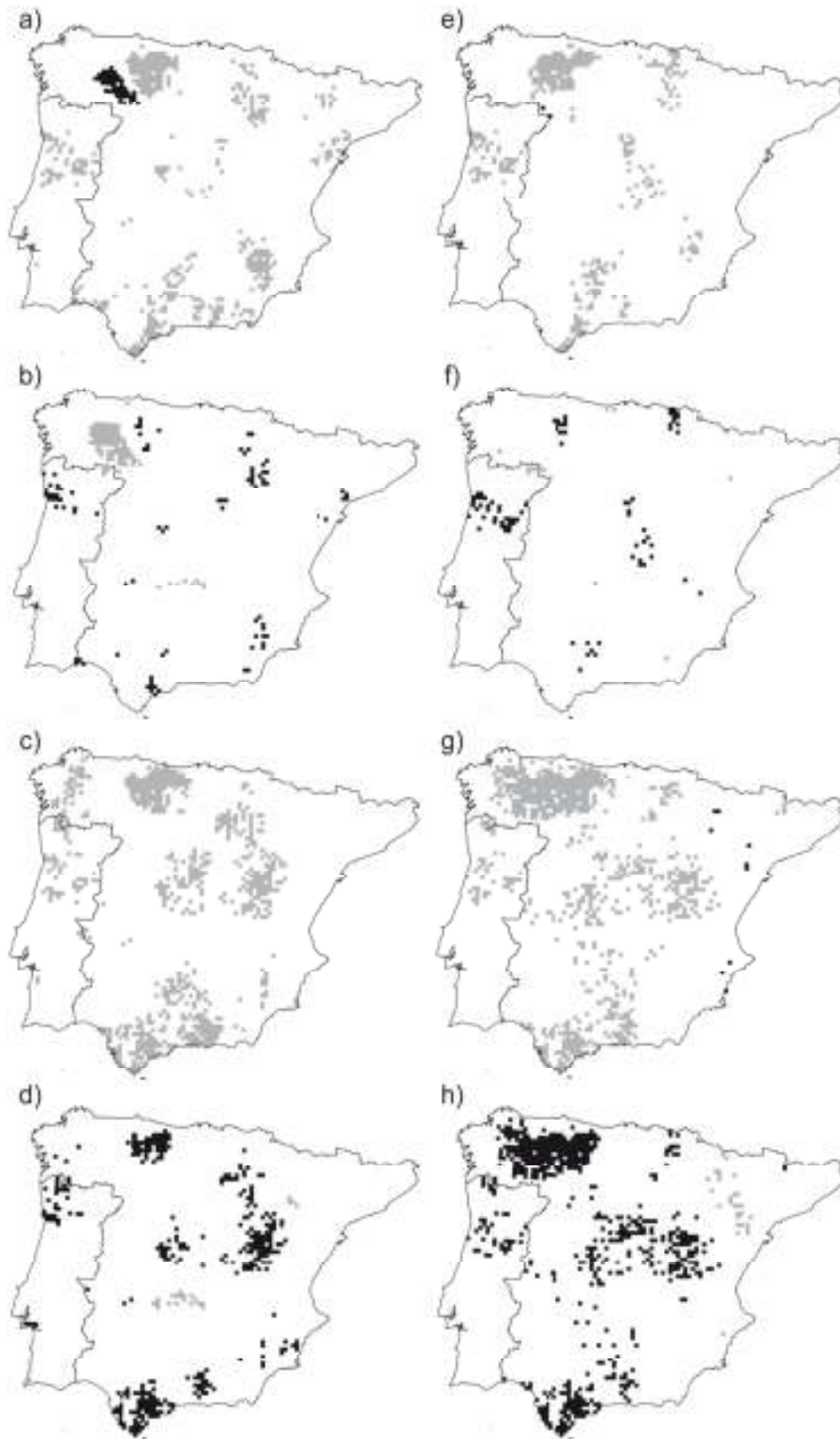


Figure 3. Performance of RNAs (a-d) and N2000 (e-h) networks in representing taxonomic and functional beta diversity components (turnover and nestedness) at subregional scale (100 km radius windows). Grid cells representing the centre of those 100-km-radius windows with significantly higher (black cells) 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} .

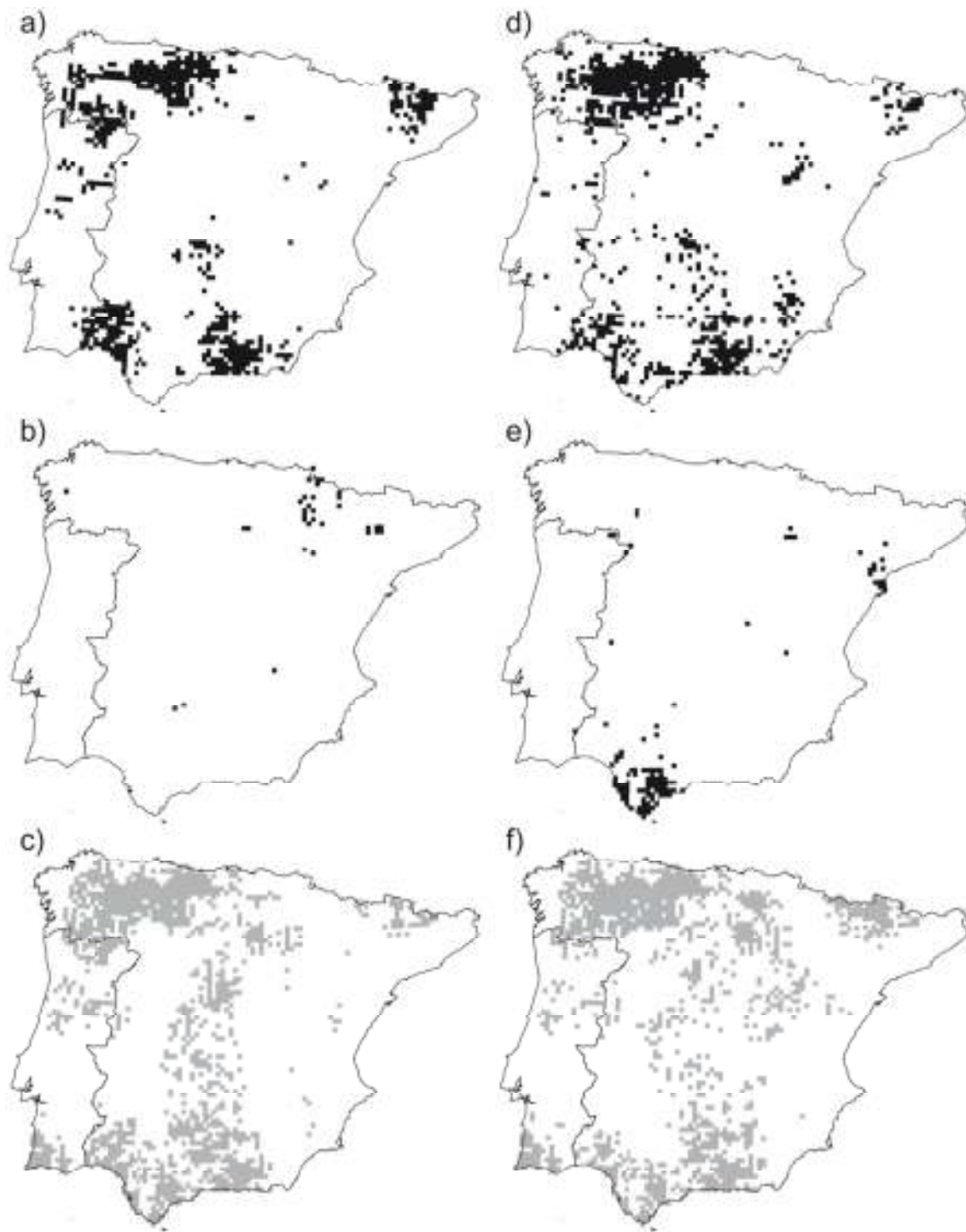


Figure 4. Performance of RNAs (a-c) and N2000 (d-f) networks in representing α , β and γ functional diversity at subregional scale (100-km-radius windows). a) and d) windows for which α diversity is significantly higher in protected than in unprotected cells; b) and e) windows for which γ diversity was 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.

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 & Pfaff, 2009). This is true of 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; Mann-Whitney U 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. in press).

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 65 species (13%) that occur completely outside the RNA network, 15 are Iberian endemics with high vulnerability (Millán et al., in press; Sánchez-Fernández et al., 2008b). Moreover, in the case of the 26 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 (Fig. A1). 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 & 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 km², approximating to that of our windows (31 400 km²).

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 & Child, 2009; Devictor et al., 2010; Forest et 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. 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).

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 would be expected by chance. 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 & 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 & 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 species replacement between protected sites is higher than random, whilst trait replacement is lower, seems to suggest that spatial turnover within protected area networks is mainly driven by spatial and historical constraints and less so by environmental sorting, as it is easier find a higher trait replacement (i.e. environmental dissimilarity) between equivalent random sites. 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 showed 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 total 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 Natura2000 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 freshwater biodiversity (e.g., Hermoso & Clavero, 2011; Sánchez-Fernández et al., 2013) and the need of explicitly consider their biota and environments into conservation planning at European level. 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 (Abellán et al., 2007; 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 freshwater 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 other ecosystems 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 aquatic macroinvertebrates 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 (Strecker et al., 2011; Devictor et al., 2010; Abellán et al., 2013). 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).

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Supplementary material

Figure A1. Location of grid cells where “gap species” occur (i.e. those not represented in any protected area at a threshold of 50%). A, All species; B, vulnerable species.

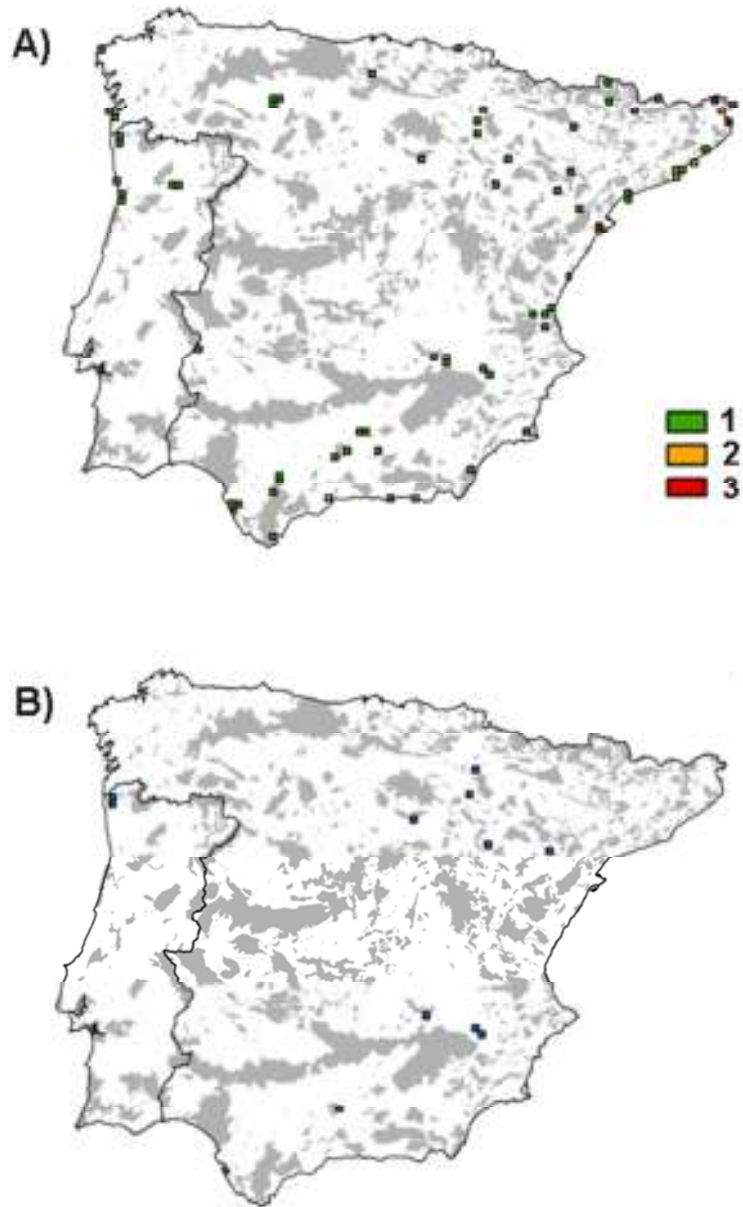


Table A1. Comparison of taxonomic and functional α diversity (median $\pm$ SD) between protected and unprotected grid cells at Iberian scale. Significance was assessed by nonparametric Mann–Whitney U tests.

	Threshold	Protected	Unprotected	<i>U</i> -statistic	<i>P</i>
<i>Taxonomic diversity</i>					
RNAs	1	10 $\pm$ 17.0	6 $\pm$ 12.9	814626	< 0.001
	25	13 $\pm$ 17.5	6 $\pm$ 14.0	623307	< 0.001
	50	15 $\pm$ 17.9	6 $\pm$ 14.3	460201	< 0.001
	75	17 $\pm$ 19.4	7 $\pm$ 14.4	287963	< 0.001
	90	17.5 $\pm$ 19.6	7 $\pm$ 14.6	190224	< 0.001
N2000	1	9 $\pm$ 16.0	4 $\pm$ 10.6	638977	< 0.001
	25	12 $\pm$ 17.3	5 $\pm$ 12.2	895040	< 0.001
	50	13 $\pm$ 18.2	6 $\pm$ 13.0	751946	< 0.001
	75	16 $\pm$ 19.4	6 $\pm$ 13.5	540462	< 0.001
	90	16.5 $\pm$ 20.6	7 $\pm$ 14.0	358216	< 0.001
<i>Functional diversity</i>					
RNAs	1	0.268 $\pm$ 0.08	0.247 $\pm$ 0.09	530804	< 0.001
	25	0.270 $\pm$ 0.07	0.255 $\pm$ 0.09	387514	< 0.001
	50	0.271 $\pm$ 0.07	0.257 $\pm$ 0.09	287422	< 0.001
	75	0.273 $\pm$ 0.07	0.258 $\pm$ 0.09	180156	< 0.001
	90	0.273 $\pm$ 0.08	0.258 $\pm$ 0.09	120039	< 0.001
N2000	1	0.263 $\pm$ 0.08	0.232 $\pm$ 0.10	356280	< 0.001
	25	0.266 $\pm$ 0.07	0.251 $\pm$ 0.09	504469	< 0.001
	50	0.269 $\pm$ 0.07	0.255 $\pm$ 0.09	437074	< 0.001
	75	0.270 $\pm$ 0.07	0.256 $\pm$ 0.09	317764	< 0.001
	90	0.270 $\pm$ 0.08	0.258 $\pm$ 0.09	214261	0.003

Table A2. Representation of taxonomic and functional γ diversity in protected area networks at Iberian scale (protected) for different protection thresholds and comparison with the values expected from 1,000 random draws of an equal number of grid cells (random).

Network	Threshold	$\gamma_{\text{protected}}$	γ_{random}	<i>P</i>
<i>Taxonomic diversity</i>				
RNAs	1	477	463	< 0.001
	25	449	431	0.002
	50	419	404	0.040
	75	382	364	0.055
	90	351	326	0.037
N2000	1	484	478	0.001
	25	472	461	0.004
	50	458	443	0.002
	75	440	414	< 0.001
	90	405	382	0.012
<i>Functional diversity</i>				
RNAs	1	0.284	0.283	0.095
	25	0.281	0.283	0.920
	50	0.283	0.283	0.692
	75	0.282	0.283	0.646
	90	0.285	0.282	0.059
N2000	1	0.282	0.282	0.434
	25	0.282	0.283	0.765
	50	0.284	0.283	0.131
	75	0.285	0.283	0.063
	90	0.282	0.283	0.736

Table A3. Representation of taxonomic and functional beta diversity (β_{SOR}) and its decomposition in nestedness (β_{NES}) and turnover (β_{SIM}) in protected area networks (Protected) at Iberian scale across different protection thresholds and comparison with the values expected from 1,000 random draws of an equal number of grid cells (Random).

Network	Threshold	β_{SIM}			β_{NES}			β_{SOR}		
		Protected	Random	P	Protected	Random	P	Protected	Random	P
<i>Taxonomic diversity</i>										
RNAs	1	0.9952931	0.9952410	0.540	0.002809765	0.002888144	0.328	0.9981028	0.9981292	0.002
	25	0.9911104	0.9906279	0.064	0.005027810	0.005681436	0.008	0.9961382	0.9963094	0.002
	50	0.9866012	0.9858582	0.180	0.007379509	0.008561903	0.022	0.9939807	0.9944201	0.002
	75	0.9766507	0.9765143	0.970	0.012814420	0.014157220	0.274	0.9894651	0.9906715	0.002
	90	0.9652331	0.9654714	0.886	0.018580790	0.020751280	0.364	0.9838138	0.9862227	0.002
N2000	1	0.9971007	0.9970365	0.012	0.001724865	0.001799092	0.006	0.9988255	0.9988355	0.002
	25	0.9952859	0.9950127	< 0.001	0.002697699	0.003026270	0.002	0.9979836	0.9980389	0.002
	50	0.9928408	0.9924585	0.038	0.004044368	0.004568587	0.008	0.9968852	0.9970270	0.002
	75	0.9883894	0.9877729	0.176	0.006407057	0.007402056	0.008	0.9947964	0.9951749	0.002
	90	0.9812587	0.9809809	0.786	0.010412210	0.011472980	0.202	0.9916709	0.9924538	0.002
<i>Functional diversity</i>										
RNAs	1	0.9903451	0.9909953	0.002	0.00650441	0.00603762	0.002	0.9968495	0.9970330	0.002
	25	0.9795386	0.9819263	0.002	0.01368930	0.01207427	< 0.001	0.9932279	0.9940006	0.002
	50	0.9670745	0.9721515	0.002	0.02197082	0.01855651	< 0.001	0.9890454	0.9907080	0.002
	75	0.9408807	0.9518428	0.002	0.03928814	0.03186513	0.008	0.9801688	0.9837079	0.002
	90	0.9049145	0.9262835	0.006	0.06300666	0.04826227	0.006	0.9679212	0.9745458	0.002
N2000	1	0.9670745	0.9721796	0.002	0.02197082	0.01853756	0.002	0.9890454	0.9907171	0.002
	25	0.9897171	0.9905612	0.002	0.00687048	0.00632402	< 0.001	0.9965876	0.9968852	0.002
	50	0.9834505	0.9855476	0.002	0.01113055	0.00966901	< 0.001	0.9945811	0.9952166	0.002
	75	0.9713965	0.9760498	0.002	0.01920146	0.01599141	0.002	0.9905979	0.9920412	0.002
	90	0.9529096	0.9616508	0.002	0.03179427	0.02546044	< 0.001	0.9847039	0.9871112	0.002

Table A4. Comparison of taxonomic and functional α diversity between protected and unprotected grid cells at subregional scale (100-km-radius windows) for different protection thresholds. It is shown the percentage of windows for which α diversity was significantly greater in protected than in unprotected grid cells.

Network	Threshold	% windows
<i>Taxonomic diversity</i>		
RNAs	1	44.8
	25	55.0
	50	50.3
	75	43.3
	90	38.0
N2000	1	55.7
	25	72.2
	50	68.0
	75	64.0
	90	52.7
<i>Functional diversity</i>		
RNAs	1	50.3
	25	29.4
	50	26.0
	75	20.9
	90	14.9
N2000	1	30.1
	25	33.2
	50	30.3
	75	23.6
	90	17.0

Table A5. Representation of taxonomic and functional γ diversity in protected area networks at subregional scale (100-km-radius windows) for different protection thresholds. It is shown the percentage of windows for which γ diversity was significantly greater within protected areas than random.

Network	Threshold	% windows
<i>Taxonomic diversity</i>		
RNAs	1	26.3
	25	15.5
	50	14.1
	75	13.2
	90	11.9
N2000	1	19.8
	25	22.2
	50	17.1
	75	16.5
	90	18.2
<i>Functional diversity</i>		
RNAs	1	7.5
	25	5.0
	50	1.4
	75	3.5
	90	4.3
N2000	1	2.7
	25	2.1
	50	4.7
	75	1.4
	90	6.3

Table A6. Representation of taxonomic β diversity in protected area networks at subregional scale (100-km-radius windows) for different protection thresholds. It is shown the percentage of windows for which beta diversity (β_{SOR}) and its decomposition in nestedness (β_{NES}) and turnover (β_{SIM}) was significantly higher or lower among protected areas than random.

Network	Threshold	β_{SIM}		β_{NES}		β_{SOR}	
		% higher	% lower	% higher	% lower	% higher	% lower
RNAs	1	0.34	12.96	8.98	1.72	1.05	44.88
	25	0.80	14.91	6.53	4.38	0.46	50.02
	50	2.13	19.57	4.04	4.30	0.04	61.30
	75	0.19	28.09	7.41	2.41	0.00	55.90
	90	0.00	26.06	9.72	0.00	0.00	47.05
N2000	1	0.76	2.31	0.42	2.18	0.13	42.79
	25	1.76	4.36	0.00	4.99	0.00	59.19
	50	0.09	14.77	3.59	0.60	0.00	66.20
	75	0.00	14.97	3.43	0.09	0.00	66.80
	90	0.55	21.90	6.93	0.46	0.55	61.83

Table A7. Representation of functional β diversity in protected area networks at subregional scale (100-km-radius windows) for different protection thresholds. It is shown the percentage of windows for which beta diversity (β_{SOR}) and its decomposition in nestedness (β_{NES}) and turnover (β_{SIM}) was significantly higher or lower among protected areas than random.

Network	Threshold	β_{SIM}		β_{NES}		β_{SOR}	
		% higher	% lower	% higher	% lower	% higher	% lower
RNAs	1	0.00	68.62	0.00	8.98	0.00	79.49
	25	0.38	66.49	0.38	10.44	0.38	78.86
	50	0.00	30.39	14.96	1.17	0.00	50.91
	75	0.00	71.72	0.00	11.66	0.00	77.53
	90	0.00	70.76	0.00	6.52	0.00	67.09
N2000	1	NA	NA	NA	NA	NA	NA
	25	0.00	68.58	0.00	12.0	0.00	87.42
	50	0.34	36.83	24.16	1.32	0.00	56.94
	75	0.00	76.39	0.00	8.33	0.00	85.85
	90	0.00	71.03	0.00	13.17	0.00	78.28

Chapter 4:

How far could the alien boatman *Trichocorixa verticalis verticalis* spread? Worldwide estimation of its current and future potential distribution



Marismas de Odiel (Huelva)

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Abstract and keywords

Invasions of alien species are considered among the least reversible human impacts, with diversified effects on aquatic ecosystems. Since prevention is the most cost-effective way to avoid biodiversity loss and ecosystem problems, one challenge in ecological research is to understand the limits of the fundamental niche of the species in order to estimate how far invasive species could spread. *Trichocorixa verticalis verticalis* (Tvv) is a corixid (Hemiptera) originally distributed in North America, but cited as an alien species in three continents. Its impact on native communities is under study, but it is already the dominant species in several saline wetlands and represents a rare example of an aquatic alien insect. This study aims: i) to estimate areas with suitable environmental conditions for Tvv at a global scale, thus identifying potential new zones of invasion; and ii) to test possible changes in this global potential distribution under a climate change scenario. Potential distributions were estimated by applying a multidimensional envelope procedure based on both climatic data, obtained from observed occurrences, and thermal physiological data. Our results suggest Tvv may expand well beyond its current range and find inhabitable conditions in temperate areas along a wide range of latitudes, with an emphasis on coastal areas of Europe, Northern Africa, Argentina, Uruguay, Australia, New Zealand, Myanmar, India, the western boundary between USA and Canada, and areas of the Arabian Peninsula. When considering a future climatic scenario, the suitability area of Tvv showed only limited changes compared with the current potential distribution. These results allow detection of potential contact zones among currently colonized areas and potential areas of invasion. We also identified zones with a high level of suitability that overlap with areas recognized as global hotspots of biodiversity. Finally, we present hypotheses about possible means of spread, focusing on different geographical scales.

Corixidae • Potential distribution • Alien species • Global change • Wetlands

1. Introduction

One of the most important human impacts on a wide range of ecosystems is the introduction of alien species (e.g., McKinney & Lockwood, 1999; Clavero & García-Berthou, 2005; Lockwood et al., 2007; Butchart et al., 2010), this being a problem of particular concern in aquatic ecosystems (Bunn & Arthington, 2002; Dudgeon et al., 2006) with possible impacts at different levels of organisation (Simon & Townsend, 2003). Alien species are a non-random subset of the aquatic biota and, although insects dominate the world's freshwater ecosystems, they are almost unrepresented in the lists of alien species (Karatayev et al., 2009; Strayer, 2010). In this sense, examples of the distribution, major impacts and vectors of invasive plants, fishes, mollusc and decapods are quite numerous (see Strayer, 2010 and references therein). However, the scientific knowledge on alien aquatic insects and their effects on biodiversity and ecosystems processes is very scarce. This is especially true for species considered to be of little importance for the economy and the general public (Kenis et al., 2009).

Trichocorixa verticalis verticalis is one of the few strictly aquatic insects (i.e., all their life cycle stages are aquatic) that can be considered as an “alien” species because it has been moved outside of its native range, following the definitions of Rabitsch (2008) and Strayer (2010).

Trichocorixa verticalis verticalis (Fieber, 1851) (hereinafter Tvv) is a small corixid (Hemiptera) (< 5.5 mm, Fig. 1) originally distributed in North America and the Caribbean islands. However, this boatman has been recorded as an alien species in South Africa, New Caledonia, Morocco, Portugal and Spain, being the only water bug recognized so far as an alien species in Europe (Rabitsch, 2008; Rabitsch, 2010). The invasion of Tvv seems to be more widespread in the Palearctic, where it has been present in the Iberian Peninsula since at least 1997 and was first reported in Andalucía (Spain) by Günther (2004). It has since been recorded from various areas of southern Portugal (Sala & Boix, 2005), south-west Spain (Millán et al., 2005; Rodríguez-Pérez et al., 2009; Van de Meutter et al., 2010a; and authors unpublished data) and Morocco (L'Mohdi et al., 2010).

The success of this corixid as an alien species has been mainly attributed to its capacity: i) to live in brackish and saline waters in both the juvenile and adult

phases (Van de Meutter et al., 2010b), ii) to be passively-transported (Sailer, 1948), and iii) to survive partial desiccation, extreme salinity or freezing in the egg stage (Kelts, 1979). Although this species is considered euryhaline (Sailer, 1948; Hutchinson, 1993), it usually inhabits highly mineralized water bodies like ponds or coastal wetlands. Furthermore, TvV is the only corixid found in the open sea (Gunter & Christmas, 1959). Adults of TvV also have a good ability to fly overland, which is likely to explain their colonization of closed-basin lakes in south-west Europe (e.g., numerous isolated lakes and temporary ponds throughout Andalusia (Rodríguez-Pérez et al., 2009).

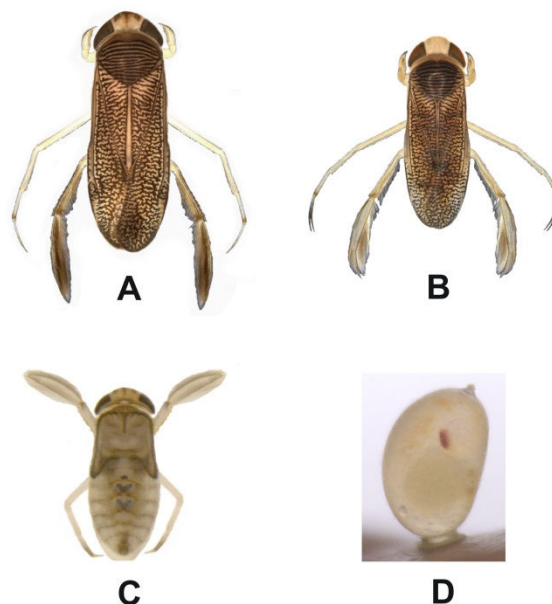


Figure 1. Different stages of *Trichocorixa verticalis verticalis*: (A) Adult female; (B) Adult male; (C) Nymph and (D) Egg.

Whether this corixid is causing loss of native aquatic invertebrate populations is still partially unclear and under study, but it is the dominant hemipteran in many of the invaded sites where it is found (Rodríguez-Pérez et al., 2009; Van de Meutter et al., 2010a) and where it reproduces it is more abundant than native corixids (Rodríguez-Pérez et al., 2009). Thus, the establishment of this species out of its native range could be considered as a threat to aquatic biodiversity, especially for local corixid species. This species also has the potential to cause major changes across food webs via trophic cascades, being one of the few

predators that can survive in highly mineralized aquatic ecosystems (Wurtsbaugh, 1992).

Since prevention of invasions is the most cost-effective way to avoid biodiversity loss and nature conservation problems (Bax et al., 2001; Leung et al., 2002), one challenge in biological invasions is to understand the limits of the fundamental niche of the species, since this information allows us to map the set of places where the species might inhabit (i.e., the potential distribution). Identification of environmentally suitable areas for invasive species can offer great opportunities for preventing or slowing invasions (Guisan & Thuiller, 2005; Jeschke and Strayer, 2008). For this purpose, ecological niche modelling has recently been used to identify the potential distributions of a number of invasive species and provide information to decision-makers (e.g., Peterson, 2003; Aragón et al., 2010; Gallardo et al. 2012). These models are designed to identify the environmental conditions in which species can maintain populations, and then to project these suitable conditions into geographical space, leading to spatial hypotheses on potential distribution (e.g., Aragón et al., 2010; Thuiller et al., 2005a). These models are often coupled to climate-change models to predict how the geographic ranges of species could shift following changes in environmental conditions (e.g., Oberhauser & Peterson, 2003; Roura-Pascal et al., 2004; Thuiller et al., 2005b; Arribas et al., 2012; Capinha et al., 2012).

This study aims to estimate the potential distribution of *Tvv* according to the conceptual and methodological guidelines proposed by Jiménez-Valverde et al. (2011). We used complementary techniques (derived from distribution and physiology) to obtain areas of potential distribution of *Tvv* (i.e., zones with invasion risk at a global scale), taking into account both current and future climatic conditions (a climate change scenario for the year 2100). This study represents the first attempt to estimate potential areas of invasion by *Tvv* and may be considered a useful tool to understand and prevent future invasions of this taxon in aquatic ecosystems worldwide.

2. Methods

Different modelling methods may be arranged along the gradient of potential-realized distribution according to their ability to model any concept (potential distribution refers to the places where a species could live, while realized distribution refers to the places where a species actually lives; see Jiménez-Valverde et al. (2008). Since the required complexity of the modelling technique strongly depends on the precise aims, in this study we decided to use a multidimensional-envelope procedure (MDE) because it provides a picture close to the potential distribution (not the realized one; see Araújo & Peterson, 2012 for a review on uses and misuses of this procedure).

When estimating species' fundamental niches, single procedures are likely to misrepresent the true range of climatic variation that those species are able to tolerate (Sánchez-Fernández et al., 2012), and it is recommendable to consider multiple methodologies (Jiménez-Valverde & Lobo, 2011). Here, the potential distribution of *Tvv* was estimated applying a multidimensional envelope procedure (MDE) based on both i) climatic data obtained from observed occurrences, and ii) thermal physiological data derived from experimental analyses. Potential distributions can be briefly considered here as the regions in which the climatic conditions are suitable for a species, according to its observed occurrences and physiological limits (Jiménez-Valverde et al., 2011; Soberón & Nakamura, 2009 for details).

Estimating potential distribution from occurrences (PD_o)

We used an established procedure which maximizes the capacity to represent geographically the potential distribution of a species based only on distributional data (Aragón et al., 2010; Jiménez-Valverde et al., 2011; Sánchez-Fernández et al., 2011).

Biological and climatic data

Because species distribution models that do not incorporate global data could misrepresent potential distributions (Sánchez-Fernández et al., 2011), we compiled all available distributional data of *Tvv* from the literature. This included

published records in more than 100 years of research (1908-2011), unpublished data from sampling in invaded areas (mainly the Iberian peninsula), and data from environmental agencies' reports and the GBIF (Global Biodiversity Information Facility, 2007). Records with taxonomic uncertainties, or doubtful or imprecise localities, were not considered in the development of predictive maps. The dataset gathered contained 152 records (species/date/locality) for *Tvv*, including both native and invaded zones (Fig. 2). As the spatial units for this study were grid cells at a resolution of 0.4°, these records were summarized in a total of thirty occurrences (0.4° grid cells).

Climatic data were obtained from WORLDCLIM, version 1.3 (<http://www.worldclim.org>, Hijmans et al., 2005). WORLDCLIM contains climatic data obtained by interpolation of climate station records from 1950–2000. Nineteen climatic variables were used as predictors (see Table S1 in Supporting Information). Data from all these variables were extracted at the same resolution (0.4°) as biological data.

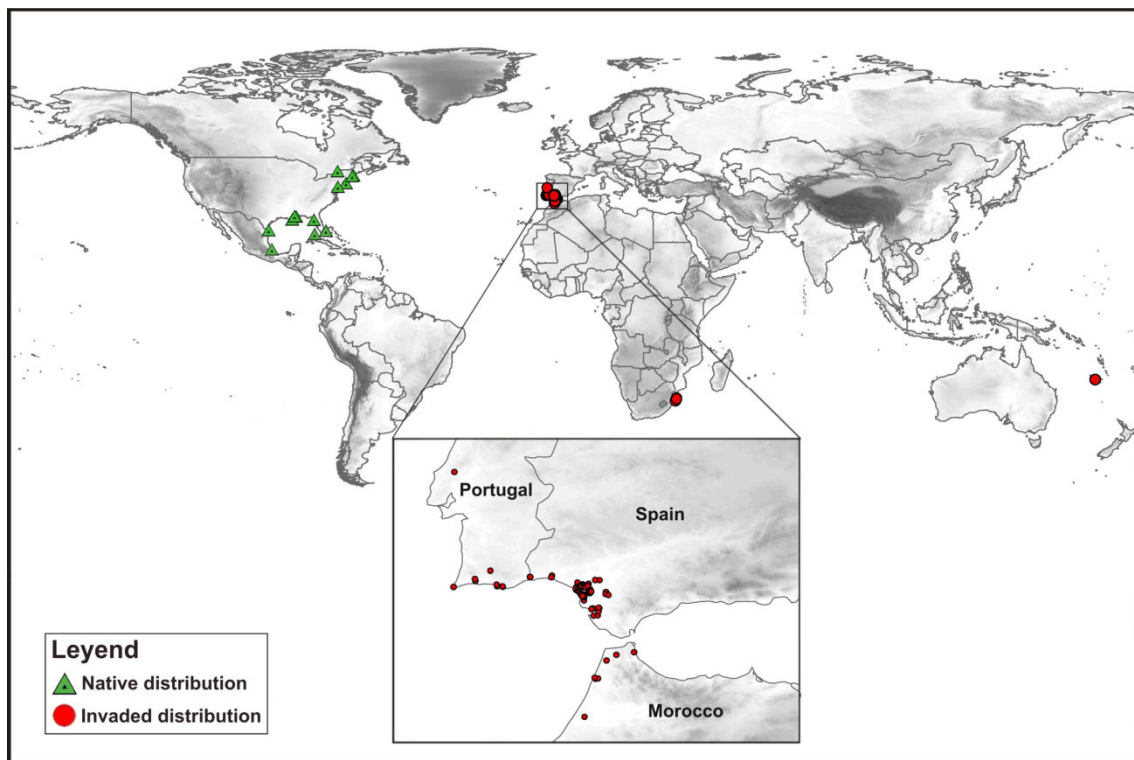


Figure 2. Current known distribution of *Trichocorixa verticalis verticalis*. Map of native (triangles) and invaded (circles) distribution areas of *Trichocorixa verticalis verticalis*, with a close-up of the Iberian Peninsula and Morocco.

Selecting relevant variables and MDE procedure

We used a multidimensional envelope procedure (MDE) to obtain a map with the potential distribution of *Tvv*. Firstly, and because MDE procedures are highly dependent on the number of selected predictors (Beaumont et al., 2005), we estimated climatic variables considered to be relevant for the species distribution. The minimum set of climatic variables needed to explain the occurrence of *Tvv* was calculated using ecological-niche factor analysis in the Biomapper package (ENFA; Hirzel et al., 2002; Calenge & Basille, 2008). This procedure computes uncorrelated factors that can explain both species marginality (the distance between the species optimum and the average climatic conditions in the study area) and specialization (the ratio of the ecological variance in the climate of the study area to that associated with the focal species). Factors were retained or discarded based on their eigenvalues relative to a broken-stick distribution (Hirzel et al., 2002). Climatic variables selected as relevant predictors were those showing the highest correlations (factor scores > 0.30) with the retained ENFA factors.

Then, the maximum and minimum scores (extreme values) for all these relevant climatic variables were calculated in all cells with observed presence of *Tvv*, selecting as suitable grid squares all those with climatic values falling within that range and designating as unsuitable all cells outside it. Distributional information from both the native range and invaded regions is recommended to improve prediction maps (Jiménez-Valverde et al., 2011; Broennimann & Guisan, 2008). Thus, the extreme values were used to derive a binary distributional hypothesis about the areas having climatically suitable conditions (potential distribution), assuming that recorded occurrences reflect the full spectrum of climatic conditions in which the species can survive and reproduce. Then a map with the potential distribution (PD_0) for *Tvv* was obtained.

Estimating potential distribution from physiological data (PD_{PH})

The potential distribution of a species can be considered to be the regions in which the climatic conditions fall within its thermal limits. Data on upper thermal limits (UTL) and lower thermal limits (LTL) were used to define *Tvv*'s thermal biology. These thermal limits were assessed by means of thermal ramping experiments (Coccia et al. unpublished data) and were obtained considering the

extreme values from different combinations of temperature and conductivity during acclimatization.

These values were considered because they are the most reliable and repeatable measures of thermal limits in aquatic insects. Following the same procedure as above, suitable grid squares were considered as all those meeting two conditions: i) lower value of "maximum temperature of the warmest month" (MaxTWM) than UTL and higher value of "minimum temperature of the coldest month" (MinTCM) than LTL; i.e., the thermal values falling within the range designated as suitable by physiological experiments. In the same way, following the same procedure as above, a binary potential distribution map was derived from these physiological thermal limits (PD_{PH}).

Refining the Potential Distribution Map

To be conservative, we combined the potential distribution maps showing the climatically inhabitable areas for *Tvv* using both methods into a single map (PD_{CL}). This new map showed all areas than can be considered as climatically suitable for *Tvv* (under current climatic conditions), considering at least one of the two procedures used ($PD_{CL} = PD_O + PD_{PH}$). Then, as this species mostly inhabits water bodies related with coastal environments, the PD_{CL} map was refined using altitude data as a surrogate of marine-related environments. Therefore, we removed all areas (grid cells) that presented an altitude higher than the highest altitude at which the species has been detected. We thus obtained a final potential distribution map (PD_{CR}) showing the climatically suitable (under current conditions) lowland areas (Fig. 3).

Climatic optimum distances

To obtain a continuous value of climatic suitability within the PD_{CR}, we calculated Mahalanobis distances (a measure of multidimensional non-Euclidean distance, MD) from each cell to the mean of the hypervolume of the selected variables, with reference to the species presence records. This procedure has been widely used in spatial ecology (e.g., Farber & Kadmon, 2003; Etherington et al., 2009). The same predictors selected by ENFA were used to obtain MD. This process has previously been proposed as a useful tool to estimate area

favourability for a species (Calenge et al., 2008), and was carried out using Statistica 8.0 software (StatSoft, 2008). Thus, the final representation of the potential distribution for *Tvv* is a map with continuous values of favourability (or climatic suitability) within its potential distribution, ranging from 0 (low suitability) to 100 (high suitability) (Fig. 4).

Future potential distribution

The extreme values found above (those obtained from both current distribution and physiology) were projected with respect to a future climate scenario, to estimate the potential dynamics of invasion risk areas through time (i.e., combining current (PD_{CR}) and future (PD_F) model outputs, see Fig. 5). Effects of climate change on the potential distribution were predicted considering a climate change Community Climate Model scenario (CCM3) for the year 2100. This prediction assumed a scenario of CO_2 duplication in the atmosphere (Govindasamy et al., 2003), and is approximately equivalent to the average of the current scenarios proposed by The Intergovernmental Panel on Climate Change (Dai et al., 2001). Projected changes in aquatic habitats under climate change are based on the fact that land-based variables could be representative of climatic conditions found in inland waters, since the temperatures in these two systems are strongly correlated (Webb et al., 2003; Caisse, 2006), especially in shallow waterbodies in lowland areas (Vannote et al., 1980) where *Tvv* lives.

3. Results

Potential distribution under current climatic conditions

Isothermality (BIOCLIM3) and Temperature Annual Range (BIOCLIM7) were the most relevant climatic variables identified by ENFA, and therefore these variables were used in the MDE procedure. Isothermality is defined by the relationship between Mean Diurnal Range and Temperature Annual Range, and is a quantification of how large the day-to-night temperature oscillation is in comparison to the summer-to-winter oscillation (see Hijmans et al., 2005). Both variables presented negative signs, indicating that *Tvv* preferably inhabits aquatic habitats in areas with relatively constant temperature and with limited variation

during the year. These climatic preferences are generally related to coastal areas, where the physical properties of the sea allow a smoothing effect of extreme temperatures.

Tvv presented a broad potential distribution under current climatic conditions (PD_{CR}) around the world (see Fig. 3). This corixid seems to have inhabitable conditions in temperate areas, mainly in coastal areas where Isothermality and Temperature Annual Range are generally limited (Fig. 4). Nevertheless, broad areas in South America, Australia, Asia and Europe present a priori suitable conditions for the establishment of the species. Within this PD_{CR}, the areas with higher suitability are coastal areas of Europe (including the Mediterranean islands), Turkey, Tunisia, Egypt, Myanmar, India, Argentina, Uruguay, Australia, New Zealand, the western boundary between USA and Canada, some areas of the Arabian Peninsula and the Persian Gulf (see Fig. 4).

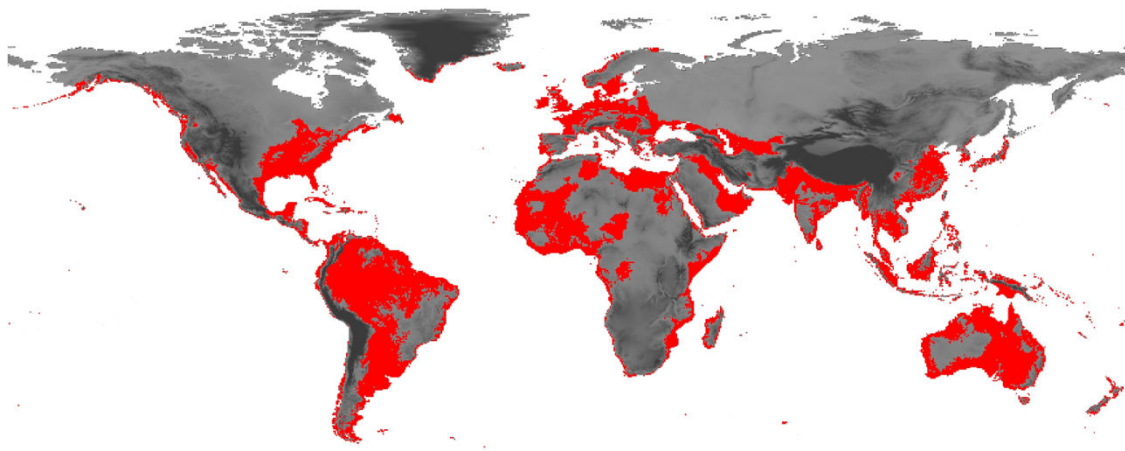


Figure 3. Current potential distribution. Map of worldwide potential distribution of *Trichocorixa verticalis verticalis* based on current climatic conditions.

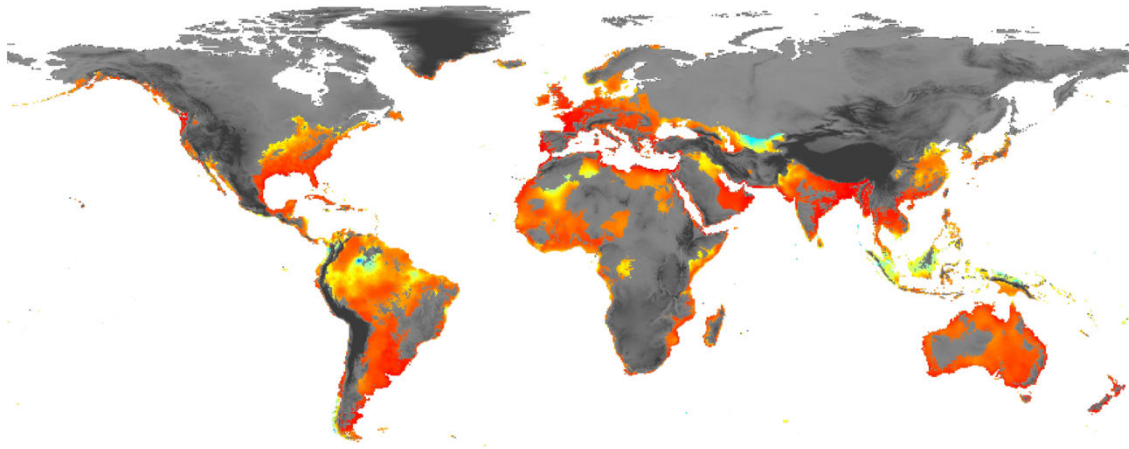


Figure 4. Climatic suitability within the current potential distribution. Map of worldwide current potential distribution of *Trichocorixa verticalis verticalis*. showing the climatic favorability from red (very high suitability) to light blue (very low suitability). These values were calculated applying Mahalanobis distances within the area defined in Fig. 3.

Potential distribution under climate change

Under the CCM3 scenario, the future climatic suitability of Tvv is very similar to the current potential map (Fig. 5). In general, it seems that the potential dynamics of invasion risk areas through time will be low, since almost all potential cells were maintained, with only a few additions and subtractions. In this sense, the models estimated an expansion towards higher latitudes that is visible mainly in Eastern Europe and Asia (e.g., the Baltic Republics and Ukraine), and to a lesser extent in North America. At the same time, this shift towards northern latitudes was accompanied by a reduction of suitable areas in Africa (mainly Algeria), and the loss of suitability in some cells of North America (USA and Canada).

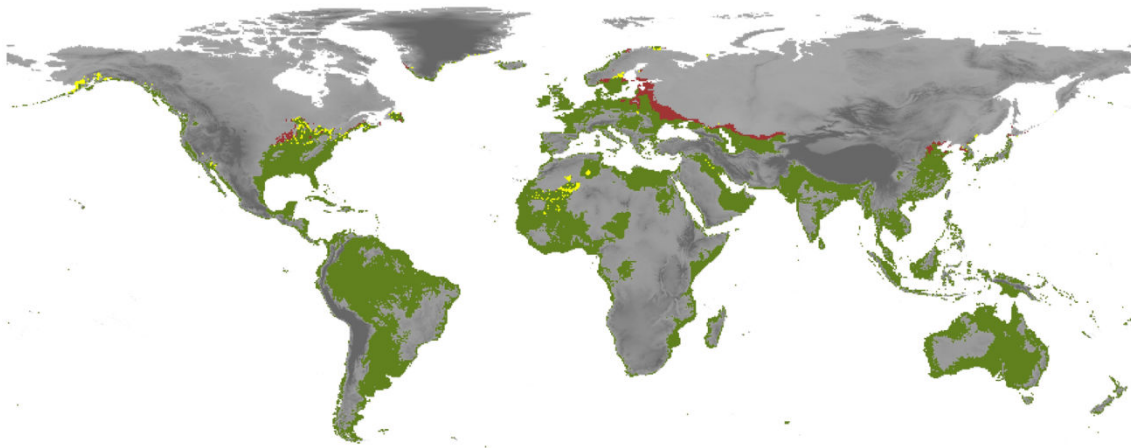


Figure 5. Future potential distribution of *Trichocorixa verticalis verticalis*. This map shows the worldwide future potential distribution of *Trichocorixa verticalis verticalis*. Predictions were based on the Community Climate Model scenario (CCM3) for the year 2100. The concordance between current and future periods is shown in green. Areas labeled in brown are new areas with environmental suitability for future conditions, while yellow cells represent areas where suitable climatic conditions are predicted to be lost in the future.

4. Discussion

Areas of risk invasion and conservation implications

The potential distribution maps produced here represent the first attempt to estimate the global potential distribution of the alien boatman *Trichocorixa verticalis verticalis*. The most effective way to deal with introduced species, short of keeping them out, is to discover them early and attempt to eradicate or at least contain them before the extent of spread and proliferation reaches the critical threshold (Simberloff, 2003; Pluess et al., 2012). Among our findings, one of major concern is the detection of areas highly suitable for TvV in global biodiversity hotspots. Areas like the Mediterranean basin, Northern Africa, New Zealand, the Indo-Burma Region and, to a lesser extent, the Atlantic forest in South America, are particularly important given the high suitability of invasion for TvV. These areas are considered important for worldwide conservation according to different global

biodiversity priority templates such as the biodiversity hotspot concept (Myers et al., 2000), crisis ecoregions (Hoekstra et al., 2005) and Global 200 biologically valuable ecoregions (Olson & Dinerstein, 1998). Our results are useful for detecting the potential connection zones between the current distribution areas (native or invaded) and other suitable areas. These zones should be kept under observation as the most likely future areas of invasion. Thus, major efforts (sampling programs, trade vigilance, biomonitoring efforts) are recommended to prevent future invasions of aquatic ecosystems in these potential areas, especially in high-risk potential contact zones (e.g., coastal wetlands in France, Italy, some areas of Northern Africa and numerous Mediterranean islands).

Western Europe has been already highlighted as a recipient area sensitive to invertebrate biological invasions (Devin et al., 2005; Devin & Beisel, 2008). Strictly within the Mediterranean basin; it is interesting to note that there are so far few records of *Tvv*. To date records nearby are concentrated in Andalusian wetlands (Spain), the Algarve (Portugal) and in the Atlantic coast of Morocco, all to the west of the Strait of Gibraltar. However, samples from the Smir wetland (eastern Morocco; L'Mohdi et al., 2010) within the Mediterranean basin support the possibility that this corixid can colonize extensive areas within this basin. In Spain, Portugal and Morocco, numerous records are from protected areas such as National Parks (Doñana National Park, Southern Spain), Ramsar sites (Andalusian and Moroccan wetlands) or nature reserves (Algarve, Portugal). Biological invasions in protected areas are of global concern (Usher, 1988; Lovejoy, 2006) and illustrate the difficulty of managing and controlling alien species, especially invertebrates.

Invasive species coupled with climate change represent two of the most pervasive aspects of global environmental change (Rahel & Olden, 2008). Generally, at regional scales, a shift of species' ranges towards higher altitudes and latitudes in accordance with their thermal preferences represents the most expected ecological impact of climatic change (Parmesan & Yohe, 2003), as detected for several aquatic macroinvertebrates (Domish et al., 2011). However, in the case of *Tvv*, potential dynamics of invasion risk areas (Fig. 4) considering future climate changes seem to be quite limited. This may be due to the low variability in the climatic conditions of the coastal areas and also because this

species seems to have limited capacity to colonize water bodies in areas at high altitude. However, this restriction appears more related with habitat availability than with the apparently wide thermal tolerance of *Tvv*. Nevertheless, further experiments are needed to confirm the sensitivity response to temperature changes of this species.

Possible ecological impacts and means of dispersal

Although insect species are extremely rare among aquatic invaders (Karatayev et al., 2009), *Tvv* presents traits that enable it to be an important aquatic insect invader: wide potential distribution (also in a climate change context), close relationship to coastal and transitional ecosystems which are less sensitive to drought (Van de Meutter et al., 2010b; Sailer, 1948; Kelts, 1979; Hutchinson, 1993), ability to exploit habitats with a high level of human impact (Van de Meutter et al., 2010a), and possible capacity to be passively-transported by ships or birds (as eggs, larval and adult stages).

Humans have historically facilitated the spread of aquatic invasive species through intentional stocking, infrastructure construction, releases from aquaria and trade routes (Rahel, 2007). International trade has been reported to be among the most important vectors of alien species (Hulme, 2009). Recently, Diez et al. (2012) suggested that extreme climatic events, like strong winds, large waves and high-magnitude storms, may further promote the transport, introduction and establishment of non-native species, since these events often create resource pulses that non-native species are able to utilize. Furthermore, migratory waterbirds are another plausible means by which invertebrates can colonize new areas (Green & Figuerola, 2005).

In this sense, several studies have considered two potential means of dispersal for *Tvv*: one at an intercontinental scale (e.g., from America to Europe or Africa), and another at a more local scale (e.g., from Spain to Morocco and vice-versa or among nearby wetlands). Some studies have suggested that the presence of this corixid outside its native zone may be explained by the introduction of the fishes *Gambusia affinis*, especially in South Africa and New Caledonia (Jansson, 1982; Jansson, 1999), or *Fundulus heteroclitus*, particularly in Spain (SW Europe) (Sala & Boix, 2005). However, the maritime trade, which represents 90% of

international trade (IMO, 2012), may potentially play a crucial role in dispersing Tvv. Ships can transport entire coastal organism assemblages across oceanic barriers and into bays, estuaries, and inland waters (Carlton & Geller, 1993; Ricciardi, 2006). Alien invertebrates are often transported on the surface of container ships or inside containers, as well as in ballast waters or attached to submerged objects including ballast tanks (Tamelander et al., 2010; Briski et al., 2011; Briski et al., 2012). Invertebrate propagules may suffer extreme conditions during transport (Klein et al., 2010), but the wide thermal and salinity tolerance (Van de Meutter et al., 2010b and Coccia et al. unpublished data] of Tvv, together with its capacity to survive partial desiccation and to overwinter at the egg stage (Kelts, 1979; Aiken & Malatestinic, 1995), may allow it to survive in these environmental conditions. Furthermore according with the BWM Convention (BWM Convention, 2004) ships entering Mediterranean waters from the Atlantic Ocean (Straits of Gibraltar) should undertake ballast water exchange before entering the Mediterranean Sea. This procedure could be another option to explain the Atlantic records of Tvv in invaded zones (Portugal, Spain and Morocco).

Our results suggest that major maritime trade routes between commercial harbours, especially in the Atlantic (e.g., New York, Buenos Aires), as well as in Europe and Asia (Kaluza et al., 2010), are potential routes of Tvv spread. In the era of trade globalization and intensification of shipping trade, this dispersal mechanism is likely to be especially important in countries with emerging economies such as India, United Arab Emirates and China. Their rapid economic development, including an explosive growth in international trade, has already increased the potential for new introductions (Yan et al., 2001). These new and relevant links in international trade may affect pathways for the spread of aquatic alien species, particularly euryhaline ones from coastal and transitional aquatic ecosystems, such as Tvv. Gaps in border controls were demonstrated to be related to alien insect invasions (Bacon et al., 2012), so major efforts in terms of trade vigilance and ballast water management are recommended to prevent future spreads of Tvv.

Small-scale dispersal of species is mainly due to natural means such as passive transport by wind (Sailer, 1948) or migratory waterbirds (Green & Figuerola, 2005; Sánchez et al., 2012). Waterbirds have already been shown to

disperse dipterans (Green & Sánchez, 2006; Frisch et al., 2007), and corixid eggs can be abundant in their faeces within the Tvv range (Figuerola et al., 2003), although their viability after gut passage has not been assessed. Birds could accelerate spread across high-risk potential contact zones between currently invaded areas (e.g., Spain and Morocco) and potential areas of invasion with high level of suitability, such as coastal wetlands of France, North Africa, and Mediterranean islands. Large numbers of migratory waterbirds move through SW Spain and Morocco (Rendón et al., 2008), making this flyway a potential major invasion route for Tvv between Africa and Europe.

Moreover, invasion of alien species is considered among the major threats to wetland ecosystems in a worldwide context, also under future global change (Junk et al., 2012). Whether this species is contributing or not to the loss of aquatic macroinvertebrate populations in some ecosystems is still under study (Van de Meutter et al., 2010a), but it is already the dominant species in several invaded saline wetlands (Rodríguez-Pérez et al., 2009). Furthermore, environmental disturbances generally influence the invasion success of aquatic organisms (Mächler & Altermatt, 2012), and Tvv appears to be better than native corixids at coping with human impacts and exploiting artificial wetlands (Van de Meutter et al., 2010a). In this sense, and considering the wide potential geographic range and possible capacity to be passive-transported, the establishment of this species outside of its native range may be considered as a threat to aquatic macroinvertebrate biodiversity, especially to native corixid species.

A negative impact on other invertebrates is also possible. Tvv is the only corixid present in several salt pan complexes in south-west Spain, and research in its native range shows it has the potential to limit the distribution of brine shrimp *Artemia*, the dominant grazer regulating phytoplankton abundance in these hypersaline systems (Wurtsbaugh, 1992). Given the extensive overlap between the predicted distribution of Tvv and the current distribution of *Artemia* at a global scale (Muñoz & Pacios, 2010), the spread of Tvv has the potential for a major impact on the distribution and abundance of brine shrimp.

Prospects for the future

Strong efforts are required to survey carefully the aquatic ecosystems in areas that are suitable for *Tvv*, according to our models. In many parts of the world, little attention is paid to corixids, and *Tvv* is still not present in taxonomic keys used outside North America. For this reason, it is likely that many existing populations outside the native range have so far been overlooked. Indeed, retrospective study of old samples confirmed that *Tvv* has been in the Iberia peninsula since at least 1997, but no one realized it was present prior to Günther (2004). The maps provided by this study can be used as a tool (combined with new field research) to reduce uncertainty in geographically or taxonomically questionable records coming from areas identified as suitable by our model. This could be the case of *Trichocorixa verticalis* reported without subspecies level (*Tv*) in Cuba (Naranjo et al., 2010) or Western Canada (Kenner and Needham, 2004), since our maps have shown these areas to be highly suitable for *Tvv* presence (Fig. 2). Others records of *Tv* were recently reported in saline wetlands of north-western Iran (Ahmadi et al., 2011), which our maps did not detect as a suitable area for *Tvv* invasion. These records necessarily require more research effort to clarify taxonomic doubts at the sub-species level, as correct taxonomic information is crucial for modeling studies on invasive species. Once these records (or new future records) are confirmed, they can be incorporated into our model to improve estimates of *Tvv* potential distributions.

On the other hand, genetic studies are advisable to establish whether the populations in South Africa and New Caledonia, or Europe and Africa, have a common origin, and clarify whether there have been multiple introductions from the native range. Furthermore, genetic studies are also required to clarify the separation of *Tv* into subspecies, and to address possible differences in their capacities to be invasive.

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Supplementary material

Table S1. Climatic variables

Set of Bioclimatic variables considered. Variables were derived from the monthly data. A quarter is a period of three months (1/4 of the year).

Code	Bioclimatic Variables
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7) (* 100)
BIO4	Temperature Seasonality (standard deviation *100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

General conclusions



Laguna del Hito (Cuenca)

Chapter 1

1. Mountainous national parks in Spain have been shown to contain a substantial percentage (almost 70%) of the overall Iberian biodiversity with respect to aquatic macroinvertebrates at family level. The Spanish national parks with the highest richness were “Picos de Europa” and “Cabañeros”.

2. Maximum altitude and habitat type (presence of lotic habitats) were the most important variables related to different community compositions. Meanwhile, lithology (siliceous substrate), land use (percentage of the catchment area with non-irrigated agriculture) and, in particular, habitat type (presence of lotic systems) seemed to be the most important factors for predicting family richness in the national parks as a whole.

3. Selecting several diverse lotic and lentic water bodies at different altitudes seems to be essential for representing the widest range of Iberian macroinvertebrate diversity. Coleoptera family richness may be used as a macroinvertebrate biodiversity surrogate in Iberian mountainous protected areas because it was seen to display the highest correlation with the other taxonomic groups and remaining richness (RR) values. This taxonomic indicator could be complemented with the use of Odonata family richness in case of standing waters.

Chapter 2

4. The results highlighted a limited concordance between assemblage patterns of waterbirds and macroinvertebrates, which may be related to their contrasting responses to environmental gradients. Some climatic variables related with temperature seemed to affect waterbirds more than macroinvertebrate assemblages, while factors directly related with aquatic ecosystems, such as water chemistry, precipitation or hydroperiod, seemed to affect different components of the macroinvertebrate community.

5. The analysis detected a negligible or inverse relationship in patterns of richness. The wetlands with higher waterbird richness values showed significantly lower richness in Hemiptera and macroinvertebrate families, and no significant relationship with Coleoptera. The results of species richness models suggested that different processes, or the same processes operating in different directions, may underlie the observed species richness patterns of waterbirds and aquatic macroinvertebrates.

6. These outcomes pointed to the limited potential of using waterbirds as aquatic biodiversity indicators in Mediterranean wetlands, and the need for caution when using them as “flagships”. Thus, protected area management focusing only on waterbirds is not likely to be sufficient to ensure the conservation of aquatic macroinvertebrate biodiversity. An integrative analysis of different biological assemblages, using datasets from different taxonomic groups, is a necessary precursor for successful conservation policies.

Chapter 3

7. At the Iberian scale, protected area networks tended to include the cells of highest diversity (both taxonomic and functional) of water beetles, as revealed by the alpha diversity assessments. With respect to gamma diversity, contrasting results for taxonomic and functional diversity were found: while Iberian reserves performed relatively well in representing taxonomic diversity, they did not cover greater functional diversity than would be expected by chance. These patterns were not congruent at smaller spatial scales for taxonomic diversity, with a considerable percentage of 100-km-radius windows showing no significant differences in alpha diversity between protected and unprotected areas, and most showing no significant differences in total species representation (gamma diversity).

8. Beta diversity (both taxonomic and functional), which was mainly the result of species/trait replacement between sites, was always significantly lower than could

be expected by chance at the Iberian scale. However, deconstructing beta diversity into its spatial turnover and nestedness components again provided contrasting results for taxonomic and functional diversity: while protected area networks showed a significantly lower turnover and higher nestedness than random for functional diversity, the opposite pattern was observed for taxonomic diversity, suggesting that the processes underlying these beta diversity values are different. Although the results at smaller spatial scale were more ambiguous, they generally pointed to the same pattern.

9. No important qualitative differences between the two studied protected area networks were found. Nevertheless, the Natura2000 network allowed most of the species of conservation concern to be represented.

10. Overall, these findings highlight the contrasting performance of reserve systems for the maintenance of taxonomic and functional freshwater diversity, and point to a bias in environmental representation within protected area networks. Importantly, such a mismatch calls for caution when using any one diversity component as a surrogate for others, and emphasizes the importance of adopting an integrative approach to biodiversity conservation in aquatic ecosystems. Finally, these results also highlight the importance of considering the influence of spatial scale when evaluating the effectiveness of protected area systems.

Chapter 4

11. Recent sampling activities detected large populations of the previously unrecorded alien Hemiptera *Trichocorixa verticalis verticlis* (Tvv) in numerous wetlands designated under the Ramsar Convention in Andalusia (South of Spain).

12. The predictive maps of current potential distribution obtained suggest that Tvv may expand well beyond its current range and find inhabitable conditions in temperate areas across a wide range of latitudes. Bearing in mind the future

climatic scenario, the suitability area showed only limited changes compared with the current potential distribution.

13. The results identified potential contact zones among currently colonized areas and potential areas of invasion (e.g., coastal wetlands in France, Italy, some areas of Northern Africa and numerous Mediterranean islands). These zones should be kept under observation as the most likely future areas of invasion and great effort (sampling programmes, trade vigilance, biomonitoring efforts) are recommended to prevent future invasions of aquatic ecosystems in these potential areas.

14. Zones with a high level of suitability for Tvv overlapped areas recognized as global biodiversity hotspots (Mediterranean basin, New Zealand, Indo-Burma Region and, to a lesser extent, the Atlantic forest in South America) and hence are particularly important and need further effort and research. Possible means of spreading, depending on the different geographical scales, can be proposed. For example: the expansion of international maritime trade may offer new pathways for the spread of alien aquatic species, particularly euryhaline ones from coastal and transitional aquatic ecosystems, such as Tvv. The small-scale dispersal of species seems to be related to natural means such as passive transport by wind, extreme climatic events or migratory waterbirds.

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*Paisajes del Sureste Ibérico familiares en estos años. Al centro una foto de grupo y abajo un bonito recuerdo de São Miguel (Azores, Portugal). En la portada principal: foto de la Laguna de los Majano (Setiles, Guadalajara, CLM).
(Fotos: SG & Ecología Acuática)*