UNIVERSIDAD DE MURCIA

DEPARTAMENTO DE ECOLOGÍA E HIDROLOGÍA

Diversity Patterns in Freshwater Ecosystems: new Insights using Water Beetles at different Spatial Scales

Patrones de Diversidad en Ecosistemas Acuáticos Continentales: nuevas Aportaciones usando Coleópteros a diferentes Escalas Espaciales

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2015

UNIVERSIDAD DE MURCIA

Faculty of Biology
Department of Ecology and Hydrology

Doctoral programme “Biodiversity: conservation and management of species and their habitats”

Diversity patterns in freshwater ecosystems: new insights using water beetles at different spatial scales

Dissertation submitted by

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to obtain the PhD degree with the European Mention

form the University of Murcia

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A mis padres,
por desprenderse de su salud para que
yo pudiera tener la mejor formación posible.

A mi prima Esther,
por sus carcajadas,
por las notas de su saxofón,
porque hubiera sido una excelente médico.

A mis abuelos,
por enseñarme a vivir con humildad.

A las nuevas generaciones,
con la esperanza de que aprendan a vivir
de forma sencilla para que los demás,
sencillamente, puedan vivir.

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Resumen

“*If we admit that human life can be ruled by reason, then all possibility of life is destroyed*”.

(Into the Wild, Christopher McCandless)

‘Blanco’ stream in Bojadillas (Nerpio, Albacete)

Author: Ecología Acuática/CREA

La diversidad biológica, en cualquiera de sus niveles jerárquicos (desde los genes a los ecosistemas), no se encuentra distribuida de manera homogénea en el planeta Tierra. Existen, por tanto, regiones y ecosistemas que poseen mayores valores de biodiversidad que otros. El conocimiento y la comprensión de los patrones espaciales de biodiversidad (a diferentes escalas y desde diferentes enfoques), así como los procesos asociados a los mismos, resulta clave para la conservación de dicha variedad. En este sentido, el estudio de las faunas locales desde diferentes perspectivas (taxonómica, ecológica y funcional), de los procesos por los que éstas se configuran, y de su variación a diferentes escalas espaciales, se han convertido en algunos de los retos más interesantes para disciplinas como la ecología de comunidades, la biogeografía y, más recientemente, también desde la perspectiva de la macroecología.

La tesis profundiza en el estudio de estos tópicos, y para ello se centra en unos ecosistemas y un grupo de organismos que ofrecen numerosas ventajas a la hora de abordarlos, como son los ambientes acuáticos continentales y sus respectivas comunidades de coleópteros. Y es que, a pesar del esfuerzo realizado durante los últimos años, la información sobre los patrones de diversidad a diferentes escalas para este tipo de ecosistemas es muy escasa, especialmente para determinados grupos de organismos como los invertebrados en general y los insectos en particular.

Los ambientes acuáticos continentales son el hábitat de una cantidad de especies desproporcionadamente alta en relación a la superficie que ocupan (casi el 6% de las especies descritas, a pesar de que cubren sólo un 0,8% de la superficie mundial), por lo que están considerados como puntos (ecosistemas) calientes de biodiversidad. Sin embargo, estos sistemas se hayan muy alterados por la actividad humana, lo que ha hecho que se sean reconocidos como unos de los ambientes más amenazados del mundo. De hecho, las tasas de pérdida de biodiversidad en ecosistemas acuáticos son mucho mayores que en los terrestres. Esto es especialmente evidente en los ambientes acuáticos de la cuenca del Mediterráneo, un ejemplo de ecosistemas muy interesantes a la par que amenazados. Por lo tanto, profundizar en el conocimiento de su composición y distribución parece una tarea urgente y necesaria para mejorar su estado de conservación.

Una de las ventajas más importantes de utilizar ecosistemas acuáticos para estudiar los patrones de diversidad, tanto a escala local como global, es que son sistemas claramente delimitados en el espacio y que pueden muestrearse de manera sencilla y económica, y que nos permiten dividirlos de forma relativamente fácil en 2 tipos principales con objeto de testar ciertas hipótesis biogeográficas. Estos tipos son: lóticos o aguas corrientes y leníticos o aguas estancadas. Otra de las diferencias más notables que existe entre ambos tipos de hábitat es su estabilidad a largo plazo. Los hábitats leníticos, particularmente los de pequeño tamaño, tienen una permanencia muy limitada a escala geológica. Cuando una localidad desaparece, no hay conexión física con sitios similares, de ahí que sus habitantes se vean forzados a buscar una nueva localidad. Los hábitats lóticos, en cambio, pueden ser considerados permanentes a escala geológica y se mantienen conectados a otros sistemas similares por medio de la red de drenaje. Algunos estudios han demostrado que para invertebrados acuáticos, el tipo de hábitat (lótico o lenítico) es un buen predictor de las capacidades dispersivas de las especies que los habitan. Bajo tales premisas, se puede detectar una interesante asimetría: entre el conjunto de especialistas lóticos existen ciertos taxones con alta capacidad de dispersión y otros muchos con baja capacidad de dispersión, mientras que entre los especialistas leníticos sólo existen taxones con alta capacidad de dispersión (aquellos que presentaran una baja capacidad de dispersión se habrían extinguido). Por tanto, debería ser posible detectar diferencias en los gradientes de diversidad latitudinal entre los especialistas lóticos y leníticos, ya que las especies de los primeros serán más dependientes de factores históricos (por ejemplo distancia a los refugios glaciares), mientras que los segundos estarán más cercanos al equilibrio con las condiciones climáticas actuales.

En el caso concreto de los hábitats de aguas estancadas, la gran heterogeneidad ambiental del sureste ibérico da como resultado una alta diversidad de cuerpos de agua leníticos naturales y artificiales, por lo que se trata de una región ideal para investigar la composición (riqueza, rareza, endemicidad) y estructura (anidamiento) de sus comunidades, así como los mecanismos responsables de ambas. A pesar de la enorme tasa de pérdida de humedales mediterráneos, nuestro conocimiento sobre la importancia de la biodiversidad de

estos hábitats permanece limitado para otros grupos que no sean plantas y vertebrados, y existe una necesidad urgente de estudios sobre las comunidades de invertebrados de los sistemas acuáticos continentales con vistas a profundizar en su ecología y conservación.

Entre los invertebrados, el grupo de los insectos, pero particularmente el orden Coleoptera (comúnmente conocidos como escarabajos), es el más diversificado. Dentro de este orden, las especies capaces de prosperar en el medio acuático (como adulto, como larva, o en ambas fases), se reconocen como auténticos escarabajos acuáticos. Se trata de un grupo muy heterogéneo, integrado por diferentes familias que han colonizado este medio en diferentes momentos de su evolución, y cuya amplia variedad de estrategias de vida les ha permitido ocupar prácticamente todos los ambientes acuáticos, a excepción del mar abierto, las cumbres más elevadas y los polos. Actualmente se conocen unas 12.600 especies, si bien se estima que podrían existir hasta 18.000 en todo el mundo. Así, cada año es común que se describan nuevas especies para la ciencia pertenecientes a este grupo, incluso en zonas como Europa, donde su taxonomía se encuentra relativamente bien estudiada. Varios estudios han probado el excelente papel de los escarabajos acuáticos como indicador de biodiversidad, ya que sus patrones de riqueza, endemicidad y rareza suelen reflejar patrones similares de otros grupos que ocupan los mismos hábitats. Así pues, el conocimiento de los patrones de distribución de los coleópteros acuáticos, así como los procesos que, a diferentes escalas, conforman dicha distribución, pueden ser clave a la hora de comprender los patrones generales de distribución de la biodiversidad acuática.

La presente tesis tiene como principal objetivo profundizar en el conocimiento que se tiene sobre los patrones de diversidad en ecosistemas acuáticos continentales, de su variación a diferentes escalas espaciales y de los principales procesos que los determinan. Para ello, se ha trabajado un amplio rango de enfoques y perspectivas (diversidad taxonómica, funcional y ecológica), y a distintas escalas espaciales (desde comunidades del sureste ibérico a listados regionales en el Paleártico occidental). En el primer capítulo, se estudian las faunas locales de coleópteros asociadas a ambientes leníticos y su contribución al total de la biodiversidad acuática. En el siguiente capítulo, se aborda esta misma cuestión a

una escala espacial más amplia, a la vez que se explora la forma en la que se organizan dichas faunas (mediante el análisis de sus patrones de anidamiento) y las variables que pueden explicar dicha organización. En el tercer capítulo, se profundiza en el conocimiento de los factores que condicionan las comunidades acuáticas, a través de un estudio de los rasgos biológicos y ecológicos de los taxones. Durante el estudio de las comunidades de coleópteros acuáticos llevado a cabo en los capítulos anteriores, se descubrió una nueva especie para la ciencia, perteneciente a uno de los géneros destacados como más interesantes en el capítulo 3, y cuya descripción formal se presenta en el capítulo 4, que se completa con el análisis de la distribución del resto de endemismos ibéricos del género. Por último, en el capítulo 5 se amplía la escala geográfica para examinar si los patrones de diversidad (alfa, beta y gamma) de coleópteros acuáticos a lo largo de un gradiente latitudinal están condicionados por las diferencias en la estabilidad (a largo plazo) de los hábitats en los que viven.

En el **capítulo 1** se analiza cómo contribuye la riqueza de coleópteros acuáticos encontrada en una selección de ambientes leníticos, representativos de la provincia de Albacete, a la biodiversidad total del grupo en el área de estudio. A una escala más detallada se estudia la biodiversidad que aporta cada uno de los 6 tipos de hábitats estancados previamente tipificados. Además, se identifican las especies amenazadas asociadas a este tipo de ambientes y se testa la existencia de taxones indicadores de cada uno de dichos tipos de hábitat. La calidad de los inventarios fue comprobada mediante curvas de acumulación, y a continuación se realizaron análisis de ordenación (NMDS) y de similaridad (ANOSIM) en base a las faunas locales para testar la coherencia de la clasificación de tipos de hábitat establecida a priori. Por último, se analizó la presencia de especies indicadoras (mediante el test IndVal). Los hábitats leníticos estudiados, además de albergar un buen número de especialistas, también parecen ser de gran importancia para un amplio rango de especies facultativas, lo que pone de manifiesto el papel crucial que juegan en la dinámica metapoblacional de muchas especies. Sin embargo, del total de especies catalogadas como endémicas amenazadas, sólo una (*Ochthebius irenae*) es considerada especialista de hábitats leníticos, ya que el resto (*Nebrioporus baeticus*, *O. delgadoi* y *O. tudmirensis*) son especialistas de ambientes lóticos que aparecieron en cubetas salineras asociadas a arroyos salinos. El tipo de hábitat lenítico que registró mayor número de especies fue “pozas naturales”, debido probablemente a su mayor heterogeneidad y carácter permanente. Este tipo de ambiente, junto con “lagunas endorreicas”, hábitat en el que se observaron especies endémicas amenazadas típicas de medios salinos cercanos, se pueden considerar como los hábitats más interesantes. Todos los tipos de hábitat, excepto “lagunas kársticas”, presentaron especies indicadoras. La identificación de estas especies podría constituir una herramienta útil para el control y seguimiento de cuerpos de agua estancada tipificados y evaluar su estado de conservación. El hecho de que las lagunas kársticas no contaran con taxones indicadores, unido al elevado número de especies que albergaron y a su carácter permanente, refleja el papel crucial que este tipo de sistemas pueden jugar como área de paso durante la fase seca de otros ambientes (alimentación, refugio, etc) en los movimientos de dispersión de las especies.

En el **capítulo 2** se estudió la contribución de los cuerpos de agua estancada a la biodiversidad total del área de estudio de manera análoga al capítulo 1, y además se identificaron las principales variables ambientales que determinan la composición de sus faunas, los patrones de anidamiento de las mismas y los factores ambientales responsables de estos patrones. Para alcanzar los objetivos establecidos, se prospectaron 95 cuerpos de agua leníticos del sureste de la península ibérica, asignados a 8 tipos de hábitat diferentes (al incluir ahora ambientes costeros). Además de los anteriormente mencionados NMDS y ANOSIM, se testó la relación entre las matrices biótica y ambiental mediante el test BIOENV y se analizó el anidamiento a través de las métricas NODF y T. Los resultados muestran que los ecosistemas estudiados en un área que sólo representa el 23% del territorio peninsular, recogen hasta 35% del total de especies de la región íbero-balear. Las “pozas naturales” constituyeron claramente el tipo de hábitat que albergó mayor riqueza de especies, mientras que las “salinas interiores”, a pesar de su baja riqueza, aportaron el mayor número de endemismos ibéricos. No obstante, el componente lótico proveniente de zonas aledañas resultó clave tanto en la elevada riqueza del primero como en el gran número de endemismos del segundo. Cuando se analizaron todas las estaciones de manera conjunta, la conductividad fue la variable que mejor explicó las diferencias en la composición de las faunas, siendo el nivel de perturbación y una combinación de nivel de perturbación, altitud

y conductividad las variables más explicativas para los subconjuntos de estaciones dulces y salinas, respectivamente. Las faunas del conjunto de estaciones mostraron un patrón significativamente anidado, siendo el nivel de perturbación la variable más explicativa. Cuando los sitios dulces y salinos fueron analizados de forma independiente también se detectó un patrón significativamente anidado en ambos casos, mostrando un mayor anidamiento el subconjunto de estaciones dulces que el de salinas. Al igual que para el conjunto de sitios, el nivel de perturbación fue de nuevo la variable más explicativa para la submatriz dulce, jugando la conductividad un papel prácticamente irrelevante. Con los sitios salinos, en cambio, ocurrió justo al revés.

En el **capítulo 3** se estudian los rasgos biológicos y ecológicos que predominan en las comunidades de coleópteros acuáticos de ambientes mediterráneos y las relaciones entre la diversidad taxonómica y de rasgos biológicos y ecológicos de los principales géneros de escarabajos acuáticos. También se estudia el grado de congruencia entre ambos tipos de rasgos y se discuten los principales factores que podrían estar influyendo en la configuración de las comunidades asociadas a diferentes hábitats (básicamente filtrado del hábitat e interacciones bióticas). Para alcanzar dichos objetivos, se elaboró una lista con los géneros de coleópteros acuáticos presentes en el sureste de la península ibérica a partir de las muestras procedentes de 212 estaciones lóticas y leníticas (asignadas a 15 tipos de hábitat). Posteriormente, para los taxones observados se elaboraron sendas matrices que incluyeron la codificación tipo "fuzzy" de 40 categorías de rasgos biológicos y 54 de rasgos ecológicos, recopilados a partir de bibliografía y datos propios. Las 2 matrices resultantes se sometieron a un análisis FCA (Fuzzy Correspondence Analysis). Finalmente, la correlación entre ambas matrices se evaluó mediante un análisis de co-inercia. Los resultados mostraron que la riqueza de especies de las familias de coleópteros acuáticos estuvo significativamente relacionada con su diversidad de rasgos, tanto biológicos como ecológicos. No obstante, hubo familias que presentaron una gran diversidad de rasgos biológicos a pesar de contar con una moderada diversidad taxonómica. Al mismo tiempo, algunas familias presentaron una diversidad de rasgos biológicos menor que otras mucho más ricas taxonómicamente. Para los rasgos biológicos, los géneros fueron separados fundamentalmente en base al tipo de alimento, hábitos alimenticios y tipos de respiración y reproducción. Para los ecológicos, los géneros fueron separados en función de su distribución longitudinal, hábitat local y preferencias en la velocidad de la corriente, sin que se detectaran diferencias claras a nivel de suborden. Los resultados apuntan hacia un predominio de procesos de filtrado del hábitat en arroyos de cabecera mientras que factores de tipo biótico, por ejemplo competencia entre especies, serían más relevantes en hábitats a priori menos estresados como los ambientes leníticos.

Como resultado del estudio taxonómico detallado de las comunidades acuáticas realizado en los capítulos anteriores, se detectó una nueva especie para la ciencia que se describe en el **capítulo 4**. Se trata de *Stictonectes abellani,* coleóptero acuático perteneciente a la familia Dytiscidae, habitante común de los arroyos temporales de la parte central del macizo de Sierra Morena y con una amplia distribución en el cuadrante suroccidental de la península ibérica. A pesar de que dicha familia está bien estudiada en la península Ibérica, la nueva especie habría pasado desapercibida por el carácter críptico de las especies del género. No obstante, un estudio detallado de su morfología externa y genitalia permite distinguirla de las otras 7 especies ibéricas del género, y en particular de *S. optatus*. También se examinó el árbol filogenético de las especies del género para determinar la ubicación de *Stictonectes abellani* dentro del mismo. Además, se estimó la distribución potencial y las preferencias ambientales de las 3 especies del género consideradas endémicas de la península ibérica hasta la fecha. Para ello se elaboraron modelos bioclimáticos, a partir de los datos de presencia de las especies, basados en variables climáticas (resumidas mediante PCA) y geológicas. Estos modelos apenas mostraron solapamiento entre las zonas de mayor adecuación ambiental para los endemismos ibéricos *S. abellani*, *S. occidentalis* y *S. rebeccae*. La especie nueva prefiere áreas montanas de naturaleza silícea y clima continental mediterráneo con cierta influencia atlántica (inviernos suaves y húmedos y veranos cálidos y secos). El modelo sirvió además para localizar las áreas en las que centrar futuros esfuerzos de muestreo a la hora de descubrir nuevas poblaciones. La nueva especie presenta un alto interés de conservación debido a su destacada singularidad genética dentro del género y también por el elevado grado de amenaza que presenta (rango geográfico relativamente pequeño y marcada preferencia por uno de los hábitats más impactados dentro de la península ibérica).

En el **capítulo 5** se estudian los patrones de diversidad gamma, beta (incluyendo la descomposición en sus componentes de reemplazamiento y anidamiento) y alfa de coleópteros acuáticos del Paleártico occidental en un gradiente latitudinal que abarcó desde Marruecos hasta Suecia. El objetivo principal fue testar si existen diferencias en los patrones latitudinales de diversidad para especies de medios lóticos y leníticos, ya que estos hábitats tienen diferentes persistencias a largo plazo, lo que condiciona la capacidad de dispersión de las especies que los habitan. Mediante modelos lineares generalizados (GLM) se testó, en primer lugar, la ausencia de relación entre la riqueza regional (gamma diversidad) y el área de las regiones establecidas. A continuación, mediante el mismo procedimiento, se analizó la variación latitudinal de la riqueza regional, la riqueza local (alfa diversidad), la variación de las faunas entre regiones (beta diversidad), la contribución a la beta diversidad de los componentes de reemplazamiento y anidamiento, y la contribución de las faunas locales a las faunas regionales, así como la relación entre la riqueza regional y la riqueza local. Se encontraron patrones latitudinales opuestos de diversidad gamma para especialistas lóticos y leníticos, y así, mientras que para los primeros ésta disminuyó hacia la parte norte del gradiente, para los segundos lo hizo hacia la parte sur del mismo. La diversidad beta disminuyó con la latitud en todos los casos, sin embargo, los factores subyacentes fueron diferentes en función del tipo de hábitat. La relación entre diversidad alfa y latitud mostró tendencias similares, aunque menos apuntadas, que las obtenidas para diversidad gamma y latitud. Así pues, la diversidad alfa (tanto para sitios lóticos como leníticos) parece estar condicionada por sus respectivas faunas regionales. Estos resultados remarcan la importancia de la capacidad de dispersión de las especies junto con los ciclos glaciares-interglaciares del Pleistoceno en la configuración de los gradientes de diversidad del Paleártico occidental.

General Introduction

"El indígena de una tribu puede reconocer con facilidad cuándo sus acciones están creando un beneficio o un perjuicio en sus vecinos y en su entorno (otra cuestión es que se inhiba, o no, de aplicar el perjuicio). En muchos aspectos su vida es dura, y el conflicto y la competición están presentes, pero el control es sencillo. Para el ser humano actual, en cambio, la vida sigue siendo dura en muchos sentidos, el conflicto y la competición siguen igualmente vigentes, pero el control es cada vez más difícil. La acción benéfica, considerando un marco temporal y espacial amplio, es ahora extraordinariamente difícil. Como resultado de los procesos de globalización y complejización podemos alimentar daños profundos e incluso irreversibles a la naturaleza, a nosotros mismos y a otras personas sin ser adecuadamente conscientes de ello, e incluso hacerlo bajo la percepción de que estamos beneficiando o beneficiándonos".

(El mundo necesita terapia, Pedro Jara)

Colymbetes fuscus

Author: Jesús Arribas

The importance of understanding biodiversity patterns

Biodiversity, at any of its hierarchical levels (genes, taxa and ecosystems), is distributed heterogeneously across the Earth (Gaston 2000), with certain areas displaying higher biodiversity values than others. Understanding the biodiversity patterns and the mechanisms underlying them, at different spatial scales and through distinctive approaches, are key issues to establish conservation priorities (Gaston & Blackburn 2000; Myers et al. 2000). More concretely, the study of local faunas assembling from a given regional pool and their spatial variation have become some of the most interesting challenges for disciplines such as community ecology, biogeography and, more recently, macroecology (Gaston & Blackburn 2000).

Several methods and metrics have been developed in order to measure the different attributes of biodiversity. Most of them are based on species inventories allowing for comparison among areas and are referred both to composition (e.g. richness, rarity, endemicity), and structure (e.g. turnover and nestedness) (Gaston & Blackburn 2000). A very popular metric employed in macroecology is gamma diversity or regional pool richness, whereas alpha diversity or local pool richness is one of the most commonly used in community ecology. Another interesting metric is beta diversity, which measures the degree of change among communities, both at intra-regional (among localities) and inter-regional (among regions) scales. While gamma and alpha diversities are well established measures, beta diversity is a more controversial one, and has recently become the subject of much theoretical and methodological discussion (Baselga 2012; Carvalho et al. 2012).

Studying biodiversity: from local assemblages to latitudinal patterns

The way in which local faunas are assembled is generally determined by the combined influence of local abiotic factors, biotic interactions and the regional species pool (Cornell & Lawton 1992). Concerning abiotic factors, the classical view of community ecologist has consisted of investigating the constraints that environmental filters pose on species occurrence (Weiher & Keddy 1999). Apart from the exclusively taxonomic point of view mentioned above, the process by

which local faunas are assembled can also be approached through a functional perspective. In this sense, the 'habitat templet hyphotesis' suggests that the habitat provides a templet upon which evolution forges life history traits of species (Southwood 1977; Townsend & Hildrew 1994). In other words, the assembly of local faunas would be the result of habitat filtering processes by which concrete species traits are selected as a function of the constraints imposed by the abiotic factors. Such approach provides some advantages which allow for a better understanding of the assembly process, among which are most traits which respond to environmental variations (Richards et al. 1997; Miller et al. 2010; Statzner & Bêche 2010; Dolédec et al. 2011), and trait responses are predictable and allows for large-scale comparisons (Statzner et al. 2001; Menezes et al. 2010). From the initial publication of few direct tests on this concept (Statzner et al. 1994; Townsend et al. 1997), the use of species traits to evaluate the ecosystem functional integrity has become popular, especially in freshwaters (Culp et al. 2011). The relationship among taxonomy, habitat use and both ecological and biological traits, could therefore provide insights on what factors are important in structuring biological communities (Cooper et al. 2008). A strong habitat filter could lead to trait conservatism in close relative species, which would allow for the existence of hypediverse taxonomic groups showing low ecological and biological trait diversity (Bêche & Statzner 2009). On the other hand, high ecological and biological trait diversity in taxonomically poor communities, would point to biotic interactions as the main force in structuring communities (De Bello et al. 2009).

On the other hand, as mentioned above, among the factors influencing local faunas (alpha diversity), one that has received much attention is its dependence on the regional pool of species (gamma diversity; see a review in Gaston & Blackburn 2000), mainly in relation to the existence of community saturation (Caley & Schluter 1997). Thus, a linear relationship between local and regional diversities would suggest that local communities are simply a subsample of the available regional pool. Otherwise, an asymptotic curve would suggest the existence of other (abiotic or biotic) factors operating at local scale (Cornell & Lawton, 1992).

Going beyond the species composition of single localities, beta diversity tackles how this composition varies among localities. Such metric can be, in addition, partitioned into components due to turnover and/or nestedness (Baselga 2010). In this sense, one of the most popular ways to study how assemblages are structured within a certain region, consists of investigating the existence of nestedness patterns (Ülrich et al. 2009). In a perfectly nested system, assemblages from the poorest localities are subsets of the assemblages occurring at the richest sites. The concept of nestedness has been tackled in a number of different disciplines, but specially in biogeography from the first half of the 20th century (Hultén 1937; Darlington 1957; Daubenmire 1975; Hausdorf & Henning 2003) to investigate the patterns in species composition in islands (Hecnar et al. 2002), landscape patches (Tellería & Santos 1995), mountain peaks (Bruun & Moen 2003), ponds, lagoons and lakes (Hecnar & Mcloskey 1997). The first authors developing formal tests on nestedness were Patterson & Atmar (1986) and Patterson (1987). They showed that patterns could be the result of an extinction sequence on island and fragmented habitats. Nowadays, nestedeness is accepted to be caused by a number of different process which often interact among themselves such as selective extinction (Patterson & Atmar 1986), competition (Simberloff & Martin 1991), nested habitats (Cutler 1994) and habitat heterogeneity (Wright et al. 1998). Again, the study of the role played by abiotic factors and anthropogenic stress seems crucial to understand such structure. Such fact is of special concern for conservation purposes in relation to the management of protected area networks (Snodgrass et al. 2000; Baber et al. 2004).

By expanding the spatial scale it is also possible to investigate the trends exhibited by local and regional diversity patterns in a latitudinal gradient. The general trend of decreasing richness from the equator to the poles is considered the oldest ecological pattern known (Hawkins 2001). The debate about their causes and how they interact among themselves has been intense in the last two decades (Currie 1991; Rohde 1997; Rosenzweig & Sandlin 1997; Willig et al. 2003). Multiple hypothesis have been proposed to explain the diversity latitudinal patterns (see reviews in Pianka 1966 and Willig et al. 2003), the most prevalent being those related to energy and water availability (Currie 1991; Allen et al. 2002), area size (Rosenzweig 1995), biotic interactions (Pianka 1966) and the evolutionary time (Rohde 1992). As a variant of the latter, or at least clearly linked to it, the hypothesis of long term habitat stability has been proven to exert a strong

influence when shaping the Western Palaearctic faunas in combination with the glacial-interglacial cycles and the dispersal ability limitations of species (Hof et al. 2008; Ribera 2008). Most of the studies on diversity gradients are based on gamma diversity, with less attention on alpha diversity and beta diversity (Hillebrand 2004; Heino 2011). However, the use of this last metric in studies tackling latitudinal diversity gradients has become popular in recent years (Hof et al. 2008; Hortal et al. 2011; Baselga et al. 2012; Boyero et al. 2012). Thus, the study of its nestedness and turnover components has been proven as a useful tool to investigate the role of dispersal and the recolonization processes after the last glacial maximum (Hof et al. 2008; Baselga 2010; Dobrovolski et al. 2011; Hortal et al. 2011; Baselga et al. 2012; Villéger et al. 2013). So far, most of the studies have shown that the latitudinal gradients for gamma diversity are normally steeper than those for alpha diversity (Hillebrand 2004), since, as stated above, local richness is generally considered to be the result of the combined influence of the regional pool, local abiotic factors and biotic interactions (Cornell & Lawton 1992).

Freshwater ecosystems: interest and particularities

This thesis focuses on freshwater ecosystems because of several reasons:

i) They are recognised as biodiversity hotspots since they harbour 6% of all described species despite covering only 0.8% of the global surface (Dudgeon et al. 2006). They are also considered as highly threatened habitats due to the numerous pressures they suffer (Strayer & Dudgeon 2010) and further research is needed to better know their communities and understand the processes configuring them. All the stated above gains importance in the current context in which the majority of natural habitats are strongly disturbed by human activity, which, together with the increasing rate of environmental change in the last decades, is leading to a huge biodiversity loss (Sala et al. 2000; Barnosky et al. 2011). This fact is specially grave in aquatic ecosystems, which are among the most threatened worldwide (Sala et al. 2000; Dudgeon et al. 2006). In comparison with terrestrial ecosystems, aquatic conservation science is still lagging in quality and quantity of empirical studies as well as in systematic conservation planning (Abell 2002).

ii) These ecosystems can be easily classified into two different main classes according to the type of flow: lotic or current waters and lentic or standing waters (Millán et al. 2006; Hof et al. 2008; Ribera 2008). One of the most distinctive features between these two kinds of habitats is their long term stability. Lentic water bodies have a limited permanence in terms of time and space (especially those which are small sized), and once a locality vanishes, there is no physical connection with other similar sites, their inhabitants are forced to look for a new locality. However, lotic habitats can be considered as permanents at geological scale and they remain connected to other similar systems by means of the drainage network. A number of studies have suggested that this kind of habitat, as indicator of long term habitat stability, is a good predictor of dispersal abilities of the species inhabiting them (Ribera 2008). This contrasting dispersal ability of species typical of lotic and lentic environments allows to test some biogeographical hypotheses concerning the variation of diversity patterns across latitude.

iii) The great environmental heterogeneity of the Iberian southeast results in a high diversity of water bodies, both natural and artificial (Ribera 2000; Abellán et al. 2005; Millán et al. 2006). They are very diverse in terms of conductivity, current velocity and temporality (Millán et al. 2006). Some types of lentic habitats found in the Iberian Peninsula, concretely the inland saline ones, are practically confined to this area in a European context. This is of high interest in terms of biodiversity since inland saline habitats, despite its low richness, harbour a high number of endemic species (Moreno et al. 1997; Velasco et al. 2006; Millán et al. 2011). Finally, the fact that the Iberian Peninsula has the highest number of endemic water beetles in comparison with any other area in Europe (Sánchez-Fernández et al. 2008) increases the importance of understanding the factors involved in configuring the fauna of this region. Such environmental gradients are key factors in the habitat filtering process which will determine the community composition (Ribera 2000; Bonada et al. 2007). They also mediate the existence of different faunas associated to different habitat types in the region (Moreno et al. 1997; Millán et al. 2006; Velasco et al. 2006). This makes the Iberian southeast ideal to investigate the factors shaping community composition in Mediterranean freshwater ecosystems.

iv) Despite their importance and the effort developed by ecologists and biogeographers during the last years, several questions on the community ecology and biogeography of freshwater ecosystems (mainly belonging to the Mediterranean basin) remain unresolved. To date, studies on the biodiversity of small standing waters are mainly focused on Central and Northern Europe, the studies carried out in the Mediterranean region being scarce (Boix et al. 2008). Besides, although nestedness has been widely used to investigate the structure of communities (Meyer & Kalko 2008; Elmendorf & Harrison 2009), including inland aquatic macroinvertebrate communities (Angeler et al. 2008; Wissinger et al. 2009), very few studies have examined the factors underlying nestedness in inland aquatic ecosystems, including the relative importance of different factors in different habitat types (Baber et al. 2004; Heino et al. 2009). In addition, and despite the high rate of Mediterranean wetland loss, our knowledge about the importance of its biodiversity is limited for other groups different to vertebrates and plants (Grillas et al. 2004; Paton 2005). It exists, therefore, an urgent need to conduct studies about the communities of invertebrates from freshwater Mediterranean ecosystems in order to go deeper in their ecology and conservation.

Why water beetles?

The lack of information about diversity patterns is highly remarkable in the case of invertebrates. Despite its huge diversity and importance for humankind, this group has received little attention from conservation policies, resulting in the negative consequences mentioned above (Diniz-Filho et al. 2010; Cardoso et al. 2011). Within invertebrates, insects constitute the most numerous group, the order Coleoptera being undoubtedly the most diverse on Earth. Beetles, the common name for which organisms belonging to the order Coleoptera are known, occur in almost all habitats, except for the open oceans, the highest mountainous peaks and the poles (Beutel & Leschen 2005). Those species able to inhabit aquatic ecosystems (as larve, adult or both phases) are named as 'true aquatic beetles' (Jäch & Balke 2008). It consists of a very heterogeneous group, formed by different families which have colonized the aquatic environment at different stages of their evolution (Hunt et al. 2007). The high variety of life strategies they present allows

them to inhabit all kinds of freshwater habitats. Currently, around 12,600 species are worldwide known, although recent researches estimate that they could reach the number of 18,000 (Jäch & Balke 2008). Water beetles have been demonstrated to show a good performance as biodiversity surrogates (Bilton et al. 2006; Sánchez-Fernández et al. 2006; Picazo et al. 2010; Guareschi et al. 2012), i.e. their diversity patterns tend to predict those from other components of aquatic biodiversity. Thus, looking deeply into the ecology, biogeography and taxonomy of water beetles seems crucial for improving the understanding of aquatic biodiversity distribution and its conservation. Such research should take into account not only the local but also the regional scale, not only the taxonomic but also the functional approach, and not only the assemblage composition (species inventories) but also their spatial structure (e.g. nestedness patterns).

Objectives and thesis structure

The main goal of the present thesis is to investigate the composition and structure of water beetles assemblages in freshwater ecosystems, their performance at different spatial scales and the mechanisms underlying them, especially focusing on the lotic-lentic divide. Thus, it is expected that all this information leads to a better knowledge of the determinants that affect species distribution and community composition, so that it can contribute to improve Nature conservation policies. More especifically, this thesis aims to:

1. Assess how standing waters contribute to the whole regional diversity of water beetles, and more concretely the contribution of each lentic habitat type in terms of richness, rarity and endemicity (chapters 1 and 2).
2. Determine the main variables shaping water beetle assemblages in Mediterranean ecosystems (chapter 2).
3. Investigate if water beetle assemblages in lentic habitats are structured following a nestedness pattern and the factors responsible for the structure detected (chapter 2).

4. Study the relationships among taxonomic, biological and ecological trait diversity of water beetles in Mediterranean ecosystems, and the main factors underlying them (Chapter 3).
5. Look deeply into the taxonomy and distribution of water beetle assemblages (chapter 4).
6. Evaluate to what extent the alpha, beta and diversity patterns of water beetles across a latitudinal gradient in the Western Palaearctic are mediated by long-term habitat stability (chapter 5).

This manuscript is structured in five chapters corresponding to five scientific articles. Chapters 1, 2, 3 and 4 have been already published in international peer-reviewed journals indexed in SCI, while chapter 5 has been recently submitted for publication and it is under review (see appendix 1 for more details). These five chapters (articles) are:

Chapter 1 Picazo P, Moreno JL, Millán A (2010) The contribution of standing waters to aquatic biodiversity: the case of water beetles in southeastern Iberia. *Aquatic Ecology*, **44**, 205-216.

Chapter 2 Picazo P, Bilton DT, Moreno JL, Sánchez-Fernández D, Millán A (2012) Water beetle biodiversity in mediterranean standing waters: assemblage composition, environmental drivers and nestedness patterns. *Insect Conservation and Diversity*, **5**, 146-158.

Chapter 3 Picazo P, Millán A, Dolédec S (2012) Are patterns in the taxonomic, biological and ecological traits of water beetles congruent in Mediterranean ecosystems? *Freshwater Biology*, **57**, 2192-2210.

Chapter 4 Millán A, Picazo F, Fery H, Moreno JL, Sánchez-Fernández D (2013) *Stictonectes abellani* sp. n. (Coleoptera: Dytiscidae: Hydroporinae) from the Iberian Peninsula, with notes on the phylogeny, ecology and distribution of the Iberian species of the genus. *Zootaxa*, **3745**, 533-550.

Chapter 5 Picazo P, Millán A, Sánchez-Fernández D, Ribera I. Habitat stability determines the latitudinal gradients of diversity in Western Palaearctic water beetles. *Global Ecology and Biogeography*, under review.

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Chapters

“Cuando las dinastías pusieron la grandeza del poder por encima de la grandeza de la vida, la delgada tierra y la tupida selva no bastaron para alimentar, tanto y tan rápidamente, las exigencias de reyes, sacerdotes, guerreros y funcionarios. Vinieron las guerras, el abandono de las tierras, la fuga a las ciudades primero, y de las ciudades después. La tierra ya no pudo mantener el poder. Cayó el poder. Permaneció la tierra. Permanecieron los hombres sin más poder que el de la tierra”.

(Los cinco soles de México, Carlos Fuentes)

‘Arazas’ river in ‘Puente del Fresno’ (Parque Nacional de Ordesa)

Author: Ecología Acuática

Chapter 1

The contribution of standing waters to aquatic biodiversity: the case of water beetles in southeastern Iberia

‘Lavajo del Roblecillo’ pond (Pozorrubielos de la Mancha, Cuenca)

Author: Félix Picazo

Introduction

The Mediterranean Basin is considered to be one of the world's biodiversity hotspots (Myers et al. 2000). While recent decades have witnessed severe biodiversity losses in the region, almost certainly associated with increased human activity, the southeast of the Iberian Peninsula still retains a rich and endemic biota (Médail & Quézel 1997). Arthropods represent more than 80% of all known animal species, and within them, water beetles make up a hyperdiverse group with about 18,000 estimated species (Jäch & Balke 2008) and usually contribute greatly to the total aquatic biodiversity of a given area. Water beetles also are a well-known group of insects in the Iberian Peninsula (Ribera et al. 1998; Ribera 2000; Sánchez-Fernández et al. 2008b) and certainly one of the best known groups of insects in southeastern Iberia (Millán et al. 2001a; 2001b; 2002; 2006). Furthermore, they have been shown to be good indicator of wider biodiversity in aquatic ecosystems (Bilton et al. 2006; Sánchez-Fernández et al. 2006), and water beetle hotspots (some combination of high species richness and high occurrence of rare, endemic and/or threatened species) are usually accompanied by similar patterns in other macroinvertebrate groups.

Biodiversity is one of the main evaluation criteria used in the protection of wetlands, and a number of studies have emphasized the high species richness of these systems (Williams et al. 2003; De Meester et al. 2005; Hof et al. 2006). Despite this, apart from some concrete studies (e.g. Boix et al. 2008), the aquatic invertebrate communities of these habitats are relatively poorly known in much of southern Europe. Furthermore, stagnant waters in the Mediterranean region are threatened because of changing agricultural practices, as the region moves from extensive to intensive farming, a transformation that is mainly associated with overexploitation of aquifers, alterations of natural drainage patterns, eutrophication, and the introduction of alien species (Battisti et al. 2008).

Thus, more information on lentic biodiversity and its contribution to regional biodiversity in Mediterranean Europe is necessary. Since water beetles have been demonstrated to be good biodiversity surrogates and Albacete province is representative of the semiarid Mediterranean region, the identification of indicator species of naturalness and their distribution patterns in this region would provide valuable information for monitoring and conserving these kinds of ecosystems.

Hence, the main aims of this study were:

1. Analyzing the contribution of standing waters to local water beetle biodiversity and distinguishing which species are exclusive to these water bodies.
2. Determining the relative contribution of different lentic habitat types to such biodiversity.
3. Identifying the threatened species associated with lentic habitats.
4. Identifying indicator species of naturalness for the different lentic habitat types.

Materials and methods

Study area

The area considered in this work is the administrative province of Albacete (figure 1), which has an area of 14,858 km^2. Albacete is representative of the southeast of Iberian Peninsula, with a continental Mediterranean climate and an altitudinal range of 300–2,000 m.a.s.l. A large part of the province is semiarid with a mean annual precipitation of 350–400 mm although in the southwestern mountains precipitation is usually between 700 and 1000 mm (Fernández 1998). Underlying rocks are mainly calcareous, with Jurassic and Cretaceous limestones in the mountains and sedimentary detritic Tertiary basins on the plains. Saline water bodies are a common feature of this area, being associated to evaporite outcrops (Triassic-Keuper) and/or semiarid endorheic basins (Casado & Montes 1995).

Habitat types

Sampling sites were assigned to habitat types according to environmental and ecological features following Millán et al. (2002) and Abellán et al. (2005). These authors distinguished eighteen main types of habitat, nine of them lentic. In this work, a total of 26 sites covering six standing water habitat types which span the entire spectrum of lentic habitat types in the region, with the exception of reservoirs, were sampled (table 1). These habitats types were rice fields, karstic lagoons (mostly associated with continuous underground drainage systems), natural ponds (associated with small and continuous superficial drainage systems), endorheic lagoons, artificial ponds (for irrigation and livestock watering), and continental salt-pans.

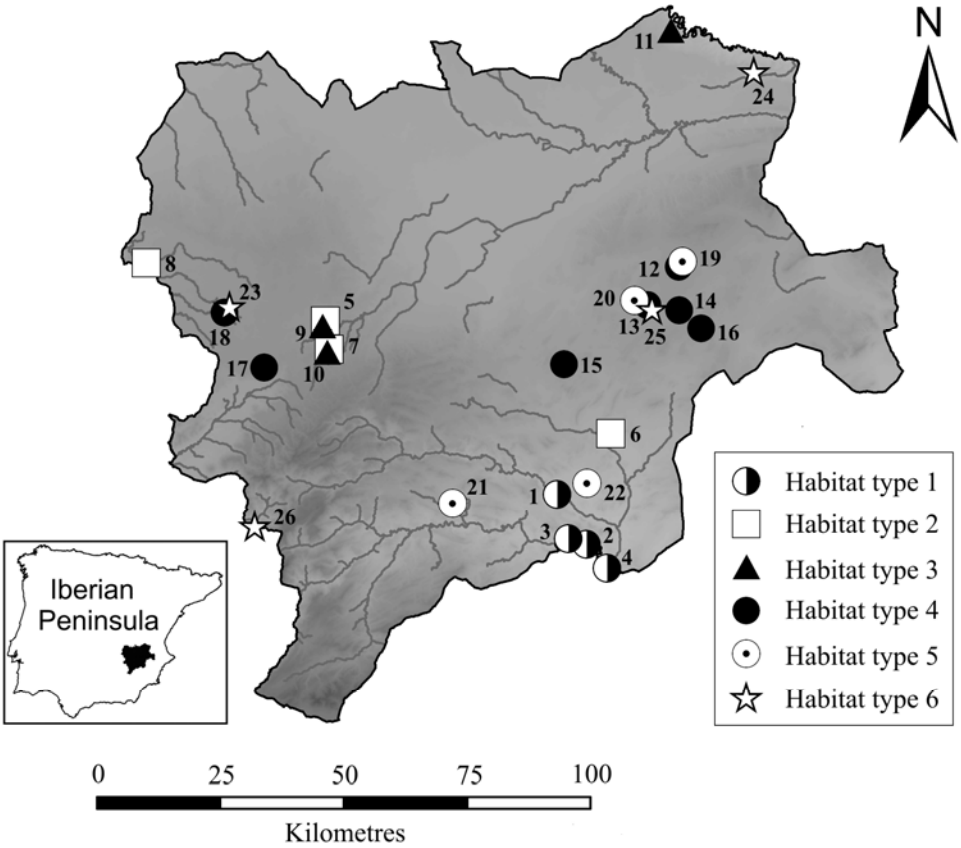

Figure 1 Study area showing sampling sites and habitat types (1, rice fields; 2, karstic lagoons; 3, natural ponds; 4, endorheic lagoons; 5, artificial ponds; 6, continental salt-pans).

Sampling and sample processing

The species list (see table S1) was compiled from field samples collected between 1981 and 2008, with most sampling taking place between 1994 and 2003. Most sites (70%) were visited at least twice. Despite some differences in sampling methodology over this period, localities were consistently sampled until no further species were found. Samples were taken with pond nets (pentagonal or triangular, 20–30 cm deep, 500 μm to 1 mm mesh) and in all cases sampling was stratified,

Table 1 Sample sites. Habitat types (HT): 1, rice fields; 2, karstic lagoons; 3, natural ponds; 4, endorheic lagoons; 5, artificial ponds; 6, continental salt-pans. Size: small (10 m2-0.1 ha), Medium (0.1-1 ha, large (1-5 ha). Depth: shallow (<2 m), deep (>2 m). Cond.: mean conductivity (μS/cm).

	Site	HT	Altitude	Size	Depth	Cond.	Temporary
1	Puente de Isso	1	429	Medium	Shallow	723	Yes
2	El Hondón	1	341	Medium	Shallow	476	Yes
3	Cenajo	1	351	Medium	Shallow	510	Yes
4	Las Minas	1	322	Large	Shallow	475	Yes
5	Laguna de Ojos de Villaverde	2	900	Large	Deep	408	No
6	Laguna grande de Alboraj	2	600	Medium	Deep	3430	No
7	Laguna del Arquillo	2	1000	Large	Deep	470	No
8	Lagunas de Ruidera	2	840	Large	Deep	900	No
9	Poza en Ojos de Villaverde	3	900	Small	Shallow	850	No
10	Charca en el Arquillo	3	1000	Small	Shallow	750	No
11	Toyo en Tabaqueros	3	580	Small	Shallow	1400	Yes
12	Laguna del Salobrejo	4	940	Large	Shallow	11000	Yes
13	Laguna de Pétrola	4	860	Large	Shallow	13210	Yes
14	Lagunas de Corral Rubio	4	870	Medium	Shallow	20000	Yes
15	Laguna de Ontalafia	4	840	Large	Shallow	9540	No
16	Laguna del Saladar	4	870	Large	Shallow	43000	Yes
17	Laguna de la Sanguijuela	4	1024	Medium	Shallow	700	Yes
18	Laguna de Pinilla	4	960	Large	Shallow	37000	Yes
19	Balsa en Salobrejo	5	940	Small	Shallow	1400	No
20	Charca artificial en Pétrola	5	860	Small	Shallow	1500	Yes
21	Charca en Elche de la Sierra	5	650	Small	Shallow	1450	Yes
22	Laguna de los Patos	5	500	Medium	Deep	2620	No
23	Salinas de Pinilla	6	960	Medium	Shallow	90000	Yes
24	Salinas en Casas de Ves	6	571	Small	Shallow	230000	No
25	Salinas en Pétrola	6	860	Medium	Shallow	86200	Yes
26	Rezume salino en Siles	6	760	Small	Shallow	290000	No

including all microhabitat types considered suitable for aquatic beetles. Samples were preserved in 70% ethanol and taken to the laboratory, where they were processed and identified to species level. In order to minimize uncertainty due to insufficient knowledge of their distribution and/or taxonomy, species of the families Sphaeriusidae, Chrysomelidae, Curculionidae, Georissidae, Scirtidae, Limnichidae and Heteroceridae were not included in this study, which was restricted to the following families, themselves comprising the vast majority of water beetles present in Iberia: Gyrinidae, Haliplidae, Paelobiidae, Dytiscidae, Hydrophilidae, Helophoridae, Hydrochidae, Hydraenidae, Elmidae and Dryopidae. The habitat preferences of species (running; running and standing; standing) were obtained from Ribera et al. (2003). Species which are considered threatened (those included in the High or Very High vulnerability categories), and endemic species follow Sánchez-Fernández et al. (2008a). Finally, the species recorded in this study and the contribution of standing waters to the local species pool were analyzed using the latest species checklist available for Albacete province (Abellán et al. 2004; unpublished data).

Collector's curves

This method was used to determine whether the number of species recorded across the standing waters sampled, both for all species recorded and only lentic species, represented a relatively complete inventory for the study area. Collector's curves are widely employed to evaluate the quality of inventories (e.g., Soberón & Llorente 1993; Hortal et al. 2004), and represent the expected accumulated number of species encountered within a certain geographical area as a function of collecting effort (Soberón & Llorente 1993; Colwell & Coddington 1994; Gotelli & Colwell 2001). The slope of the collector's curve determines the rate of species accumulation at a given level of sampling effort. This slope diminishes with sampling effort as new species are found, reaching a hypothetical value of 0 when all species are detected. As the shape of this relationship depends on the order in which individuals were recorded, this order was randomized 100 times to obtain a smoothed accumulation curve (using the EstimateS 6.0 software package; Colwell 2000). The Clench function was fitted to smoothed data, and the asymptotic value (i.e., the species richness predicted for an ideally unlimited sample size) was computed. The ratio of recorded to predicted species richness (the asymptotic score) was used as a measure of completeness of the inventory.

Multivariate analysis

Non-metric MDS ordinations (PRIMER 6.0 software package, Clarke & Warwick 1994) were employed to explore whether samples taken from different sites were distinct based on their water beetle community composition. Furthermore, the ANOSIM (ANalysis Of SIMilarities) routine, also in the PRIMER 6.0, was used to compare within- and between-group similarities (Clarke 1993). In a robust classification, similarities between sites that are in the same group should be substantially greater than similarities between sites that are in different groups. The key output from this analysis is the R statistic, which ranges from -1 to 1. The R statistic equals 1 if all sites within classification groups are more similar to each other than any sites from different groups. Similarly, R = 0 if inter-site similarities between and within classification groups are the same. A negative value for R would indicate that sites within a classification group are more similar on average to sites in the other groups than to those in their own group. Although the R statistic is a useful comparative measure of the degree of separation of sites, a Monte Carlo permutation test was also carried out to determine whether the R statistic is significantly different from zero (Clarke 1993). In addition, IndVal analysis (Dufrêne & Legendre 1997) was performed (using abundance data) to identify of naturalness species within each habitat type using PC-ORD version 4.20 software (McCune & Mefford 1999). This analysis estimates the indicator value (IV) based on the relative abundance and occurrence frequency of each species in each previously defined habitat type. A Monte Carlo permutation test was also used to test the significance of each value.

Results

Standing water species list for Albacete

A total of 125 species of water beetles belonging to 11 families were collected: Gyrinidae (5 species), Haliplidae (6), Noteridae (1), Paelobiidae (1), Dytiscidae

(53), Helophoridae (7), Hydrochidae (3), Hydrophilidae (28), Hydraenidae (17), Elmidae (2), and Dryopidae (2). Ten species were Iberian endemics, although only one endemic species, *Ochthebius irenae*, showed a clear preference for standing water bodies. Other endemic species such as *Graptodytes castilianus*, *Helophorus seidlitzii* and *Hydraena atrata* were habitat generalists since they occur in both standing and running waters (table S1). Four threatened endemic species were also recorded, *Nebrioporus baeticus*, *Ochthebius delgadoi*, *Ochthebius irenae* and *Ochthebius tudmirensis*. Other rare and threatened species, typical of standing waters, were *Gyrinus suffriani*, *Hydaticus seminiger*, and *Graphoderus cinereus*. Here, such species are found at the southern limits of their global distributions (Millán et al. 2002). Out of the 218 species recorded in the most recent checklist for Albacete province, 125 (57%) were found in this study. Of these 125, 24 species were typical of running waters, 46 species occurred in both running and stagnant waters, and 55 species (44% of those recorded in this study; 25% of the total for Albacete) were exclusive to stagnant waters (table 2). In the Albacete checklist as a whole, 65 species (30%) are exclusive to standing waters, 94 (43%) to running, and 59 (27%) are habitat generalists, following Ribera et al. (2003).

Table 2 Species richness indicating habitat preference (Ribera et al. 2003), mean and standard deviation, number of threatened species and number of endemics recorded in the six habitat types studied. Percentage in brackets are calculated over the total number of species recorded in Albacete (218 species).

	Rice fields	Karstic lagoons	Natural ponds	Endorheic lagoons	Artificial ponds	Continental salt-pans	Total
Running	3	10	16	9	6	2	24
Running/ stagnant	7	25	34	18	22	0	46
Stagnant	5	23	41	24	26	2	55
Total	15 (7%)	58 (27%)	91 (42%)	51 (23%)	54 (25%)	4 (2%)	125 (57%)
Threatened	0	1	0	4	0	2	4
Endemics	0	4	4	6	2	2	10

The collector's curve for all species recorded in standing waters, and for exclusively lentic species sensu Ribera et al. 2003, predicted an asymptotic value of 162 species (correlation coefficient r = 0.999, variance explained = 99.99%) and 70 species (correlation coefficient r = 0.999, variance explained = 99.88%) in the studied area (figure 2), respectively. In both cases, sampling completeness was therefore approximately 77%, a relatively high value for invertebrate inventories (see Sánchez-Fernández et al. 2008a).

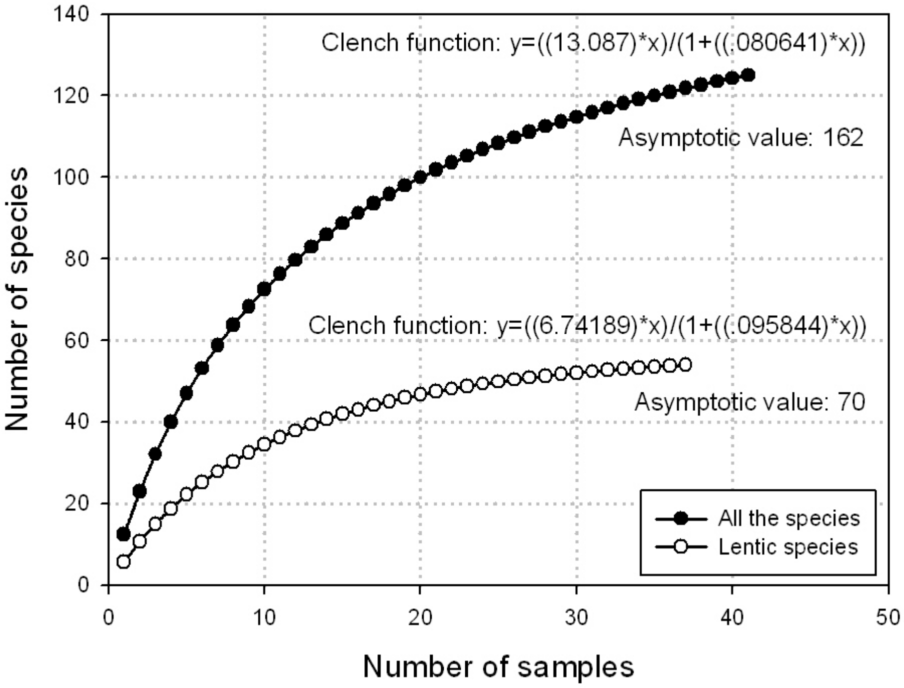

Figure 2 Collector's curves (Clench function) and asymptotic values predicted for all species recorded and exclusively lentic species sensu Ribera et al. (2003).

Habitat type, assemblages and indicator species of naturalness

The highest species and family richness was recorded in natural ponds, although the highest number of endemic and vulnerable species were recorded in endorheic lagoons. Water beetle assemblages of the six a priori defined habitat types were studied by means of MDS and ANOSIM analyses (figure 3; table 3). Minor differences were found between karstic lagoons, natural ponds and artificial ponds, while rice fields and endorheic lagoons showed the greatest differences from the other types. Continental salt-pans, with only four species but one exclusive to this habitat (*Ochthebius notabilis*) were also clearly different. IndVal analysis identified of naturalness species for five habitat types (table 4). *Hydroglyphus geminus* and *Ochthebius viridescens* were weak but significant indicators for rice fields and artificial ponds, respectively. *Ochthebius marinus* and *Hygrotus pallidulus* were good indicators for endorheic lagoons. *Ochthebius notabilis* showed the maximum possible indicator value, since it only occurs in continental salt-pans. Finally, natural ponds showed a high number of indicator species, *Hydroporus discretus* having the highest value. Karstic lagoons did not have any significant indicator species associated with them in the analysis.

Discussion

The water beetle taxa recorded from standing water bodies in this study represent 57% of the total species reported in Albacete (218 species), highlighting the importance of lentic ecosystems for regional aquatic beetle diversity. In addition, the species collected include more than one-third of the lentic water beetles recorded from the Iberian Peninsula and the Balearic Islands (Ribera et al. 1998; 2003; Millán et al. 2002), emphasizing the importance of these lentic sites at both regional and global scale.

Williams et al. (2003) have suggested that small standing water bodies may contribute the bulk of regional freshwater biodiversity, a result which may initially appear to be borne out in this study, where 57% of water beetle species known from Albacete have been recorded in the lentic sites studied. However, such data must be considered in the light of the habitat preferences of the species concerned, since a number of the taxa recorded from standing waters in this study are more characteristic of running waters, or habitat generalists, and in fact only 55 of the species found (25% of the water beetles recorded from the province as a whole) can be considered exclusively lentic in their ecological requirements. Nevertheless, they represent the 77% of the exclusively lentic species expected for the region. In this respect, running waters do indeed support more exclusive species, many of which are geographically restricted endemics (Ribera et al. 2003; Sánchez-Fernández et al. 2008a).

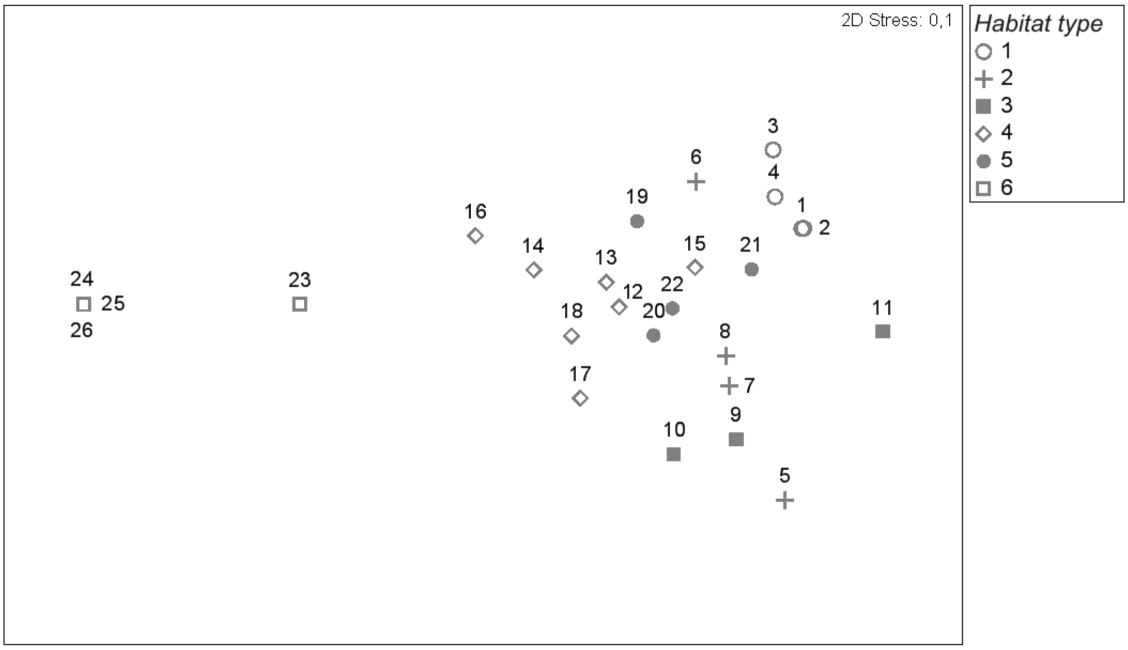

Figure 3 MDS plot showing sampling sites and habitat types (1, rice fields; 2, karstic lagoons; 3, natural pools; 4, endorheic lagoons; 5, artificial ponds; 6, continental salt-pans).

Table 3 ANOSIM analysis. Habitat type: 1, rice fields; 2, karstic lagoons; 3, natural ponds; 4, endorheic lagoons; 5, artificial ponds; 6, continental salt-pans.

Habitat type	R Statistic	Significance level (%)
Global	0.685	0.1
1 & 2	0.656	2.9
1 & 3	0.852	2.9
1 & 4	0.767	0.3
1 & 5	0.438	2.9
1 & 6	1	2.9
2 & 3	0.019	45.7
2 & 4	0.54	0.3
2 & 5	-0.083	68.6
2 & 6	0.99	2.9
3 & 4	0.73	0.8
3 & 5	0.426	8.6
3 & 6	1	2.9
4 & 5	-0.032	54.5
4 & 6	0.987	0.3
5 & 6	1	2.9

In any case, in addition to their specialist inhabitants, the importance of standing water habitats is related to the presence of a wide range of facultative species, which highlights the supporting role they are likely to play in the metapopulation dynamics of many species. Thus, an environment that includes these ecosystems as part of a mosaic of habitats is likely to support greater aquatic biodiversity as a whole (Nicolet et al. 2004). The high species richness observed in natural ponds in this study was related to the fact that such sites were always associated with small permanent drainage systems, meaning that they also typically supported a number of running water species and habitat generalists. Furthermore, most natural ponds had a relatively long hydroperiod (Abellán et al. 2005), which implies more stable environmental conditions and a higher species richness than highly temporary water bodies. In conclusion, more data are needed on the relative contribution of running and standing waters to aquatic biodiversity, and these studies should be conducted across both regions and scales.

Table 4 Significant indicator species (P value < 0.05) for each habitat type (IndVal analysis). IV: Indicator value. For natural ponds, 27 species showed significance values but only those with the higest three are presented. Karstic lagoons did not show any significant indicator species.

	Species	IV
Rice fields	*Hydroglyphus geminus*	47.9
Natural ponds	*Hydroporus discretus*	87.5
	Agabus bipustulatus	85.4
	Ochthebius dilatatus	66.8
Endorheic lagoons	*Ochthebius marinus*	54.6
	Hygrotus pallidulus	48.6
Artificial ponds	*Ochthebius viridescens*	56.2
Continental salt-pans	*Ochthebius notabilis*	100.0

Most standing water ecosystems are seriously threatened in the Mediterranean Basin (Cereghino et al. 2008), particularly as a result of agricultural activities (Martínez-Fernández et al. 2000). Taking into account the fact that the southeast of the Iberian Peninsula represents a transitional area between Europe and Africa, holding species from both continents (Ribera et al. 1996), the degradation of lentic waterbodies in this region could result in significant biodiversity loss at a European scale. Standing waters in the region support a number of rare species at the southerly or northerly edge of their ranges, where these habitats can play an important role as refuge. In addition, although there are very few narrow range endemic species of water beetle found in standing waters (Ribera et al. 2003), four endemics were collected in this study, one of them being exclusive to lentic ecosystems. These species were found in mineralized water bodies where it is more usual to find rare or endemic invertebrate species (Velasco et al. 2006; Abellán et al. 2007). A good example of this is the presence of *Ochthebius irenae*, the only known endemic species from standing saline waters in the Iberian Peninsula (Ribera & Millán 1999; Abellán et al. 2005), a taxon which is also highly threatened (Sánchez-Fernández et al. 2008a).

Although there is no simple and standardized typology for these aquatic ecosystems, the task of identify indicator species was tackled in order to form the basis of future ecosystem management and ecological research, as they may constitute characteristic assemblages for the different habitat types defined here. Even though more studies must be carried out to support the findings of this work, such results showed that rice fields, endorheic lagoons and continental salt-pans have specific water beetles assemblages which could be used as a key factor for bioassessment and conservation studies (Menetrey et al. 2005; Oertli et al. 2005). Continental salt-pans constituted a homogeneous group due to the high salt content of water, with conductivity values of about 200,000 µS/cm in many cases (Abellán et al. 2007; Gutiérrez-Cánovas et al. 2008). Under these environmental constraints, only four species were able to survive, *Ochthebius notabilis* being the best indicator species inhabiting this kind of habitat. The abandonment of salt works appears to be the principal cause of habitat loss for this species (Velasco et al. 2006). The differences between endorheic lagoons and the rest of the habitat types could also be related with the salt content, as reflected by the presence of

Ochthebius marinus and *Hygrotus pallidulus*, both of which have frequently been found in these ecosystems (Millán et al. 2001a; 2001b; 2002). Rice fields are temporary flooded ecosystems that show a short hydroperiod and pioneering species such as *Hydroglyphus geminus* are characteristic and might be the first and commonest colonizer (Gutiérrez-Cánovas et al. 2008). In this sense, the presence of indicator species in the habitat types could be a good tool for classifying stagnant water bodies and also for assessing the conservation status of water bodies.

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SUPPORTING INFORMATION: CHAPTER 1

Table S1: Species list showing their occurrence in the six habitat types studied.

Table S1

Habitat types: 1, rice fields; 2, karstic lagoons; 3, natural ponds; 4, endorheic lagoons; 5, artificial ponds; 6, continental salt-pans). Habitat preference (H): running (r), running/stagnant (r/s) or stagnant (s) sensu Ribera et al. (2003). Endemics^a and threatened^b species sensu Sánchez-Fernández et al. (2008a).

	1	**2**	**3**	**4**	**5**	**6**	**H**
Agabus biguttatus (Olivier, 1795)		x					r
Agabus bipustulatus (Linnaeus, 1767)		x	x		x		r/s
Agabus brunneus (Fabricius, 1798)			x				r
Agabus conspersus (Marsham, 1802)		x	x	x	x		s
Agabus didymus (Olivier, 1795)		x	x	x	x		r
Agabus nebulosus (Forster, 1771)		x	x		x		s
Agabus paludosus (Fabricius, 1801)		x	x				r
Agabus ramblae Millán & Ribera, 2001			x				r
Anacaena bipustulata (Marsham, 1802)		x	x				r/s
Anacaena limbata (Fabricius, 1792)				x	x		r/s
Anacaena lutescens (Stephens, 1829)			x				r/s
Aulacohthebius exaratus (Mulsant, 1844)			x				r/s
Aulonogyrus striatus (Fabricius, 1792)	x						r
Berosus affinis Brullé, 1835			x	x	x		r/s
Berosus guttalis Rey, 1883			x	x			s
Berosus hispanicus Küster, 1847	x			x	x		r/s
Berosus signaticollis (Charpentier, 1825)			x				s
Bidessus pumilus (Aubé, 1836)		x	x				s
Chaetarthria seminulum seminulum (Herbst, 1797)			x				s
Coelostoma hispanicum (Küster, 1848)	x				x		r/s
Colymbetes fuscus (Linnaeus, 1758)		x	x	x	x		s
Cybister lateralimarginalis (De Geer, 1774)	x		x	x	x		s
Dryops algiricus (Lucas, 1849)			x	x			s
Dryops gracilis (Karsch, 1881)	x	x	x	x	x		r
Dytiscus circumflexus Fabricius, 1801			x	x	x		s
Dytiscus marginalis Linnaeus, 1758			x				r/s
Dytiscus semisulcatus Müller, 1776			x				r/s
Enochrus bicolor (Fabricius, 1792)		x	x	x	x	x	s
Enochrus fuscipennis (Thompson, 1884)			x	x			s
Enochrus halophilus (Bedel, 1878)		x	x	x	x		s
Enochrus politus Küster, 1849		x	x	x			r
Enochrus salomonis (Sahlberg, 1900)	x				x		r
Eretes griseus	x						s
Graphoderus cinereus (Linnaeus, 1758)			x				s

	1	**2**	**3**	**4**	**5**	**6**	**H**
Graptodytes aequalis Zimmermann, 1918			x				s
Graptodytes castilianus Fery, 1995 [b]					x		r/s
Graptodytes flavipes (Olivier, 1795)			x				r/s
Gyrinus caspius Ménétries, 1832			x				s
Gyrinus dejeani Brullé, 1832			x	x			r/s
Gyrinus suffriani Scriba, 1855		x					s
Gyrinus urinator Illiger, 1807		x	x				r/s
Haliplus andalusicus Wehncke, 1872			x				s
Haliplus guttatus Aubé, 1836			x				s
Haliplus lineatocollis (Marsham, 1802)		x	x		x		r/s
Haliplus mucronatus Stephens, 1832		x					r/s
Haliplus obliquus (Fabricius, 1787)		x					s
Helochares lividus (Forster, 1771)	x	x	x	x	x		r/s
Helophorus alternans Gené, 1836		x	x		x		s
Helophorus brevipalpis Bedel, 1881		x	x	x	x		r/s
Helophorus fulgidicollis Motschuslky, 1860				x	x		s
Helophorus longitarsis Wollaston, 1864				x	x		s
Helophorus maritimus gr.			x	x	x		s
Helophorus nubilus Fabricius, 1776		x	x				r
Helophorus seidlitzii Kuwert, 1885 [b]		x	x	x			r/s
Herophydrus musicus (Klug, 1833)		x		x	x		r/s
Hydaticus leander (Rossi, 1790)	x	x			x		s
Hydaticus seminiger (De Geer, 1774)		x	x				s
Hydraena atrata Desbrochers des Loges, 1891 [b]			x				r/s
Hydraena rufipennis Boscá Berga, 1932					x		r
Hydrobius fuscipes (Linnaeus, 1758)			x	x	x		s
Hydrochara flavipes (Steven, 1808)	x		x		x		s
Hydrochus grandicollis Kiesenwetter in Heyden, 1870			x				r
Hydrochus ibericus Valladares, Díaz-Pazos y Delgado, 1998 [b]		x				r	
Hydrochus smaragdineus Fairmaire, 1879			x				r/s
Hydroglyphus geminus (Fabricius, 1792)	x	x	x	x	x		r/s
Hydroglyphus signatellus (Klug, 1834)		x					r/s
Hydrophilus pistaceus (Laporte de Castelnau, 1840)			x				s
Hydroporus decipiens Sharp, 1877			x				r/s
Hydroporus discretus Fairmaire & Brisout, 1859			x	x			r
Hydroporus limbatus Aubé, 1838				x			s
Hydroporus lucasi Reiche, 1866			x	x			r/s
Hydroporus nigrita (Fabricius, 1792)			x				s
Hydroporus normandi Régimbart, 1903 [b]		x	x	x	x		r

	1	**2**	**3**	**4**	**5**	**6**	**H**
Hydroporus planus (Fabricius, 1781)			x				s
Hydroporus pubescens (Gyllenhal, 1808)			x		x		s
Hydroporus tessellatus Drapiez, 1819		x	x	x			r/s
Hydrovatus clypealis Sharp, 1876		x	x				s
Hygrobia hermanni (Fabricius, 1775)			x				s
Hygrotus confluens (Fabricius, 1787)		x		x	x		s
Hygrotus impressopunctatus (Schaller, 1783)		x	x	x	x		s
Hygrotus inaequalis (Fabricius, 1777)		x	x				r/s
Hygrotus lagari (Fery, 1992)		x	x	x	x		s
Hygrotus pallidulus (Aubé, 1850)				x	x		s
Hyphydrus aubei Ganglbauer, 1892		x	x	x	x		r/s
Ilybius meridionalis Aubé, 1837		x	x				r/s
Ilybius montanus (Stephens, 1828)			x				s
Laccobius bipunctatus (Fabricius, 1775)		x	x		x		r/s
Laccobius gracilis Kiesenwetter in Heyden, 1870		x	x				r/s
Laccobius hispanicus Gentili, 1974					x		r/s
Laccobius moraguesi Régimbart, 1898	x	x		x	x		r/s
Laccobius sinuatus Motschulsky, 1849	x	x	x	x	x		r/s
Laccobius ytenensis Sharp, 1910			x				r/s
Laccophilus hyalinus (De Geer, 1774)		x	x		x		r
Laccophilus minutus (Linnaeus, 1758)		x	x	x	x		r/s
Laccophilus poecilus Klug, 1882		x	x		x		s
Limnebius furcatus Baudi, 1872		x	x		x		r/s
Limnebius gerhardti Heyden, 1870 [b]		x					r
Limnebius maurus J.Balfour-Browne, 1978		x	x	x	x		r/s
Limnebius papposus Mulsant, 1844		x	x				s
Limnoxenus niger (Zschach, 1788)			x				s
Meladema coriacea Laporte de Castelnau, 1834	x						r/s
Metaporus meridionalis (Aubé, 1838)		x	x		x		s
Nebrioporus baeticus (Schaum, 1864) [a, b]				x		x	r
Nebrioporus clarkii (Wollaston, 1862)		x	x	x			r
Noterus laevis Sturm, 1834		x	x	x	x		s
Ochthebius aeneus Stephens, 1835			x		x		r/s
Ochthebius delgadoi Jäch, 1994 [a, b]				x			r
Ochthebius difficilis Mulsant, 1844			x				r
Ochthebius dilatatus Stephens, 1829			x	x	x		r/s
Ochthebius irenae Ribera & Millán, 1999 [a, b]		x		x			s
Ochthebius marinus (Paykull, 1798)				x	x		s
Ochthebius nanus Stephens, 1829				x	x		s
Ochthebius notabilis Rosenhauer, 1856						x	s

	1	**2**	**3**	**4**	**5**	**6**	**H**
Ochthebius tudmirensis Jäch, 1997 [a, b]				x		x	r
Ochthebius viridescens Ienistea, 1988				x	x		s
Oulimnius rivularis (Rosenhauer, 1856)		x	x				r/s
Paracymus aeneus (Germar, 1824)				x			r/s
Paracymus phalacroides (Wollaston, 1867)		x	x				s
Paracymus scutellaris (Rosenhauer, 1856)		x					r/s
Peltodytes rotundatus (Aubé, 1836)		x	x				s
Rhantus hispanicus Sharp, 1882			x				s
Rhantus suturalis (McLeay, 1825)	x	x	x	x	x		s
Riolus illiesi Steffan, 1958			x				r
Stictonectes optatus (Seidlitz, 1887)			x				r
Yola bicarinata (Latreille, 1804)		x	x		x		r/s

Chapter 2

Water beetle biodiversity in Mediterranean standing waters: assemblage composition, environmental drivers and nestedness patterns

‘Laguna pequeña de Paniagua’ lagoon (Belvís de la Jara, Toledo)

Author: Ecología Acuática/CREA

Introduction

The Mediterranean Basin is one of the most important biodiversity hotspots world-wide (Mittermeier et al. 1998; Myers et al. 2000). It has supported a high human population since historical times, which, coupled with a rapid increase in anthropogenic environmental change in recent decades, is leading to a high rate of habitat loss in the region (Wilson 1988; May et al. 1995; Fontaine et al. 2007). This is especially the case for inland aquatic ecosystems in Southeastern Iberia. This area is dominated by a semi-arid climate where water bodies, and standing ones in particular, are naturally relatively rare at the landscape scale (Gómez et al. 2005).

Inland aquatic ecosystems in this region are very diverse due to the wide variation in conductivity, current velocity and temporality found (Millán et al. 2006). Such environmental gradients shape community composition (Collinson et al. 1995; Moss 1998; Ribera et al. 2003; Bonada et al. 2007), and drive the existence of typical faunas associated with the different habitat types in the region (Moreno et al. 1997; Millán et al. 2006; 2011; Velasco et al. 2006). Another feature which contributes to differences in aquatic invertebrate faunas is anthropogenic stress, particularly disruption to flow regimes, point or diffuse pollution, eutrophication, aquifer over-exploitation and exotic species introduction (Gómez et al. 2005; Velasco et al. 2006).

Specifically to standing water habitats, the great environmental heterogeneity of southeast Iberia results in a high diversity of natural and artificial lentic water bodies (Ribera 2000; Millán et al. 2006; Picazo et al. 2010), making this an ideal region in which to investigate factors structuring assemblage composition and species occurrence in Mediterranean inland waters.

In a number of previous studies, small standing water bodies such as ponds and lagoons have been reported to contribute the bulk of regional freshwater biodiversity (Bratton 1990; Collinson et al. 1995; Williams et al. 2004; Della Bella et al. 2005; Scheffer et al. 2006), giving them high conservation importance. In this sense, the existence of such lentic habitats is crucial for the survival of specialist species (Picazo et al. 2010).

On the other hand, as in many parts of Europe, recent decades have seen the loss of standing water habitats in the region due largely to aquifer over-exploitation and agricultural intensification (e.g. Cirujano et al. 1988; Hull 1997; Blaustein & Schwartz 2001; Williams 2001; Oertli et al. 2005). These processes result in a decrease in the number of sites, which may reduce the availability of refugia during drought periods, as well as a lesser environmental heterogeneity of individual sites. This is a key aspect in terms of biodiversity, as ecologically complex sites are considered as the richest in the region (Picazo et al. 2010).

To date, however, studies which examine the relative species richness of different types of inland waters have been largely confined to mid-northern latitudes, and our understanding of the relative biodiversity importance of small lentic waters at lower latitudes remains limited. Indeed, despite the rapid rate of loss of Mediterranean wetlands, our knowledge of the biodiversity importance of these habitats is limited for groups other than plants and vertebrates (Beja & Alcazar 2003; Grillas et al. 2004; Paton 2005), and there remains an urgent need for studies on the invertebrate communities of Mediterranean standing waters in order to inform their ecology and conservation. This is especially relevant in the case of the Iberian Peninsula, an area where, due to historical processes, species occurrence between lotic and lentic habitats is largely different to which detected in the rest of Europe (Ribera et al. 2003). Furthermore, some lentic habitat types found in the Iberian Peninsula, particularly inland saline water, are almost confined to it within Western Europe. This is of high interest in terms of biodiversity as although inland saline habitats have low species richness they hold a high proportion of endemics (Velasco et al. 2006; Millán et al. 2011). Finally, the fact that the Iberian Peninsula shows a higher level of water beetle endemicity than other European areas (Sánchez-Fernández et al. 2008) adds to the importance of understanding factors structuring the fauna in this region.

The degree to which regional communities demonstrate nestedness has become a key research topic in studies of isolated ecosystems in recent years (Ulrich et al. 2009). In a perfectly nested system, faunas of the species poor sites are subsets of the taxa present in richer locations. This concept has been independently developed several times in biogeography since the first half of 20th century (Hultén 1937; Darlington 1957; Daubenmire 1975; Hausdorf & Hennig 2003) to explore patterns of species composition within continental biotas and amongst isolated habitats such as islands (Hecnar et al. 2002), landscape fragments (Tellería & Santos 1995), mountain peaks (Bruun & Moen 2003), and lakes, lagoons and ponds (Hecnar & MCloskey 1997). Patterson and Atmar (1986) and Patterson (1987) first developed formal tests of nestedness, and showed that nestedness patterns could result from a sequence of extinctions on islands and in fragmented habitats, and it is now recognised that nestedness can result from a range of processes including selective extinction (Patterson & Atmar 1986), competition (Simberloff & Martin 1991), nested habitats (Cutler 1994), and habitat heterogeneity (Wright et al. 1998). Detecting and understanding the generation of nested patterns has important conservation implications, mainly related to protected area network planning, since if nestedness is high, species poor sites will hold ubiquitous species whereas less common species will be found only in richer localities (Snodgrass et al. 2000; Baber et al. 2004). Nestedness has been widely used to explore the structure of biological communities (Fleishman & Murphy 1999; Hylander et al. 2005; Meyer & Kalko 2008; Elmendorf & Harrison 2009), including the macroinvertebrate communities of lentic freshwaters (Mcabendroth et al. 2005; Angeler et al. 2008; Wissinger et al. 2009). Few studies have attempted to examine the factors underlying nestedness in freshwater systems however, including the relative importance of different factors in different habitat types (Baber et al. 2004).

Here, the importance of biodiversity and the conservation status of lentic water bodies in the southeast of the Iberian Peninsula are investigated. This area is representative of the Mediterranean semi-arid region and shows a diverse array of natural and anthropogenic inland waters (Millán et al. 2002; Picazo et al. 2010). This work is focused on water beetles, which constitute a high and functionally diverse proportion of inland water biodiversity (Jäch & Balke 2008) and have been successfully used as surrogates of overall aquatic biodiversity, both in Iberia and elsewhere (Bilton et al. 2006; Sánchez-Fernández et al. 2006).

Specifically, the addressed points were the following:

1. What proportion of Iberian freshwater biodiversity is present in lentic inland waters in Southeastern Iberia and how it is distributed across habitat types?
2. What are the key environmental drivers of water beetle assemblage composition in the region?
3. Are aquatic beetle assemblages in the regions nested, and what factors underline any nested subset pattern observed?

The present study improves our understanding of the assemblage composition and distribution of biodiversity in Mediterranean standing waters in order to help in further planning for conservation and management of such aquatic ecosystems.

Materials and methods

Study area

The study area comprised the southeast quadrant of the Iberian Peninsula, covering over 130,000 km^2 (figure 1). A large part of this area is occupied by the Southern Meseta, a relatively flat region where most of the land is under unirrigated agriculture. The majority of the study area belongs to the Tajo, Guadiana, Júcar and Segura river basins. The altitude ranges from sea level on the Mediterranean coast to over 2,000 m.a.s.l. in the Iberian and Betic mountains. This complex topography also results in notable local climatic variation. In this way, coastal and low altitude southern areas and the western part experience temperate winters and warm summers, sub-zero temperatures being very unusual, whereas the inland zone has cold winters with more extreme temperatures. Rainfall varies between 250 mm in the semi-arid southeast to more than 1000 mm in the wettest parts of the Iberian and Betic ranges (Fernández 1998). The temporal distribution of rainfall also follows this gradient, eastern areas having a high irregularity where seasonal heavy rains alternate with extended drought periods (Font 1983). As regards geology, underlying rocks are mainly calcareous, with Jurassic and Cretaceous limestones in the mountains and sedimentary detritic Tertiary basins on the plains. Nevertheless, the western part is characterised by the presence of acid soil. Saline water bodies are a common feature of this area, being associated with evaporate outcrops (Triassic-Keuper), Miocene basins filled with salt-rich marls and semi-arid endorheic basins (Casado & Montes 1995).

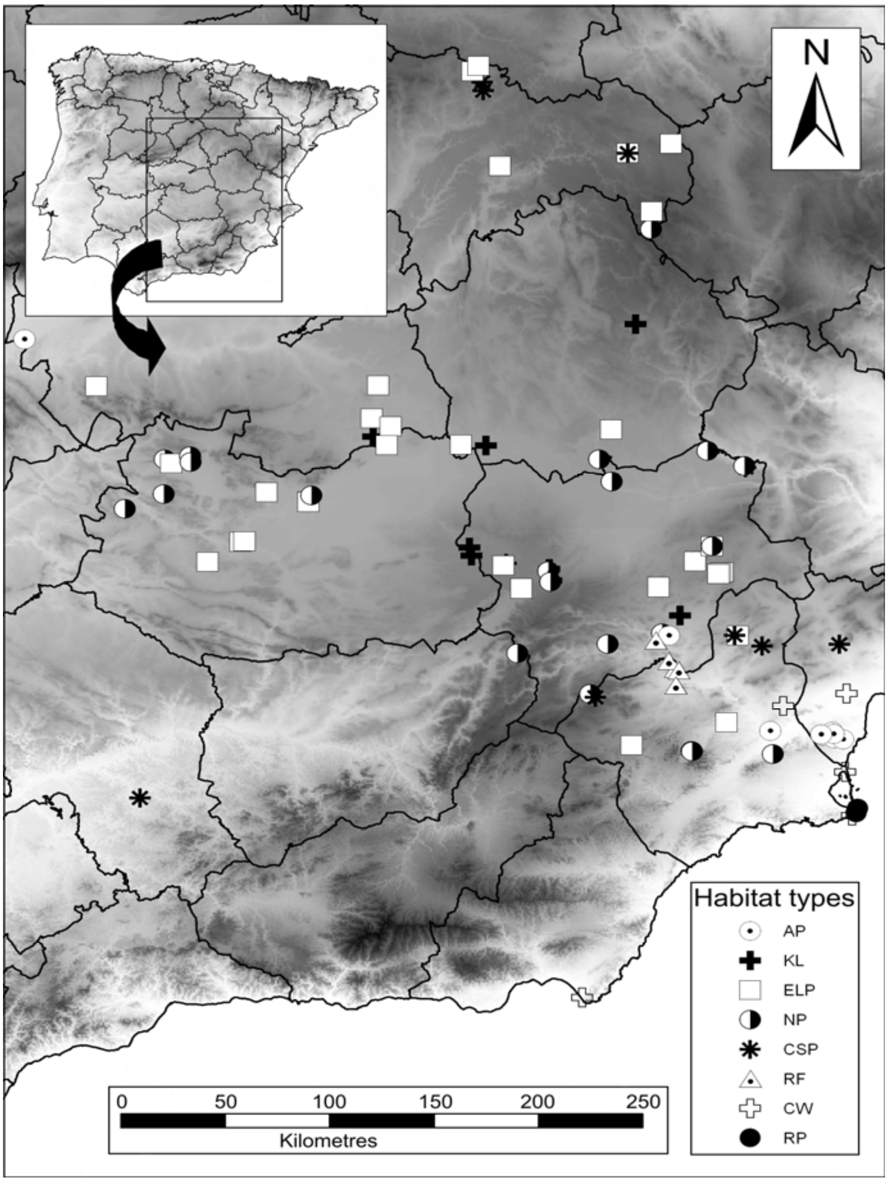

Figure 1 Study area and sampling sites by habitat type (AP, artificial pools; ELP, endorheic lagoons and ponds; KL, Karstic lagoons; NP, natural pools; CSP, continental salt-pans; RF, rice fields; RP, coastal rock-pools; CW, coastal wetlands).

Field sampling, habitat types and sample processing

A total of 95 sites (figure 1) which span the entire spectrum of lentic habitats in the region have been sampled, with the exception of reservoirs and coastal salt-pans. Sampling sites were assigned to eight different habitat types on the basis of physicochemistry, origin and hydrology, partly following the classifications of Millán et al. (2002) and Abellán et al. (2005a). These were artificial pools (for irrigation and livestock watering), karstic lagoons (mostly associated with continuous underground drainage systems), endorheic lagoons and ponds, natural pools (associated with small and continuous superficial drainage systems), continental salt-pans, rice fields, coastal rock-pools and coastal wetlands. The number of sampling sites within each habitat type was defined in order to: (i) obtain a quantitative representation of each habitat type according to their natural occurrence in the study area, and (ii) encompass the overall variability or heterogeneity within sites in each habitat type.

Nine environmental variables at each site were also recorded (see table 1). Salinity, conductivity and temperature were measured in the field using a MultiLine P4 meter (WTW, Weilheim, Germany), altitude was recorded using a GPSMAP 76S hand-held GPS (Garmin, Olathe, KS, USA) and area and maximum depth were recorded by pacing site perimeters and using a measuring tape respectively. Isolation was determined as the average distance to the five nearest sampling sites (Heino et al. 2009) using a Geographical Information System-based approach with Arc-Gis 9.2 (ESRI, Redlands, CA, USA). Despite the influence isolation has on colonisation processes, this variable was not take into account for the analyses due to the presence of unsampled water bodies which could act as stepping stones during dispersal flights, which would confound interpretation of the results obtained. Because of the extensive nature of our work, complete hydroperiod of all sampling sites were not studied. Alternatively, sites were assigned to one of three hydroperiod classes (permanent, semi-permanent and intermittent) following Williams (2006). Finally, disturbance was assessed based on a review of the literature and field observations. Such assessment was carried out following the methodology proposed by Abellán et al. (2005a, which consists of recording impacts belonging to five categories: infrastructures (fences, buildings, irrigation equipment, etc.), agriculture (direct water extraction for irrigation, aquifer overexploitation, and diffuse pollution, mainly from fertilisers), point pollution (urban effluents and other point sources), exotic species (mostly fishes and red-clawed crayfish *Procambarus clarkii*), and others (e.g. tourist pressure and eutrophication due to waterbird droppings). In this way, a site is considered as disturbed when it has three or more types of impact. At the same time, a habitat type is considered to be affected by each kind of impact when more than 50% of its sites show such impact.

Table 1 Environmental features of habitat types (AP, Artificial pools; ELP, Endorheic lagoons and ponds; KL, Karstic lagoons; NP, natural pools; CSP, continental salt-pans; RF, rice fields; RP, coastal rock-pools; CW, coastal wetlands). N, number of sampling sites within each habitat type. Disturbances observed in at least 50% of sites within each habitat type as follows: I, infrastructures; A, agriculture; E, exotic species; P, point source pollution; O, others; X, no disturbance (see text for details). SD, standard deviation. T, temperature. Temporality indicates percentage of permanent (P), near-permanent (NP) and intermittent (I) sites.

		HT							
		AP	ELP	KL	NP	CSP	RF	RP	CW
N		11	32	8	21	11	5	2	5
Disturbances		I,A,E,O	I,A,O	I,A,E	A	I	I,A,E	X	I,O
Area (m2)	Mean	10201.82	232578.97	142168.75	1000.57	21788.64	478000	5000	2006025
	SD	15538.26	376208.44	191662.36	3094.83	31913.23	412334.82	0.00	4468775.52
Altitude (m.a.s.l.)	Mean	247.91	803.09	823.75	687.86	728.36	328.40	0.00	38.00
	SD	240.01	228.12	160.26	338.70	316.23	65.71	0.00	79.50
T (ºC)	Mean	27.07	25.70	23.35	20.44	27.33	25.16	25.50	25.38
	SD	4.00	4.54	4.15	4.91	5.03	3.00	0.71	5.78
Salinity (g/l)	Mean	0.82	11.43	1.14	2.08	121.65	0.10	48.85	33.30
	SD	0.49	14.75	1.53	7.33	66.57	0.17	0.21	22.02
Conductivity (µS/cm)	Mean	1573.45	17797.66	1989.30	2916.55	179818.18	629.80	71500	50540
	SD	877.25	21561.54	2677.39	9661.99	85257.04	233.75	707.11	33535.92
Isolation (km)	Mean	14.12	24.45	26.04	24.50	39.66	12.15	21.23	47.46
	SD	24.69	12.31	18.40	10.47	36.44	2.70	0.61	56.10
Depth (m)	Mean	3.05	1.08	5.31	0.92	0.51	0.30	0.20	0.62
	SD	1.08	0.45	2.52	0.64	0.32	0.00	0.00	0.28
Temporality	P	90.91	18.75	87.50	76.19	45.45	0.00	100	100
	NP	0.00	50.00	12.50	9.52	54.55	0.00	0.00	0.00
	I	9.09	31.25	0.00	14.29	0.00	100.00	0.00	0.00

Field samples were collected between 1981 and 2008, with most sampling taking place between 1994 and 2003. Most of the sites were sampled in at least two different campaigns, these samples being taken in the early summer coinciding with the maximum activity period of beetles. Localities were consistently sampled until no further species were found by experienced investigators. Sampling was carried out by the same team, however, when new personnel were added to the sampling programme they were initially trained by experienced staff to ensure consistency of approach across years. Samples were collected with a hand net (pentagonal or triangular, 20–30 cm deep, 500 µm to 1 mm mesh –mesh sizes sufficiently small to catch all aquatic beetles), and in all cases sampling was stratified, including all microhabitat types occupied by aquatic beetles in a locality.

Field samples were preserved in 70% or 95% ethanol and taken to the laboratory, where they were processed and identified to species level. Presence–absence and abundance data, depending on which is required in each case, were then used for further analyses. Those species of Coleoptera belonging to strictly aquatic families sensu Jäch & Balke (2008), i.e. Gyrinidae, Haliplidae, Noteridae, Paelobiidae, Dytiscidae, Helophoridae, Hydrochidae, Hydrophilidae, Hydraenidae, Elmidae and Dryopidae, were included.

Habitat preferences of species (running, generalist and standing), were obtained from Ribera et al. (2003), whilst threatened species (those included in the High or Very High vulnerability categories) and endemics followed Sánchez-Fernández et al. (2008), supplemented by our own observations.

Multivariate analysis

Non-metricMDS ordinations of presence/absence data using PRIMER 6.0 (Clarke & Warwick 1994) were used to examine whether samples taken from different sites were distinct based on their water beetle assemblages. Additionally, the analysis of similarities (ANOSIM) routine, also in PRIMER 6.0, was performed in order to differentiate within- and between-group similarities (Clarke 1993). In a robust classification, similarities between sites that are in the same group should be substantially greater than similarities between sites that are in different groups. A Monte Carlo permutation test with 999 replicates was used to assess the significance of each value. Relationships between environmental variables and water beetle assemblages were explored using BIOENV (Clarke & Ainsworth 1993), again in PRIMER 6.0. Salinity was excluded from the BIOENV analysis due to its high correlation with conductivity (Spearman correlation = 0.98, $P < 0.05$). These three analyses were based on presence/absence data, with coastal rock-pools being excluded, since preliminary analyses demonstrated their assemblages were highly differentiated from all other habitat types. To better resolve the environmental variables driving assemblage composition the whole matrix was divided into freshwater and saline submatrices. Montes & Martino (1987) proposed five salinity categories for Iberian inland waters based on their invertebrate assemblages: freshwater (<0.5 g/l), subsaline (0.5–3 g/l), hyposaline (3–20 g/l), mesosaline (20–40/50 g/l) and hypersaline (>40/50 g/l), the last three being designated as authentic saline waters in our study. A cut-off point of 6,500 µS/cm allowed all the sites below this value to be placed into the two first salinity categories, whereas the rest of sites, above this value, where assigned to the last three salinity categories. So, the freshwater submatrix (<6500 µS/cm) included freshwater and subsaline sites and the saline submatrix (>6500 µS/cm) includes hyposaline, mesosaline and hypersaline ones.

Finally, an IndVal analysis (Dufrêne & Legendre 1997), was conducted to identify indicator species of naturalness within each habitat type using PC-ORD version 4.20 (McCune & Mefford 1999). This analysis estimates the indicator value (IV) based on the relative abundance and occurrence frequency of each species in each a priori defined habitat type. A Monte Carlo permutation test with 9999 permutations was used to assess significance.

Nestedness analysis

Nestedness analyses were conducted in ANINHADO 3.0 (Guimarães & Guimarães 2006), which calculates two different metrics of nestedness: matrix Temperature T, (Atmar & Patterson 1993) and a newer metric, NODF (Almeida-Neto et al. 2008). As T has recently been shown to overestimate the degree of nestedness in metacommunities (Almeida-Neto et al. 2008), NODF was primarily employed to assess nestedness. In addition, given the widespread past use of matrix temperature, the T value for the whole matrix and also for the freshwater and saline submatrices was reported to allow the results to be assessed in context.

NODF also has the advantage of being independent of matrix shape and size, but dependent on the arrangement of rows and columns, something which allows the user to test hypotheses on the causes of nestedness by ordering rows and columns (i.e. samples and species) according to a priori criteria (Almeida-Neto et al. 2008). NODF values range between 0 (no nestedness) and 100 (total nestedness). Here, three different matrices were prepared and analysed: whole matrix, freshwater submatrix and saline submatrix. In order to test the null hypothesis that NODF is not higher than expected by chance, ANINHADO employs four null models based on different kinds of randomisation. To test for passive sampling effects, the CE null model, with 1000 permutations in all cases, was used (see Guimarães & Guimarães 2006 for more details). In order to assess the possible role of environmental variables in driving nestedness, sites were ordered from low to high and *vice versa* on the basis of their values for each measured variable, and then compared the NODF values. The greater the difference between these two numbers, the higher influence the variable has on nestedness patterns (Almeida-Neto et al. 2008). This last analysis was conducted on the whole matrix and the freshwater and saline submatrices respectively.

Results

Water beetle assemblages

A total of 174 species were identified across the 95 sites sampled, of which 78 (45%) were lentic specialists, 37 (21%) lotic specialists and 59 (34%) habitat generalists (see table 2). Most habitat types were dominated by lentic and generalist species, but also included some species generally considered as exclusively lotic (table 2). Natural pools showed the highest species richness with 138 taxa recorded, and coastal rock-pools the lowest, with two species (table 2). Artificial pools contained the greatest proportion of exclusively lentic species (56%). Nineteen species (11% of the total) were Iberian endemics, most of them occurring in natural pools (15 species). Endemic taxa were particularly prevalent in continental salt-pans, where 4 of 10 species found were Iberian endemics. Finally, with respect to threatened species, natural pools and coastal wetlands had eight and six species, respectively, while karstic lagoons, continental salt-pans and endorheic lagoons showed slightly lower values, with the three threatened species occurring in karstic lagoons being lentic specialists.

Table 2 Species richness and composition of water beetle assemblages by habitat type (AP, Artificial pools; ELP, Endorheic lagoons and ponds; KL, Karstic lagoons; NP, natural pools; CSP, continental salt-pans; RF, rice fields; RP, coastal rock-pools; CW, coastal wetlands). N, number of sampling sites within each habitat type. SD, standard deviation. R, running water (lotic) specialist; g, habitat generalist; s, standing water (lentic specialist).

		Total	HT							
			AP	ELP	KL	NP	CSP	RF	RP	CW
	N	95	11	8	32	21	11	5	2	5
Richness	Total (%)	174(100)	50(29)	65(37)	89(51)	138(79)	10(6)	17(10)	2(1)	31(18)
	Mean	11.77	12.73	12.75	10.19	20.14	2.55	7.80	1.50	11.40
	SD	9.93	6.77	9.47	5.26	14.87	1.44	2.68	0.71	3.58
	r (%)	37(21)	5(10)	7(11)	7(8)	28(20)	7(70)	3(18)	0(0)	8(26)
	g (%)	59(34)	17(34)	25(38)	35(39)	52(38)	1(10)	9(53)	0(0)	12(39)
	s (%)	78(45)	28(56)	33(51)	47(53)	58(42)	2(20)	5(29)	2(100)	11(35)
Exclusive lentic species (%)			2 (7)	2 (6)	2 (4)	14 (24)	1 (50)	0 (0)	2 (100)	4 (36)
Endemics	Total (%)	19(100)	1(5)	3(15)	9(45)	15(75)	4(20)	0(0)	0(0)	5(25)
	r (%)	11(58)	1(100)	1(33)	4(44)	10(67)	4(100)	0(0)	0(0)	3(60)
	g (%)	7(37)	0(0)	1(33)	4(44)	5(33)	0(0)	0(0)	0(0)	2(40)
	s (%)	1(5)	0(0)	1(33)	1(11)	0(0)	0(0)	0(0)	0(0)	0(0)
Threatened	Total (%)	14(100)	0(0)	5(36)	3(21)	8(57)	4(29)	0(0)	0(0)	6(43)
	r (%)	7(50)	0(0)	3(60)	0(0)	5(62)	4(100)	0(0)	0(0)	4(67)
	g (%)	3(21)	0(0)	1(20)	0(0)	1(12)	0(0)	0(0)	0(0)	2(33)
	s (%)	4(29)	0(0)	1(20)	3(100)	2(25)	0(0)	0(0)	0(0)	0(0)

Habitat types and environmental drivers of species distributions

The MDS sites-habitat type plot (figure 2) suggests some overlap in species composition between a priori habitat categories, although there is a tendency for sites in individual categories to appear sequentially on the plot, as one moves from left (natural pools) to right (continental salt-pans). This fact was clearly related to conductivity, as it can be seen in the MDS sites-conductivity plot (figure 3). The stress value of 0.14 suggests that the MDS provides an accurate reflection of the relationships between sites (Clarke 1993). The a priori habitat classification was supported by the ANOSIM analysis (table 3), which revealed significant differences between habitats overall (Global R = 0.456, P < 0.001), and between most pairs of habitats. Pairwise, only artificial pools-endorheic lagoons and ponds, and natural pools-rice fields were not significantly different from each other on the basis of water beetle assemblage composition (see table 3).

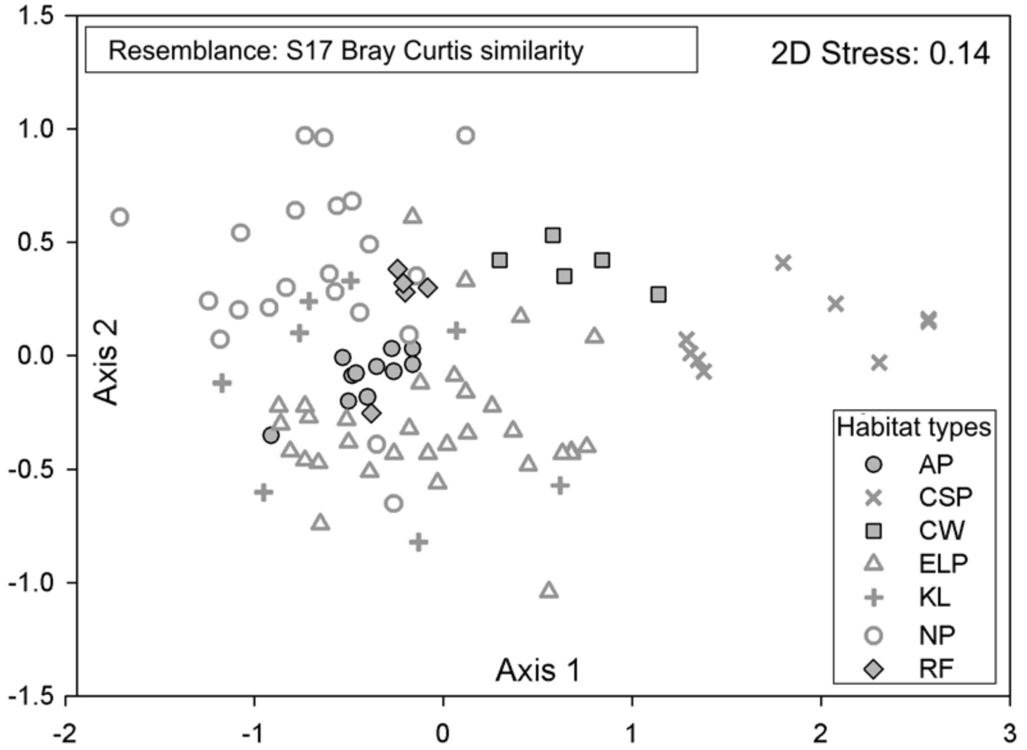

Figure 2 MDS habitat types-sampling sites plot (AP, Artificial pools; ELP, Endorheic lagoons and ponds; KL, Karstic lagoons; NP, natural pools; CSP, continental salt-pans; RF, rice fields; RP, coastal rock-pools; CW, coastal wetlands).

In the BIOENV analysis carried out on the whole matrix, a single variable, conductivity, best grouped the sites in a manner consistent with the faunal patterns (Spearman correlation = 0.55). In contrast, for the freshwater submatrix the best explanatory variable was the level of disturbance (Spearman correlation = 0.24), with a combination of disturbance, altitude and conductivity having the greatest explanatory power in the case of the saline submatrix (Spearman correlation = 0.41).

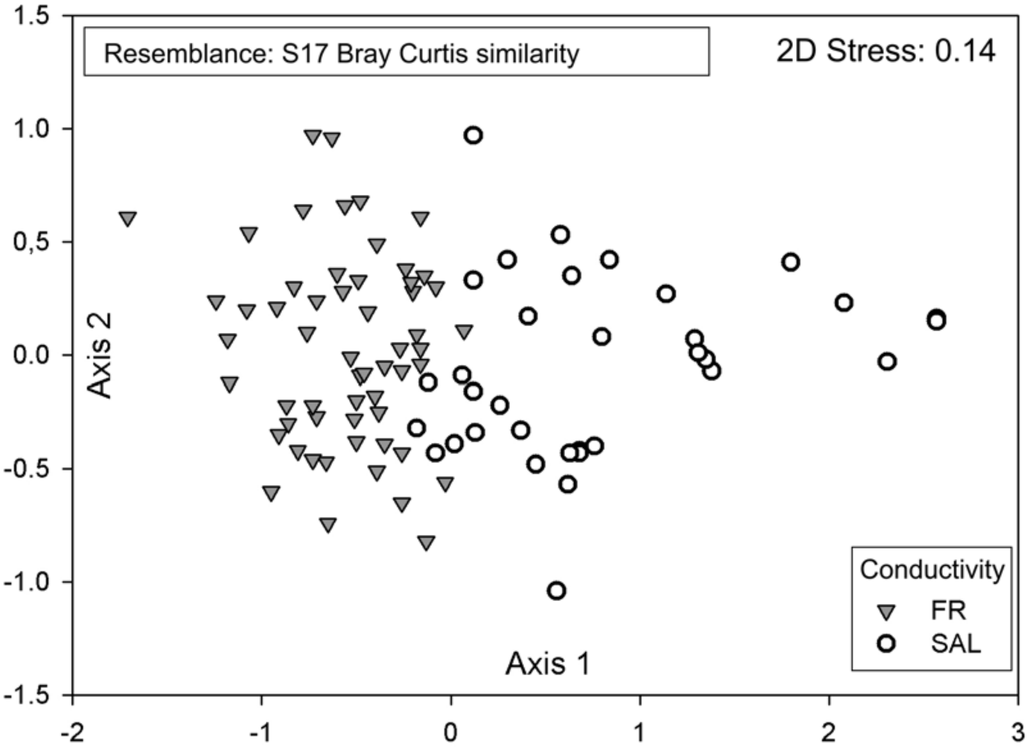

Figure 3 MDS conductivity-sampling sites plot. FR, fresh water sites; SAL, saline water sites.

Indicator species of naturalness

IndVal analysis identified indicator species for all the habitat types, except for karstic lagoons (table 4), and in some cases these species had a high indicator value (IV >50; Dufrêne & Legendre 1997). On many occasions, more than one indicator species was identified within a habitat type, and the combination of species could be considered as an indicator assemblage of the respective habitat type in the region.

Nestedness patterns

The whole matrix was highly and significantly nested (table 5), as were the freshwater and saline submatrices, although the former had a higher degree of nestedness. When exploring the influence of environmental variables on nestedness, analyses were restricted to variables most consistent with the faunal patterns, as revealed BIOENV (see above), as well as area, since this has been linked to nestedness in previous studies (Simberloff & Levin 1985; Lomolino 1996; Méndez 2004).

Table 3 Results of ANOSIM analysis (AP, Artificial pools; ELP, Endorheic lagoons and ponds; KL, Karstic lagoons; NP, natural pools; CSP, continental salt-pans; RF, rice fields; RP, coastal rock-pools; CW, coastal wetlands). * p<0.05, ** p <0.01, *** p <0.001.

Habitat type	R statistic	Significance level
Global	0.46	***
AP & ELP	0.02	n.s.
AP & KL	0.40	***
AP & NP	0.23	**
AP & CSP	1.00	***
AP & RF	0.73	***
AP & CW	0.96	***
ELP & KL	0.22	**
ELP & NP	0.41	***
ELP & CSP	0.71	***
ELP & RF	0.21	*
ELP & CW	0.53	***
KL & NP	0.20	*
KL & CSP	0.87	***
KL & RF	0.22	*
KL & CW	0.59	**
NP & CSP	0.89	***
NP & RF	0.15	n.s.
NP & CW	0.73	***
CSP & RF	1.00	***
CSP & CW	0.93	***
RF & CW	0.98	**

Overall these analyses revealed that water beetle faunas of sites having a high degree of disturbance, high conductivity, greater area and occurring at low altitude were subsets of the assemblages found in localities with low impact, low conductivity, smaller area and occurring at higher altitudes. For the whole matrix, impacts was the variable most strongly associated with nestedness, as it showed the greatest difference between NODF values when rows were arranged from high to low and from low to high (see table 6), with altitude and conductivity being sequentially less important. In the case of the freshwater submatrix, disturbance was also the most influential variable in generating the nested pattern, conductivity apparently having little impact in this case. With the saline submatrix however, conductivity was the most important factor, whilst the degree of disturbance did not markedly influence nestedness. In all cases, the influence of area on nestedness was typically intermediate (see table 6).

Table 4 Results of IndVal analysis. IV: Indicator value (only values which p<0.05 are shown.

Habitat types	Species	IV
Artificial pools	*Ochthebius viridescens* Ieniştea, 1988	62.6
	Berosus affinis Brullé, 1835	48.9
	Herophydrus musicus (Klug, 1833)	43.8
	Helochares lividus (Forster, 1771)	30.9
	Laccophilus minutus (Linnaeus, 1758)	31.2
Endorheic lagoons and ponds	*Hygrotus pallidulus* (Aubé, 1850)	40.3
Natural pools	*Agabus bipustulatus* (Linnaeus, 1767)	41.3
	Stictonectes optatus (Seidlitz, 1887)	38.1
	Anacaena lutescens (Stephens, 1829)	35.9
	Haliplus lineatocollis (Marsham, 1802)	33.2
	Hydroporus discretus Fairmaire & Brisout, 1859	32.2
	Agabus didymus (Olivier, 1795)	28.0
Rice fields	*Dryops gracilis* (Karsch, 1881)	73.7
	Hydroglyphus geminus (Fabricius, 1792)	65.2
	Aulonogyrus striatus (Fabricius, 1792)	60.0
	Hydaticus leander (Rossi, 1790)	47.2
	Rhantus suturalis (McLeay, 1825)	32.3
Continental salt-pans	*Ochthebius notabilis* Rosenhauer, 1856	78.5
Coastal rock-pools	*Calobius quadricollis* (Mulsant, 1884)	100.0
	Ochthebius subinteger Mulsant & Rey, 1861	50.0
Coastal wetlands	*Paracymus aeneus* (Germar, 1824)	96.3
	Nebrioporus ceresyi (Aubé, 1838)	80.0
	Berosus fulvus Kuwert, 1888	60.0
	Hydroporus limbatus Aubé, 1838	56.4
	Enochrus bicolor (Fabricius, 1792)	41.0
	Enochrus politus (Küster, 1849)	40.6
	Ochthebius auropallens Fairmaire, 1879	40.0
	Ochthebius bifoveolatus Waltl, 1835	40.0
	Berosus hispanicus Küster, 1847	31.5

Table 5 Nestedness values for the different matrices analysed. * p<0.05, ** p <0.01, *** p <0.001.

Metric	Matrix	Nestedness value	Null model average	p
T	Whole	7.68	18.98	***
NODF ordered	Whole	18.9	10.33	***
T	Freshwater	12.9	27.53	***
NODF ordered	Freshwater	25.68	14.42	***
T	Saline	8.97	22.40	***
NODF ordered	Saline	19.22	12.64	***

Discussion

Water beetle biodiversity and conservation

The study region makes up only 23% of the land area of the Iberian Peninsula. However, as it was demonstrated here, standing water sites within it contains at least 35% of all species recorded from the Ibero-Balearic region (Ribera et al. 1998; Ribera 2000). When only strictly lentic taxa were considered, this figure rises to 52%, emphasising the importance of still water systems in the SE of the peninsula for water beetle biodiversity. At the level of individual habitats, a number of the karstic lagoon complexes (composed of a karstic lagoon and several associated ponds and streams) in the study region (e.g. Arquillo and Ojos de Villaverde complexes) have very high local species richness, up to 72 and 45 species, respectively, of aquatic beetles being found during the sampling. Of Iberian lentic waters, only the Capmany lagoon (Ribera & Aguilera 1996) contains a greater species richness than the most species rich sites. A number of studies, in the Mediterranean region and elsewhere, have demonstrated that water beetles are excellent surrogates for aquatic biodiversity in general (Bilton et al. 2006; Sánchez-Fernández et al. 2006). Therefore, the high species richness of some standing water bodies in the region reveals their importance for the maintenance of aquatic biodiversity, at both local and regional scales.

Table 6 Environmental variables driving nestedness and values of row NODF (unordered) for the three matrices analysed. The difference between each pair of values are in brackets, with the largest ones for each matrix in bold. p<0.001 for all the cases.

			Whole		Freshwater		Saline	
row NODF (unordered)	Disturbance	From low to high	13.47	**(6.47)**	22.51	**(13.77)**	13.43	(0.08)
		From high to low	7.00		8.74		13.51	
	Altitude	From low to high	8.28	(3.90)	12.18	(6.89)	12.10	(2.74)
		From high to low	12.18		19.07		14.84	
	Conductivity	From low to high	11.46	(2.46)	15.86	(0.47)	18.64	**(8.34)**
		From high to low	9.00		15.39		8.30	
	Area	From low to high	12.22	(3.97)	19.01	(6.78)	15.58	(4.22)
		From high to low	8.25		12.23		11.36	

In contrast to the high proportion of the Iberian fauna recorded in the study, the proportion of Iberian endemics was relatively low: 11% against 20% for all the Iberian water beetles (Sánchez-Fernández et al. 2008). As stated in the introduction, this discrepancy reflects the fact that most endemic taxa in the region mostly occur in running waters (Ribera et al. 2003), and have relatively small geographical ranges, typically being restricted to individual regions or mountain systems/drainages. The fact that 40% of the species collected in continental salt-pans were Iberian endemics (Sánchez-Fernández et al. 2008) demonstrates that whilst the saline ecosystems of the region have relatively low species richness, they are of fundamental importance for the survival of a range of specialist endemic taxa (Velasco et al. 2006; Millán et al. 2011). Rare and threatened species were distributed across habitat types; most habitat types supporting between three and six species in at least one locality. Only artificial pools and rice fields, two man-made habitats, and coastal rock-pools, which are interconnected around the Mediterranean Basin (Antonini et al. 2010) did not hold any threatened species. Of all the species recorded, *Ochthebius irenae* was the only threatened endemic which is considered to be a lentic specialist (Abellán et al. 2005a; Sánchez-Fernández et al. 2008; Picazo et al. 2010), other threatened endemics being habitat generalist (three species) and lotic specialists (five species). Again such findings emphasise the low number of narrowly endemic species in standing waters, driven by the higher range size of lentic taxa (Ribera et al. 2003). However, the relatively low proportion of endemic species reported here, with the exception of continental salt-pans, does not imply that lentic waters in the region are of low conservation importance. The lentic freshwater systems studied here support a high proportion of Iberian aquatic beetles, and include populations of taxa which are extremely rare in the south of Europe, such as *Hydaticus seminiger*, *Graphoderus cinereus* and *Gyrinus suffriani* (Millán et al. 1999; 2002).

The fact that 21% of the species recorded from ostensibly lentic habitats are generally considered to be lotic specialists is likely to reflect the habitat heterogeneity of some of the sampled systems, and the practical difficulty of defining discrete lentic and lotic habitats on the ground. Natural pools are a good example, where the lotic influence is important due to the presence of small superficial drainages such as springs and other inflows. This, coupled with the limited extent of disturbance, could be one of the reasons why natural pools were the most speciose habitat type. The high proportion of lotic specialists found in continental salt-pans is similarly related to the presence of small springs, streams and seepages in association with these systems; in fact salt-pans oftlenly constitutes the source or the mouth of saline streams. Taxa characteristic of these saline lotic habitats do, it appears, utilise the adjacent lentic areas in periods of low flow, hence their frequent presence in the samples. Such findings suggest that the lentic–lotic divide is not always clear cut, but do not mean that all taxa found in both running and standing waters can be considered as generalists. Instead, many taxa, such as those of continental salt-pans discussed above, spend most of their life cycle in one habitat type, and are dependent on it for reproduction, whilst utilising another for periods, usually as adults, during low water levels. Such species depend on the presence of a range of suitable water bodies within the landscape for population persistence. Almost all the habitat types, except rice fields, supported exclusive lentic specialists. This emphasises the importance of including a good representation of a wide range of systems in any aquatic protected area network (Strayer 2006; Sánchez-Fernández et al. 2008). Good examples are natural pools (14 unique lentic specialists), coastal rock-pools and coastal wetlands (with 100% and 36% of their taxa being unique lentic specialists, respectively).

Habitat types and environmental drivers of species distribution

The MDS ordination revealed a clear gradient of water mineralisation across sites from right (higher conductivity: continental salt-pans) to left (lower conductivity: some natural pools on acid soils). Such a finding is in line with a number of previous studies which point to the importance of conductivity in shaping macroinvertebrate distributions (Moreno et al. 1997; Miserendino 2001; Bonada et al. 2005; Millán et al. 2006; Mellado et al. 2008), and is reflected in the overall BIOENV analysis across all habitat types. When freshwater and saline waters were analysed separately, the importance of impacts was revealed more clearly. This variable alone best correlated with faunal composition for freshwater sites, and was also important in saline localities, despite the remaining variation in conductivity. Hydroperiod, at least in the way it was measured (three categories), did not seem to be a key factor driving assemblage composition since many water beetles typical of standing waters could need only a few weeks to colonise temporary sites. Many aquatic ecosystems from Southern Iberia show a great resilience (Ortega et al. 1991; Moreno et al. 2010), with species having well developed dispersal abilities in order to move from drying temporary breeding sites to more permanent wetland refugia, which is especially prevalent in lentic specialist water beetles.

The results of ANOSIM analysis largely corroborated the a priori habitat classification, suggesting that, in general, these habitat types are populated by distinct water beetle assemblages. In the case of artificial pools and endorheic lagoons and ponds, the similarity is due to the low intensity of management, which allows for a high degree of naturalisation of some long established artificial pools, resulting in their biota becoming very similar to that typical of natural endorheic ponds in the region (Abellán et al. 2006; Cereghino et al. 2008). The others habitat types that showed considerable overlap in water beetle species composition were natural pools and rice fields. Both of these habitat types are freshwater and have a certain degree of water flow, as most of them are closely linked to superficial drainages. For this reason they share a number of typically lotic species, and have the lowest proportion of lentic specialists of any freshwater system in the region. In conclusion here, whilst many of the previous typologies developed for inland water bodies are very specific (National Wetland Working Group 1997; Williams 2006; Sánchez-Montoya et al. 2007) and difficult to apply in conservation management, this classification system seems, with few exceptions, to broadly reflect the main drivers of water beetle biodiversity in the region. These assemblages, together with the indicator species identified in the analyses, could be utilised for conservation planning in the future.

Nestedness patterns

Together with analyses of community composition, exploring the underlying causes of nested subset patterns in metacommunities can allow a better understanding of the factors structuring natural systems, and can be a key factor to designing an efficient protected area network (Kerr et al. 2000). Finding a certain degree of nestedness means some places are potentially more interesting than others in terms of conservation (Méndez 2004). A nested pattern across localities implies that some species have low occurrence, meaning that their risk of regional extinction is higher than others which are more widespreadly distributed. As a consequence, the importance of conserving the richest sites is not only due to their high number of species, but also because they are the sites which hold most rare taxa. However, even in the case of perfect nested structure, where a single site would hold all species present within the region, to guarantee the maintenance of biodiversity it is not enough to have species represented at single sites. Instead, effective conservation of a regional fauna requires the maintenance of effective metapopulations, which incorporates an adequate number of places where all species could be present (Cabeza et al. 2004; Abellán et al. 2005b; 2007). This point is especially important for the beetle fauna of standing waters in semi-arid areas, such as most of Southern Iberia, since individual lentic sites may have unpredictable hydroperiods, being unsuitable for many species in some seasons or years (Millán et al. 2001a; b). This forces many species to use different habitat types during their life cycles; for example endorheic ponds for breeding and karstic lagoons, artifical pools, etc. for adult survival during drought periods (Moreno et al. 1997; Picazo et al. 2010).

As discussed in the introduction, several mechanisms can drive nested structure in metacommunites. In the lentic systems studied here, as disturbance

appears to play a particularly important role in the generation of nestedness, selective extinction could be a major driver of the current nested structure. This seems particularly true in the case of freshwater sites, as revealed by the analysis of the freshwater submatrix. Anyway, since there is some overlap amongst the assemblages of different habitat types, nested habitat patterns may mainly be related to differing degrees of complexity amongst habitat types. In the case of saline localities, where conductivity appears to be the main driver of nestedness, selective colonisation by halotolerant species and the presence of nested habitats (with different values of conductivity) could be the main factors behind the pattern observed. Despite the fact that area was never the most important variable driving nestedness, the results obtained suggest that the faunas of larger sites are largely subsets of those found in smaller ones. Such a finding is in contrast to general expectations, as the greater area and/or habitat diversity of larger sites would be seen to support viable populations of a larger number of species (Gaston & Blackburn 2000). In this study, however, the largest sites are some deep karstic and endorheic lagoons, with much open water and limited marginal vegetation development, which often have relatively low water beetle species richness; smaller sites such as some natural pools, endorheic ponds and small coastal wetlands holding a much higher proportion of the regional species pool. As inter-locality habitat heterogeneity has been described as one of the most important factors eroding nestedness (Cutler 1994; Wright et al. 1998), working at a habitat rather than a regional scale, as it was attempted here (saline and freshwater), has advantages for exploring the degree to which metacommunities are nested.

Implications for management and conservation

Natural pools, which showed the highest number of species and endemics, and continental salt-pans, with a high proportion of endemics, are complex sites where a mix of lentic and lotic habitats gives them great heterogeneity, allowing them to support high aquatic biodiversity. However, this level of complexity is decreasing in many of these sites within the study area, mainly due to aquifer over-exploitation, hence the importance of maintaining the volume of flows which feed the standing fraction of these complexes. In this sense, the conservation of certain individual sites can be a key factor for the maintenance of regional aquatic biodiversity. Taking into account the nested structure, it is necessary to be careful when selecting the most interesting sites. In this way, whilst it is necessary to include the richest sites in protected area networks, this is not sufficient to fulfil all the goals such networks pursue. Despite the general nested structure detected, there are also a number of species which fall outside this pattern (i.e. they are not present in the richest sites). Therefore, it is also essential to include representation of sites which, although show a low species richness, harbour rare or endemics taxa. In addition, some habitat types that are less important in terms of species richness, threatened species and/or endemics, such as karstic lagoons and endorheic lagoons and ponds, also play a key role for the maintenance of biodiversity since they can work as an adult refuge in dry periods and as dispersal stepping stones connecting other aquatic habitats (Bilton et al. 2006).

In conclusion, this study demonstrates that standing water bodies in Southeastern Iberia harbour a relatively high proportion of the aquatic Iberian fauna, for water beetles at least, being distributed across a wide range of well-characterised aquatic ecosystems. Whilst conductivity appears as the most important driver of assemblage composition at a regional scale, independent analyses of faunal composition in saline and freshwater sites reveals the important influence of anthropogenic activity in shaping local faunas, something which is also reflected in the nestedness analyses. Although both freshwater and saline systems in the region contain significantly nested assemblages, the key drivers of nestedness apparently differ among systems, with selective extinction associated mainly with impacts, and selective colonisation due to habitat heterogeneity being key drivers in freshwater and saline systems respectively. Given the established value of aquatic beetles as surrogates of inland water biodiversity, such findings emphasise the need to maintain a range of lentic habitats for effective conservation of the regional fauna, and point to the considerable impact of human activity on the faunal composition of these systems.

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Chapter 3

Are patterns in the taxonomic, biological and ecological traits of water beetles congruent in Mediterranean ecosystems?

Hydrobius convexus

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Introduction

Understanding how species assemble locally from a given species pool requires consideration of how their traits are filtered to match local environmental conditions (Poff 1997). The ‘habitat templet’ concept suggests that the habitat provides a templet upon which evolution forges characteristic species life history traits (Southwood 1977; Townsend & Hildrew 1994). From the initial publication of a few direct tests on this concept (Statzner et al. 1994; Statzner et al. 1997; Townsend et al. 1997), the use of species traits for assessing the functional integrity of freshwater ecosystems has become popular (Culp et al. 2011), especially because most traits are predictably affected by environmental variations (Statzner & Bêche, 2010) and they enable large-scale comparisons (Statzner et al. 2001; Menezes et al. 2010). Subsequent developments in river bioassessment have shown that multiple trait-based methodologies can detect the effects of land-use disturbances (Richards et al. 1997; Dolédec et al. 2011) as well as water abstraction (Miller et al. 2010), and could help in predicting the effects of future climate scenarios on invertebrate stream communities (Bonada et al. 2007) and for biodiversity conservation (Larsen & Ormerod 2010).

However, the relative contribution of habitat (ecological traits) and biotic factors (biological traits) in the trait filtering process needs more investigation (Cooper et al. 2008). A strong habitat filter might favour trait conservatism in close relatives, thus making possible the existence of specious taxonomic groups that display low biological and ecological trait diversity (Bêche & Statzner 2009). On the other hand, biotic interactions among taxa could enable trait divergence in close relatives, thus increasing their functional diversity so that high species richness would be associated with high functional richness (De Bello et al. 2009). Here, we seek to address these contrasting expectations by studying the degree of congruence across taxa between biological traits (those which determine life history strategies) and ecological traits (those concerning the ecological requirements).

We focus on water beetles, a very specious group of 12,600 known species worldwide (3% of all Coleopteran species) that occurs in diverse water bodies (Jäch & Balke 2008), including highly stressed habitats such as saline streams or

temporary ponds (Millán et al. 2011; Picazo et al. 2012). The high richness of water beetles in southeastern Iberia is partly due to its singular biogeographical history (Ribera 2000; Millán et al. 2006), with frequent speciation processes occurring since the Pleistocene (Ribera & Vogler 2003; Ribera et al. 2011).

Our specific objectives were to determine:

1. The biological and ecological traits that predominate in beetle assemblages of Mediterranean inland aquatic ecosystems.
2. The relationships among taxonomic, biological and ecological trait diversities across the principal genera of water beetles.
3. Whether congruence occurs between biological and ecological trait diversities, together with the main factors (e.g. habitat filtering and biotic interactions) that influence them.

Methods

Sample processing

Water beetles were collected from 212 sampling sites distributed over 130,000 km^2 in the south-eastern quadrant of the Iberian Peninsula (figure 1; see Picazo et al. 2012 for detailed features of the study area). Partly following the classification of Abellán et al (2005), sampling sites were assigned to categories of inland aquatic habitat on the basis of physical and chemical features, water origin and hydrology. The sites represented the entire spectrum of inland aquatic habitats in the study area and included headwater streams (32 sites), middle reach streams (25), rivers (22), saline streams (11), springs (6), ditches (7), reservoirs (5), artificial pools (11), karstic lagoons (9), endorheic lagoons and ponds (40), natural pools (21), continental salt-pans (11), rice fields (5), coastal rock-pools (2) and coastal wetlands (5). The number of sampling sites in each habitat category was chosen to provide a quantitative representation of each inland aquatic habitat according to their natural occurrence in the study area and to encompass the overall heterogeneity among sites in each habitat. This procedure allowed the compilation of an accurate water beetle checklist from the study area.

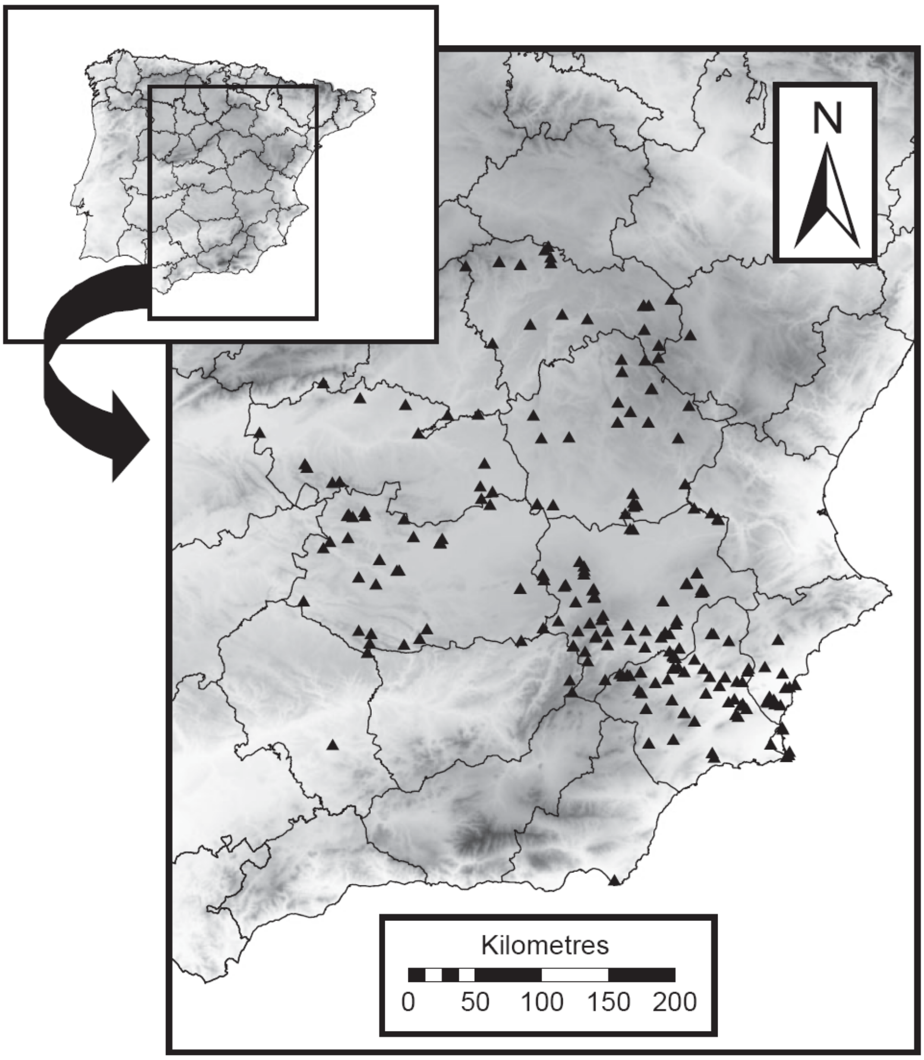

Figure 1 Location of sampling sites (figures) within the study area.

With the objective of drawing up the water beetle genera checklist from the study area, field samples were collected beginning in 1994, although most were performed between 2002 and 2008. The majority of sites were sampled at least twice during spring or early summer to coincide with the beetles' maximum activity period. Localities were consistently sampled by kick sampling into a hand net until no further morphospecies was found. Taxa belonging to coleopteran families considered as strictly aquatic sensu Jäch & Balke (2008), (i.e. Gyrinidae, Haliplidae, Noteridae, Hygrobiidae, Dytiscidae, Helophoridae, Hydrochidae, Hydrophilidae, Hydraenidae, Elmidae and Dryopidae) were included in the study. The final checklist comprised 272 water beetle species belonging to 68 genera (see table S1 in supporting information).

Biological traits and ecological traits

Several databases have been developed worldwide to conduct multiple trait-based studies (Bêche et al. 2006; Dolédec et al. 2006; Vieira et al. 2006; Tomanova & Usseglio-Polatera 2007; Tachet et al. 2010). They contain the most comprehensive available knowledge on aquatic macroinvertebrate traits at the most appropriate level of identification, the genus, since this has been demonstrated to be sufficient for assessing functional diversity of lotic invertebrate communities (Dolédec et al. 2000; Gayraud et al. 2003).

The present study incorporated the biological and ecological traits provided by Tachet et al. (2010) in their database for European macroinvertebrates, and we also used trait information from Bournaud et al. (1992) and Richoux (1994). Traits and categories were modified slightly according to the characteristics displayed by the target group in the study area: some categories that did not apply to water beetles were removed, some other categories were grouped into one, new categories that were necessary in a Mediterranean context were added (see tables 1 and 2 for details), and taxonomic information was updated according to the checklist from the study area. Ultimately, 11 biological traits comprising 40 categories and 11 ecological traits constituting 54 categories were used.

A fuzzy coding approach (Chevenet et al. 1994) quantified the affinity of each genus for each trait category and accounted for potential trait plasticity. The approach consists of assigning an affinity score ranging from 0 (no affinity) to 3 (maximum affinity) and up to 5 for those traits having a high number of selected categories, to reflect the strength of association each taxon displays for a given biological or ecological trait category. Based on an extended literature review (Bournaud et al. 1992; Richoux 1994; Tachet et al. 2010; Bonada & Dolédec 2011) and the authors' own field data (Millán et al. 2002; Abellán et al. 2004; Picazo et al. 2012), these scores were assigned according to genus requirements in the study area to take into account species plasticity (see tables S2 and S3 in supporting information for raw data). All scores were standardised so that the sums for a given genus and a given trait were 1.

Table 1 Biological traits and their categories. *, categories >1-2 cm and >2-4 cm grouped into category >1 cm; +, categories <1 and =1 were grouped into a single category; ±, larva and pupa together in one single modality; §, fine sediment, microorganisms and fine sediment >1 mm were aggregated into one category.

CODE	BIOLOGICAL TRAIT	Nº	CATEGORIES
A	Maximal size[*]	1	≤ 0.25 cm
		2	> 0.25-0.5 cm
		3	> 0.5-1 cm
		4	> 1 cm
B	Life cycle duration	1	≤ 1 year
		2	> 1 year
C	Potential number of reproduction cycles per year[+]	1	≤ 1
		2	> 1
D	Aquatic stages[±]	1	Egg
		2	Larva + pupa
		3	Adult
E	Reproduction	1	Clutches, cemented or fixed
		2	Clutches, in vegetation (endophytic)
		3	Clutches, terrestrial
F	Dispersal	1	Aquatic passive
		2	Aquatic active
		3	Aerial active
G	Resistance form	1	Diapause or dormancy
		2	None
H	Respiration	1	Tegument
		2	Gills
		3	Plastron
		4	Spiracle (aerial)
		5	Hydrostatic vesicle (aerial)
I	Locomotion and substrate relation	1	Flier
		2	Swimmer (surface swimmer included)
		3	Crawler
		4	Interstitial (endobenthic)
J	Food[§]	1	Fine sediment + Microorganisms + Detritus < 1
		2	Plant detritus ≤ 1mm
		3	Living microphytes
		4	Living macrophytes
		5	Dead animals > 1 mm
		6	Living microinvertebrates
		7	Living macroinvertebrates
		8	Vertebrates
K	Feeding habits	1	Shredder
		2	Scraper
		3	Piercer (plants or animals)
		4	Predator (carver/engulfer/swallower)

Data analyses

First, the number of species and the number of trait categories (biological and ecological) within families were counted. Simple regressions were then performed to study the relationships among taxonomic, biological and ecological trait richness. Taxon richness was log-transformed to conform with the assumption of normality. A fuzzy correspondence analysis (FCA; Chevenet et al. 1994) on the genera-by-trait categories array was used to obtain multivariate scores for genera based on their trait composition. To quantify the degree of separation among trait categories, and therefore the contribution of each trait to a given axis, correlation ratios (i.e. the amount of variance explained by trait categories along the axis scores) were computed.

To test for a co-structure, or relationship, between biological and ecological traits, co-inertia analyses were performed (Dolédec & Chessel 1994; see a review in Dray et al. 2003) both on the total arrays and on pairs of separate biological and ecological traits. The correlation between biological and ecological traits was measured using the Rv-coefficient, which is a multidimensional equivalent of the ordinary correlation coefficient between two variables (Robert & Escoufier 1976). The statistical significance of the Rv-coefficient was evaluated by a Monte Carlo permutation test. The resulting distribution of 999 replicated matches of two arrays (after random row permutations) enabled comparison with the observed Rv-coefficient. The number of simulated values higher than the observed values was estimated to be the probability (simulated) of getting the observed Rv-coefficient by chance. Co-inertia analysis provided us with two matched sets of coordinates for genera (one for biological traits and another one for ecological traits). To assess for global congruence within each family, the average distance between the biological trait and ecological requirement genus coordinates obtained along the first co-inertia axis was calculated.

Statistics and graphical outputs were computed with the ade4 library (Chessel et al. 2004; Dray & Dufour 2007) and vegan library (http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf) implemented in R freeware (R Development Core Team 2011).

Table 1 Ecological traits and their categories. *, trait categories from Tachet et al. (2010) were adapted to the study area and the target group based on own data and expertise; +, trait categories from Tachet et al. (2010) were adapted to the study area and the target group based on Ribera et al. (1998); ±, Saline water category from Tachet et al. (2010) was separated into hypo-, meso- and hypersaline categories; §, Categories equivalent to Tachet et al. (2010), but with a different denomination; ¶, trait categories from Tachet et al. (2010) were adapted to the study area and the target group based on own data and expertise.

CODE	ECOLOGICAL TRAIT	Nº	CATEGORIES
a	Local habitat (preference)	1	River channel
		2	Banks, connected side-arms
		3	Ponds, pools, disconnected side-arms
		4	Marshes, peat bogs
		5	Temporary waters
		6	Lakes
		7	Groundwaters
b	Longitudinal distribution (preference)	1	Crenon
		2	Epirhithron
		3	Metarithron
		4	Hyporhithron
		5	Epipotamon
		6	Metapotamon
		7	Estuary
		8	Otuside river system
c	Altitude*	1	≤ 750 m
		2	< 750-1500 m
		3	< 1500 m
d	Biogeographic regions$^+$	1	Transiberian
		2	Northern
		3	Southern
		4	Circummediterranean
		5	Iberian endemic
e	Substrate (preference)	1	Flags/boulders/cobbles/pebbles
		2	Gravel
		3	Sand
		4	Silt
		5	Macrophytes
		6	Microphytes
		7	Twigs/roots
		8	Organic detritus/litter
		9	Mud
f	Current velocity (preference)	1	Null
		2	Slow (≤ 25 cm s^{-1})
		3	Moderate (> 25-50 cm s^{-1})
		4	Fast (> 50 cm s^{-1})
g	Trophic status	1	Oligotrophic
		2	Mesotrophic
		3	Eutrophic

Table 2 (Continued).

CODE	ECOLOGICAL TRAIT	Nº	CATEGORIES
h	Salinity (preference)[±]	1	Freshwater ($\leq$ 1.5 g l^{-1})
		2	Hypo-, mesosaline water (> 1.5-40 g l^{-1})
		3	Hypersaline water (>40 g l^{-1})
i	Temperature (preference)[§]	1	Stenothermic cold ($\leq$ 15 ºC)
		2	Stenothermic warm (>15 ºC)
		3	Eurythermic
j	Saprobity	1	Xenosaprobic
		2	Oligosaprobic
		3	β-Mesosaprobic
		4	α-Mesosaprobic
		5	Polysaprobic
k	pH[¶]	1	≤ 6.5
		2	> 6.5-7.5
		3	> 7.5-9
		4	> 9

Results

Relationships among taxonomic, biological and ecological trait richness

Taxon richness within families was significantly linked to both the number of biological (R^2 = 0.65, P < 0.003) and ecological trait categories (R^2 = 0.91, P < 0.000). Haliplidae, Noteridae, Hygrobiidae, Elmidae, and above all, Hydrophilidae, included a higher percentage of biological rather than ecological trait categories, whereas the remaining families showed the reverse pattern; this fact was especially remarkable in the case of Hydraenidae (table 3). Hydrophilidae showed the highest richness of biological trait categories despite being the third most specious family after Dytiscidae and Hydraenidae. Dytiscidae and Elmidae were also quite diverse in terms of biological traits. In contrast, Dytiscidae, Hydraenidae and Hydrophilidae (the three most taxon-rich families) were by far the most diverse in terms of ecological traits.

Biological traits

Water beetles as a whole showed a high number of strategies, while also displaying some uniform traits across families (e.g. life cycle duration and resistance form;

figure 2). There were also families which biological traits were quite homogeneous across genera, including the highly specious Hydraenidae and other much less diverse families, such as Elmidae. Several differences occurred at the suborder level, with Adephaga displaying a high variety of categories across genera for maximal size, respiration and food, whereas Polyphaga demonstrated the same for maximal size, reproduction, respiration, locomotion, food and feeding habits.

Table 3 Number of biological trait categories, ecological trait categories and taxa richness for each freshwater beetle family (percentage over the total in brackets).

FAMILY	Biological trait categories	Ecological trait categories	Species/Genera richness
Gyrinidae	23 (58)	37 (69)	8/3 (3/4)
Haliplidae	23 (58)	29 (54)	7/2 (3/3)
Noteridae	16 (40)	21 (39)	1/1 (0/1)
Hygrobiidae	16 (40)	15 (28)	1/1 (0/1)
Dytiscidae	32 (80)	51 (94)	93/30 (34/44)
Helophoridae	20 (50)	35 (65)	9/1 (3/1)
Hydrochidae	18 (45)	29 (54)	8/1 (3/1)
Hydrophilidae	34 (85)	43 (80)	43/13 (16/19)
Hydraenidae	23 (58)	49 (91)	75/5 (28/7)
Elmidae	26 (65)	34 (63)	21/9 (8/13)
Dryopidae	24(60)	35 (65)	6/2 (2/3)
Total	**40**	**54**	**272/68**

The first three axes of the FCA performed on the biological trait array accumulated 57% of the total variance with more than half associated with the first axis (eigenvalue = 0.317; variance explained = 32.4%). Traits showing major differences across genera along the first FCA axis included food types (variance explained = 74.5%), feeding habits (74%), respiration (59.5%), reproduction (45.7%) and locomotion types (43%). Along the second axis (eigenvalue = 0.125; variance explained = 12.8%), genera were best separated according to reproduction (variance explained = 58.2%) and maximal size (38.8%). The third

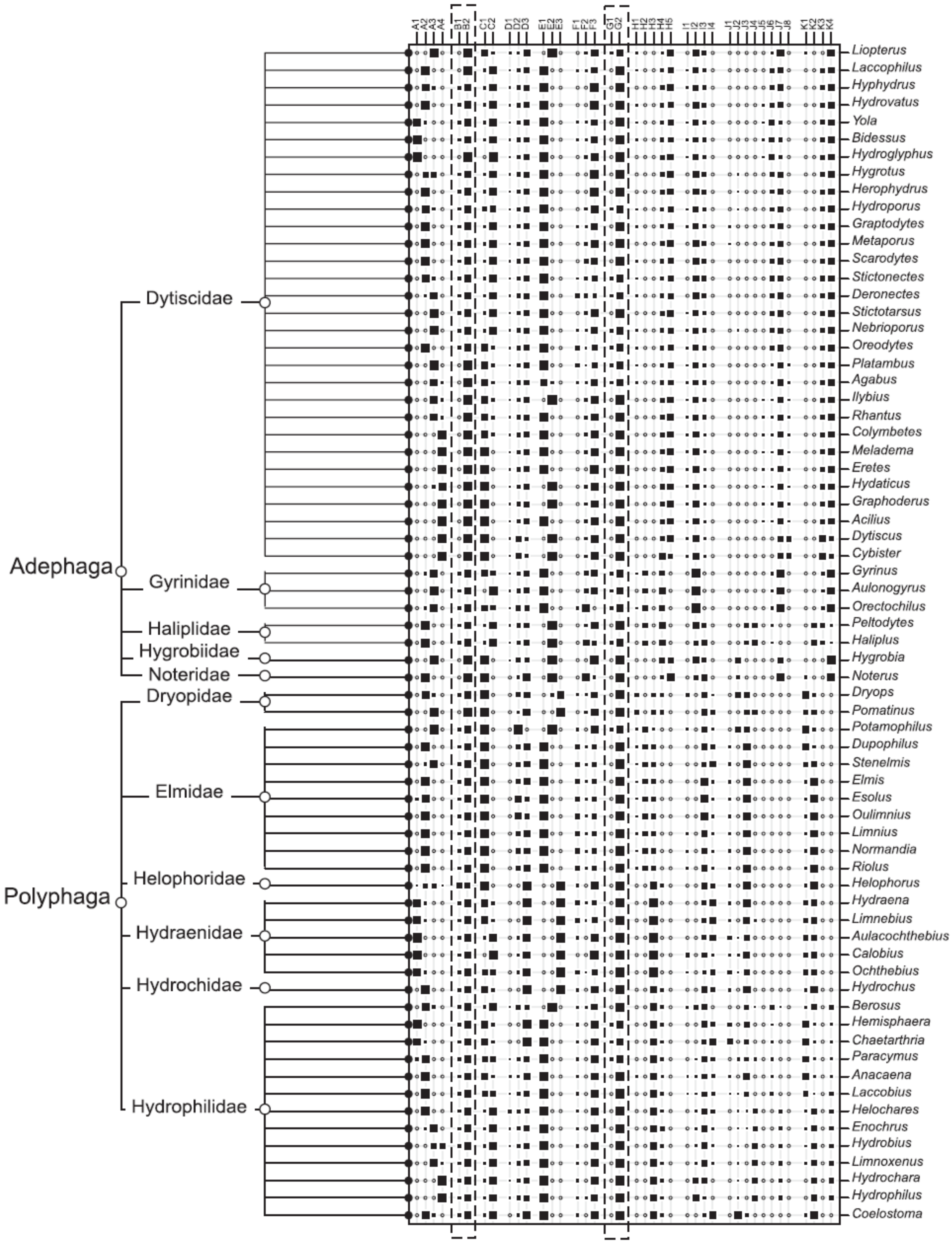

Figure 2 Biological traits of south-eastern Iberian Peninsula water beetles. Square size is proportional to the affinity of a genera for a given trait category (see trait category acronyms in table 1). Genera are arranged according to water beetle taxonomy. Dotted squares identify more uniform traits.

axis (eigenvalue = 0.110; variance explained = 11.3%), which again separated genera according to maximal size (45.5%), was not further explored.

As expected, Adephaga were opposed to Polyphaga along the first FCA axis. Adephaga genera appeared together since they generally share food types (living microinvertebrates, living macroinvertebrates, vertebrates and dead animals >1 mm), feeding habits (piercers and predators), respiration (spiracle and hydrostatic vesicle), reproduction (cemented or fixed clutches and clutches in vegetation) and locomotion types (mainly swimmers and fliers). Among Polyphaga, some Hydrophilidae genera (*Berosus*, *Enochrus*, *Hydrobius*, *Hydrochara*, *Hydrophilus* and *Limnoxenus*) presented scores close to 0 or even negative, suggesting that some of their biological trait combinations resemble those of some Adephaga genera. Polyphaga genera selected exclusive food (sediment, microorganisms and detritus ±1 mm, living microphytes and macrophytes), feeding habits (shredding and scraping), respiration (gills and plastron), reproduction (cemented or fixed clutches and terrestrial clutches) and locomotion (burrower and crawler) categories. Negative scores along the second FCA axis were mainly associated with large-sized genera (>20 mm) that lay egg clutches in vegetation (e.g. *Hygrobia* and *Potamophilus*, as well as several Dytiscidae) and small-sized genera (between 10 and 20 mm) that reproduce using terrestrial egg clutches (e.g. Dryopidae, Helophoridae and Hydraenidae). Smaller genera (<10 mm) that lay cemented or fixed clutches had positive scores along the second FCA axis (e.g. Gyrinidae, *Helochares* and *Laccobius*, as well as several Dytiscidae; figure 3).

Hydrophilidae (the third most taxon-rich family) and Dytiscidae (the most taxon-rich family) were the most heterogeneous families in terms of biological traits (figure 4). In spite of its high taxon richness, Hydraenidae showed great similarity in their biological traits, analogously to species-poor families such as Haliplidae and Gyrinidae.

Ecological traits

Water beetles as a whole displayed a considerable ecological trait heterogeneity (figure 5). In fact, contrary to what was observed for biological traits, no ecological trait showed the same pattern of selected categories across the entire group. For example, most Adephaga genera presented a very homogeneous response in terms

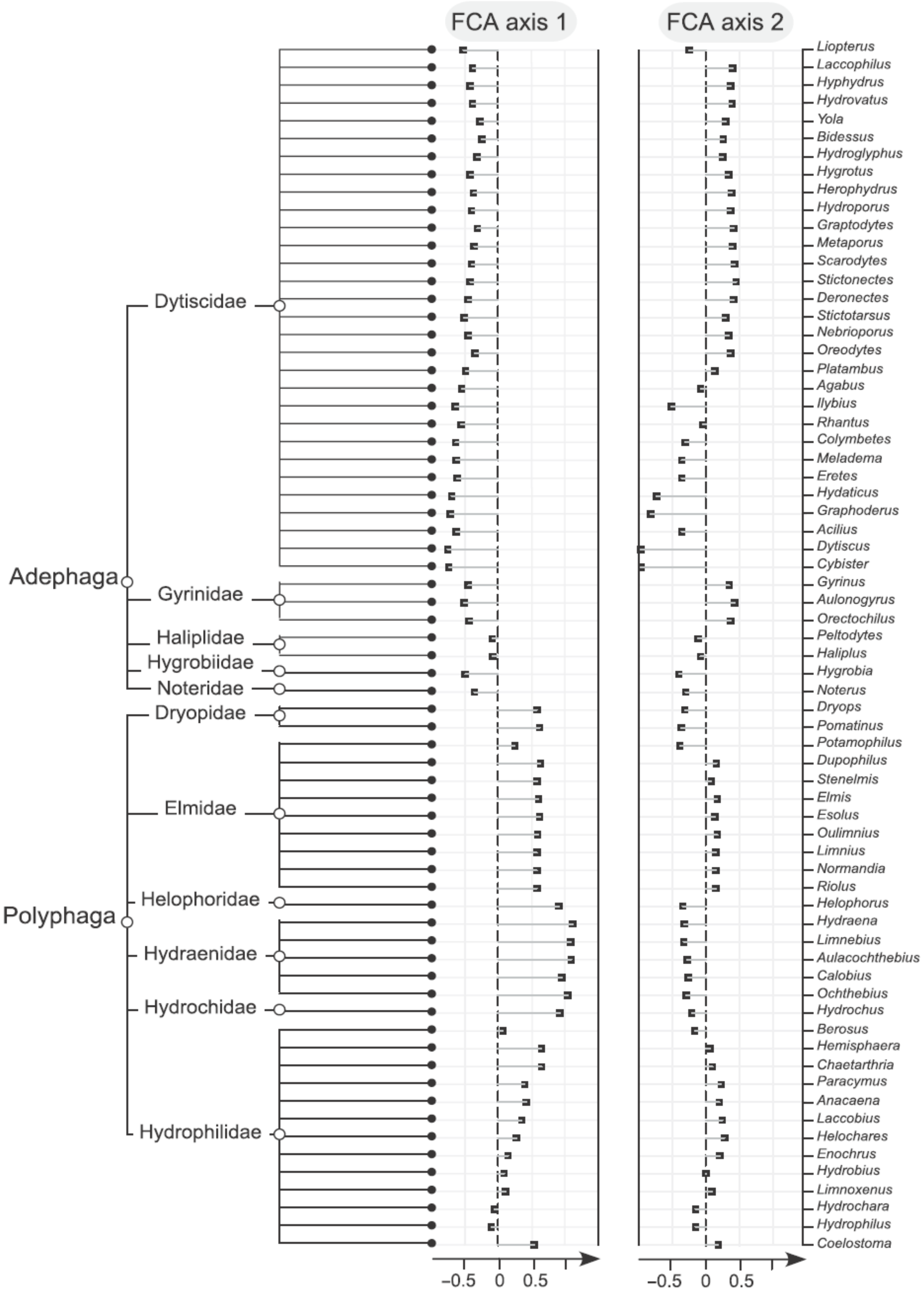

Figure 3 First two FCA axis scores of genera (dots) according to their biological traits. Genera are arranged according to water beetle taxonomy.

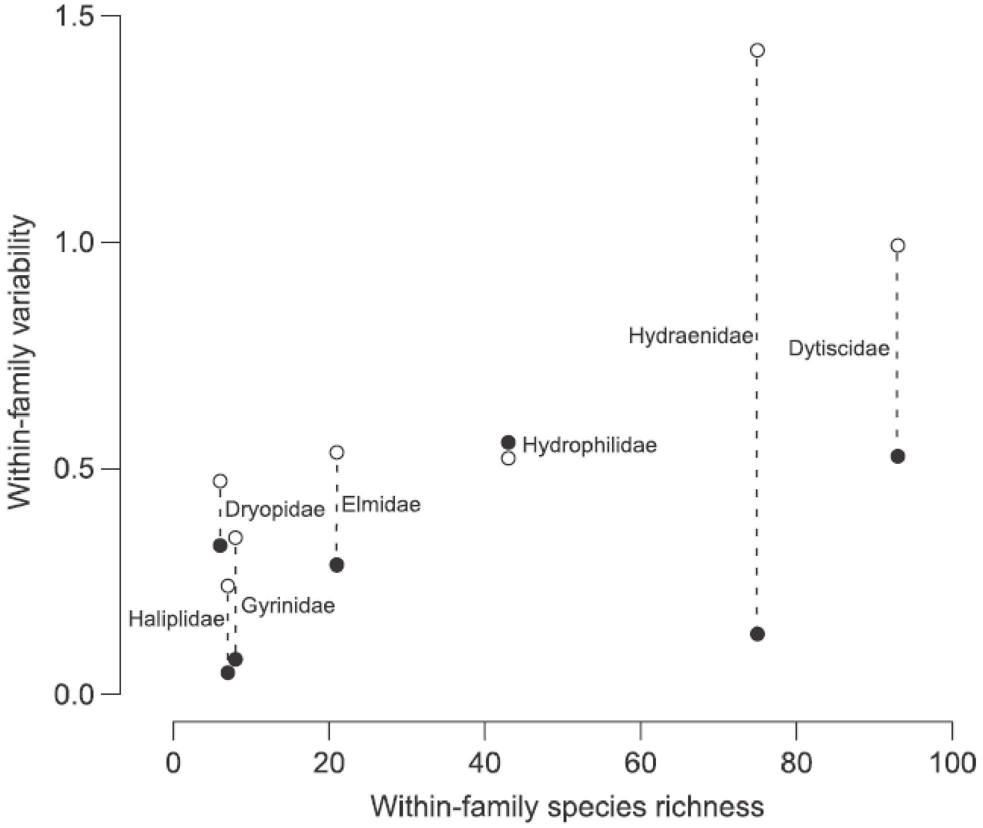

Figure 4 Within-family variability for biological (closed circles) and ecological traits (open circles) measured as the average FCA distances from genera to family centroids, as a function of taxa richness.

of salinity preferences, since they mainly selected fresh waters. In contrast, Polyphaga genera did not display a uniform pattern for such trait, although they did for temperature preferences, as many of them are eurythermic.

The first three axes of the FCA performed on ecological traits accounted for 47.4% of total variance, with more than half associated with the first axis (eigenvalue = 0.288; variance explained = 27.0%). Along the first FCA axis, the greatest differences across genera were associated with longitudinal distribution (variance explained = 54.0%), local habitat (46.4%) and current velocity preferences (48.1%). Along the second axis (eigenvalue = 0.127; variance explained = 11.9%), biogeography provided a prominent separation among genera (41.3%). The third axis (eigenvalue = 0.09; variance explained = 8.5%) did not contribute any new information.

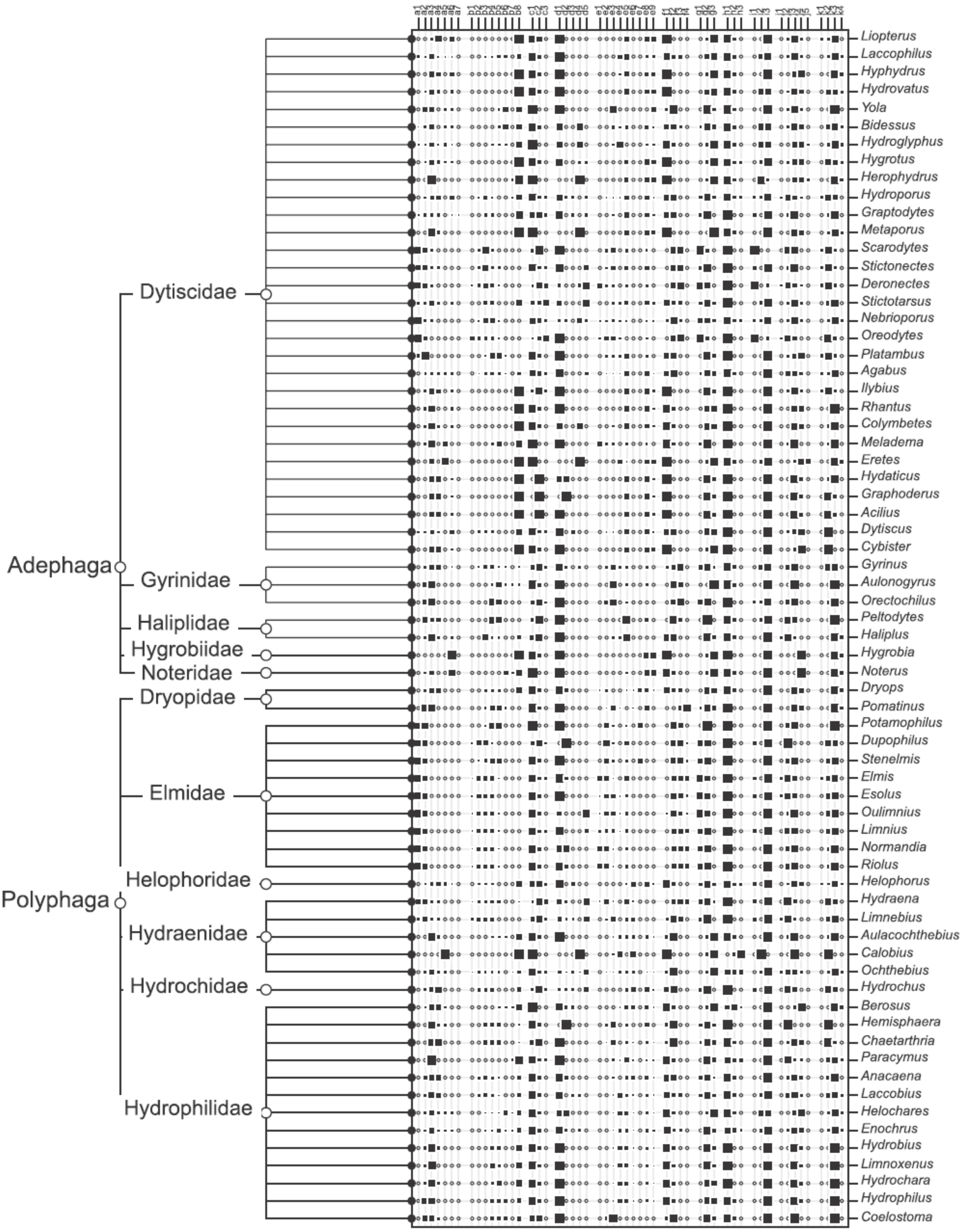

Figure 5 Ecological traits of south-eastern Iberian Peninsula water beetles. Square size is proportional to the affinity of a genera for a given trait category. Genera are arranged according to water beetle taxonomy.

Differences among suborders were not as clear as those observed for biological traits. Positive scores along the first FCA axis were associated with genera inhabiting lentic habitats such as temporary waters, lakes and other outside river systems. These habitats are generally inhabited by species belonging to *Noterus*, *Hygrobia* and several Dytiscidae genera (figure 6).

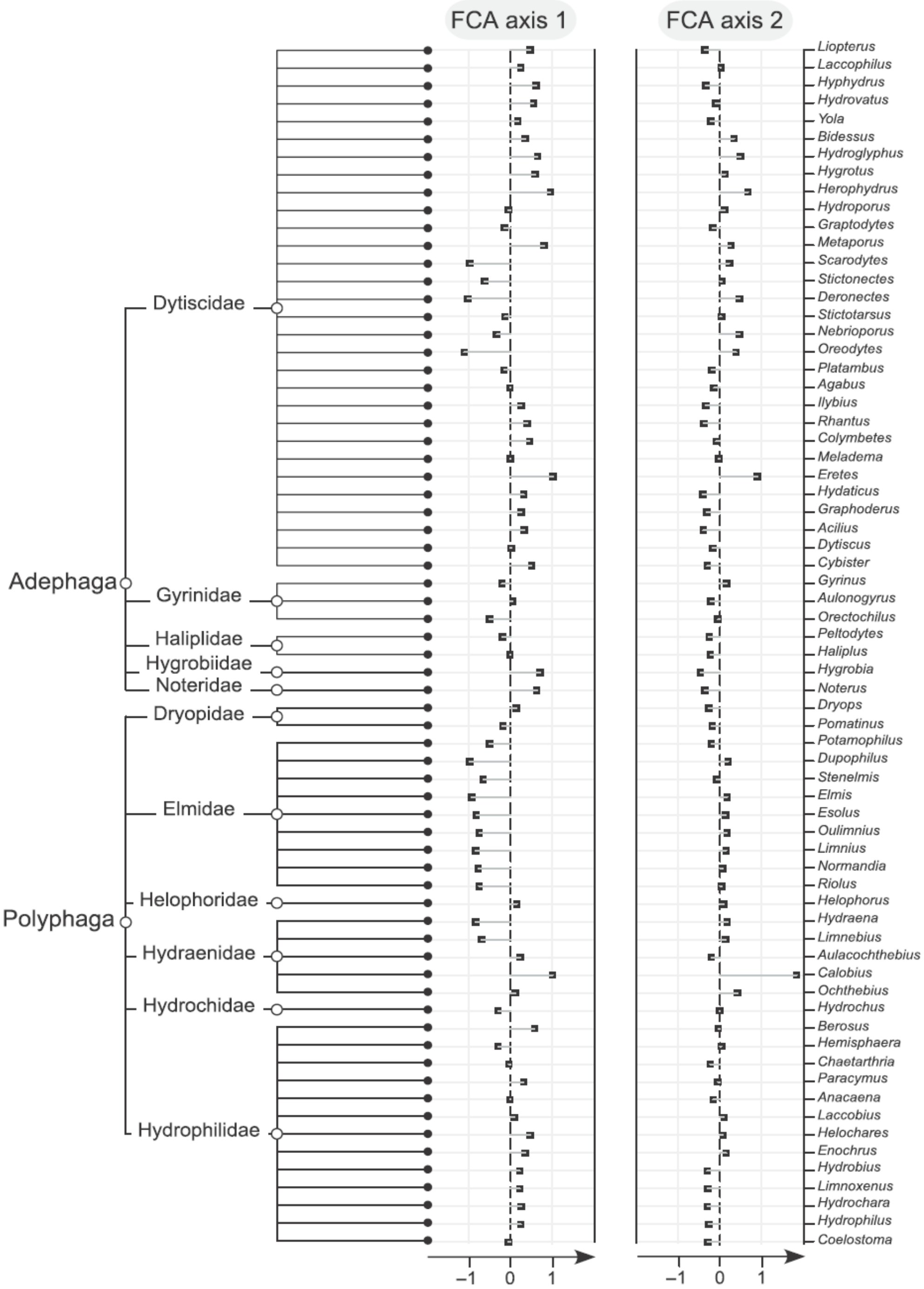

Figure 6 First two FCA axis scores of genera (dots) obtained from their ecological traits. Genera are arranged according to their water beetle taxonomy.

In contrast, the negative scores along the first FCA axis corresponded to genera inhabiting lotic habitats: river channels or connected sidearms, from crenon to hyporhithron, which prefer moderate to fast current velocity. These habitats are generally occupied by species belonging to *Deronectes*, *Scarodytes*, *Oreodytes*, *Limnebius*, *Hydraena* and Elmidae genera. In addition, Elmidae showed a great homogeneity for the majority of ecological traits across genera, whereas Hydraenidae presented the opposite pattern. The second FCA axis did not show any sharp taxonomic patterns. Hydraenidae and Dytiscidae were by far the most heterogeneous families in terms of ecological traits, as they include taxa that inhabit very different aquatic habitats (figure 4).

Relationships among biological and ecological traits

Co-inertia analysis showed a significant relationship between biological and ecological genera traits ($Rv = 0.35$, $P < 0.001$). The first co-inertia axis accounted for most of the variability (59.1%), accounting for up to 79.1% of biological trait variability and 81.4% of ecological trait variability. The varying degree of congruence was constrained by taxonomy, and co-inertia scores derived from biological traits demonstrated some structure according to taxonomy, which separated Adephaga from Polyphaga genera. In contrast, co-inertia scores associated with ecological traits were fairly randomly distributed across the taxonomic tree (figure 7).

Looking at the average distance among genus coordinates according to biological and ecological trait position grouped by family (obtained from the first co-inertia axis; see figure 7), Hydraenidae displayed the lowest degree of congruence (figure 8). In contrast, Elmidae showed the highest concordance between biological and ecological traits.

Finally, the pairwise relationships between each biological and ecological trait showed that respiration, dispersion and food types were best related to substrate and current velocity preferences, longitudinal distribution and local habitat preferences, trophic status and saprobity (table 4). Several other biological traits (maximal size, life duration, locomotion and feeding habits) were related to current velocity and longitudinal distribution preferences, whereas some others (life duration, number of reproductive cycles per year, aquatic stages, reproduction types, locomotion, feeding habits) were related to substrate preferences. Salinity and temperature preferences were only related to the number of reproductive cycles per year, whereas pH was related only to food types. Finally, no relationship was found between biological traits and altitudinal preferences.

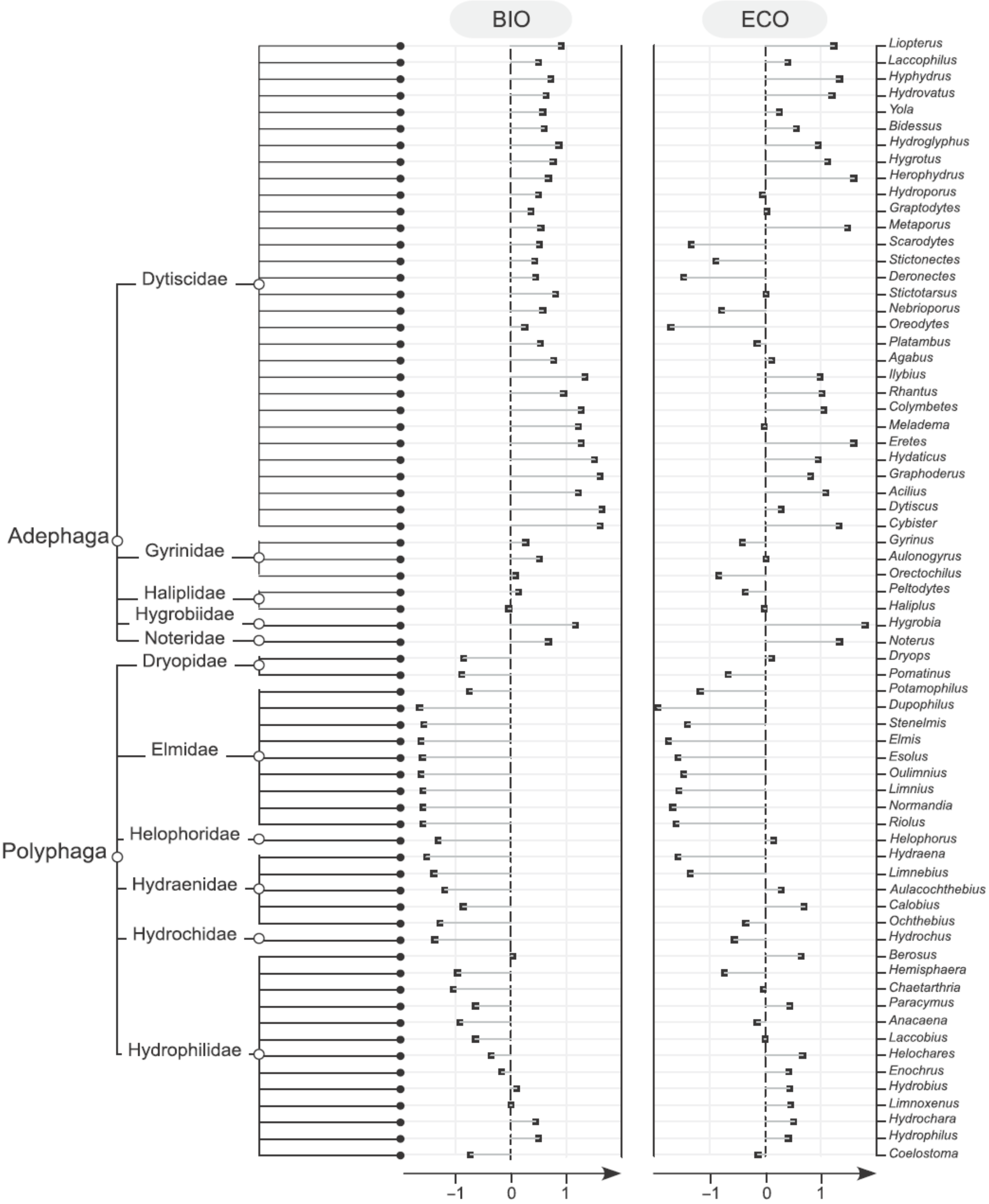

Figure 7 Results of co-inertia analysis showing the ordination of genera (dots) from their biological traits (BIO) and from their ecological traits (ECO). Genera are arranged according to their water beetle taxonomy.

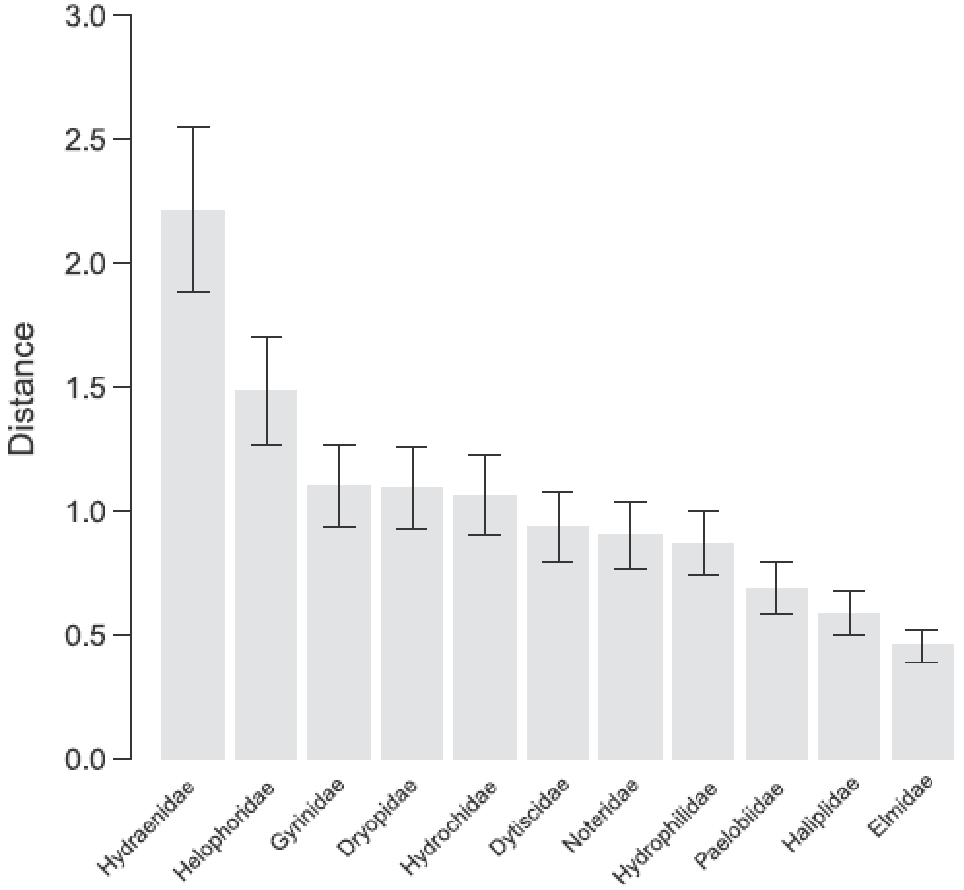

Figure 8 Within-family congruence between biological and ecological traits measured as the average Euclidean distance (±1 SE) among the first co-intertia axis sets of genera coordinates.

Discussion

Relationships among taxonomic, biological and ecological trait richness

In those cases where taxa have complementary traits, high taxon richness is expected to comprise high biological and ecological trait diversity (Petchey & Gaston 2002). In the present study, taxonomic richness was well correlated with both the number of biological and ecological trait categories used by genera within families. However, Hydrophilidae demonstrated a higher number of biological trait categories than Dytiscidae and Hydraenidae, despite its lower taxon richness in the study area (43 species for Hydrophilidae, 93 for Dytiscidae and 75 for Hydraenidae). Such a pattern has two possible origins. On one hand, in contrast to many Hydraenidae species that show narrow geographical ranges, most Hydrophilidae species display wide distributional ranges (Ribera 2000; Sánchez-

Fernández et al. 2008). In this sense, the presence of many closely related co-occurring species could have forced them to acquire different morphological and physiological characteristics to avoid intra-family competition among species. On the other hand, Hydrophilidae constitutes an older lineage than Dytiscidae (Hunt et al. 2007), so they have had more time to evolve and develop morphological and physiological adaptations.

Families displaying the highest number of ecological trait categories were also the richest in terms of taxa, which indicates that the observed ecological diversity is related to speciation processes (Hooper 1998). In this sense, families which species have colonised most aquatic habitats are the three most specious ones (Dytiscidae, Hydraenidae and Hydrophilidae), that is, they have experienced great species radiation. This pattern may be ultimately related to the avoidance of competition among closely related species and conforms to niche differentiation processes (Webb et al. 2002). In addition, population isolation due to biogeography, habitat stability and dispersal limitation may be additional keys for explaining the observed relationship between taxon richness and ecological traits (Ribera & Vogler 2003).

Despite its high taxon richness across the study area, Hydraenidae included a lower number of biological trait categories in comparison with other less rich families, such as Elmidae (21 species) or Dryopidae (6 species). The lack of concordance between biological traits and taxonomic richness for Hydraenidae could be related to a high level of endemic species; thus, a substantial percentage of their taxa have quite narrow geographical ranges (Sánchez-Fernández et al. 2008; Abellán et al. 2009; Ribera et al. 2011). Such a pattern may also indicate low inter-specific competition, which may have lessened trait divergence.

Biological traits

Two groups of taxa were clearly separated on the basis of their biological traits. Such groups corresponded to Adephaga and Polyphaga suborders, and therefore, biological traits appeared to be conservative in relation to this taxonomic level. Such segregation, mainly based on food types, feeding habits, respiration, reproduction and locomotion type, was more evident for Adephaga (even at the family level) than for Polyphaga. These patterns confirm previous findings

(Richoux 1994; Usseglio-Polatera 1994). Adephaga, which predominates in standing waters or in the depositional patches of lotic habitats, are swimmers and use hydrostatic vesicles for breathing. Food type variations among Adephaga are due to Haliplidae genera (figure 3), which are strictly herbivorous (Vondel 2005), whereas other Adephaga species feed on living or dead animal matter (Velasco & Millán 1998; Beutel & Leschen 2005). In agreement with their huge taxonomic diversity (Hanse 1999), Polyphaga genera displayed a higher biological trait variability than Adephaga. Specifically, Polyphaga genera included a greater variety of food types, feeding habits, respiration, reproduction and locomotion types than Adephaga. The evolutionary history of beetles explains such high biological trait diversity. Hydradephaga, the aquatic section of Adephaga, colonised aquatic habitats at one point in time from a single ancestor, whereas the aquatic Polyphaga come from different lineages that adapted to aquatic environments at various times throughout their evolution (Hunt et al. 2007; Morse 2009).

Generally, no trait convergence was found between these two main suborders. However, more precise information when quantifying trait categories might uncover some cases of trait convergence. For example, a few species belonging to Dytiscidae genera, such as *Deronectes* or *Oreodytes*, which prefer rheophilic freshwater habitats (primarily headwater streams), mainly use setal tracheal gills placed on the elytra surface for breathing, instead of the hydrostatic vesicle typical for Dytiscidae (Kehl & Dettner 2009). This respiration type is a clear adaptation to lotic habitats, since it decreases the need to frequently swim towards the surface for atmospheric air, thus preventing accidental drift. This respiratory strategy resembles that of Elmidae (Kodada & Jäch 2005) and represents a case of trait convergence associated with habitat filtering in constrained habitats (Webb et al. 2002; Cooper et al. 2008). Such a finding demonstrates that the occurrence of trait divergence within Dytiscidae, which has favoured niche divergence among their species (Wiens & Graham 2005), allows them to colonise very different habitats. A noticeable reverse pattern was detected for Elmidae, whose species are unusually similar in terms of biological traits and share very similar habitats, particularly riffle habitats (Kodada & Jäch 2005). In other words, they show niche conservatism (Wiens & Graham 2005) at the habitat scale.

Table 8 Pairwise correlation (*Rv*-coefficient) between biological and ecological traits (only those correlations with $p < 0.004$ are shown). *p*: simulated probability obtained from Monte Carlo random permutation test of the array rows.

Biological trait	**Ecological trait**	**Rv**	***p***
Maximal size	Local habitat	0.132	0.004
Maximal size	Longitudinal distribution	0.153	0.001
Maximal size	Current velocity (preference)	0.130	0.002
Life cycle duration	Longitudinal distribution	0.159	0.001
Life cycle duration	Substrate (preference)	0.137	0.001
Life cycle duration	Current velocity (preference)	0.133	0.003
Life cycle duration	Saprobity	0.169	0.001
Reproduction cycle per year	Substrate (preference)	0.171	0.001
Reproduction cycle per year	Salinity (preference)	0.167	0.001
Reproduction cycle per year	Temperature (preference)	0.154	0.001
Aquatic stages	Substrate (preference)	0.245	0.001
Aquatic stages	Current velocity (preference)	0.140	0.002
Reproduction	Substrate (preference)	0.205	0.001
Dispersion	Local habitat	0.297	0.001
Dispersion	Longitudinal distribution	0.347	0.001
Dispersion	Substrate (preference)	0.294	0.001
Dispersion	Current velocity (preference)	0.329	0.001
Dispersion	Trophic status	0.267	0.001
Dispersion	Saprobity	0.192	0.001
Respiration	Local habitat	0.244	0.001
Respiration	Longitudinal distribution	0.269	0.001
Respiration	Substrate (preference)	0.403	0.001
Respiration	Current velocity (preference)	0.298	0.001
Respiration	Trophic status	0.145	0.003
Respiration	Saprobity	0.194	0.001
Locomotion and substrate relation	Longitudinal distribution	0.155	0.002
Locomotion and substrate relation	Substrate (preference)	0.210	0.001
Locomotion and substrate relation	Current velocity (preference)	0.169	0.001
Food	Local habitat	0.163	0.002
Food	Longitudinal distribution	0.263	0.001
Food	Substrate (preference)	0.277	0.001
Food	Current velocity (preference)	0.234	0.001
Food	Trophic status	0.158	0.002
Food	Saprobity	0.195	0.001
Food	pH	0.154	0.001
Feeding habits	Longitudinal distribution	0.175	0.002
Feeding habits	Substrate (preference)	0.271	0.001
Feeding habits	Current velocity (preference)	0.187	0.001
Feeding habits	Saprobity	0.133	0.002

The variety of maximal body size in the four richest families is another important feature of our results. While Dytiscidae and Hydrophilidae genera show a great variety of sizes, Hydraenidae and Elmidae do not. On one hand, a diversification in size might avoid niche overlap among predators when getting food (Wilson 1975; Farlow & Pianka 2002; Woodward & Hildrew 2002), such as for Dytiscidae (larvae and adults) and Hydrophilidae (larvae) that actively hunt preys (Merritt & Cummins 1996). On the other hand, many Dytiscidae species coexist, especially in still waterbodies. The combination of both processes may have forced Dytiscidae species to interact with close relatives. Consequently, a diversification in body size would be an appropriate response to avoid competition (Farlow & Pianka 2002). In contrast, Hydraenidae and Elmidae do not actively search for their food (Jäch et al. 2005; Kodada & Jäch 2005), and interactions among similar species are probably less strong, which, together with the existence of niche divergence at the meso- or micro-habitat scale, could explain the smaller variability in body size observed in these families. Hydrophilidae genera showed a great diversity in size, food, feeding habits, reproduction, locomotion and respiration strategies. This variety concerns developmental stages as well, since most Hydrophilidae have carnivorous larvae and herbivorous adults. This considerable variety in biological strategies suggests high intra- and inter-specific competition in the past together with a high capacity for adaptation.

Ecological traits

In contrast to biological traits, and in agreement with Usseglio-Polatera et al. (2000), ecological traits were less conserved according to taxonomy. For example, families such as Dytiscidae, Hydraenidae and Hydrophilidae included some genera with specialist species, each of them inhabiting very specific habitats among a heterogeneous set of waterbodies in terms of conductivity, current velocity and permanence of water (Millán et al. 2006; Mellado et al. 2008; Picazo et al. 2012). For instance, many Dytiscidae and Hydraenidae genera include specialists from running or standing waters and fresh or saline water bodies, which explains the great variety of ecological traits within these families. The observed ecological trait overlap within families suggests the existence of niche differentiation as a consequence of the limiting effect of ecological similarity; that is, close relatives displaying similar biological traits tend to diverge in terms of ecological traits in order to avoid competition (Abrams 1983). Some key traits could explain a substantial part of this niche differentiation (Webb et al. 2002), with salinity preferences playing a prominent role, since some genera with species adapted to saline waters, such as *Nebrioporus*, *Enochrus* and *Ochthebius*, also have species typical of fresh waters (Millán et al. 2006). Only elmid genera formed a homogeneous group, suggesting niche conservatism (Webb et al. 2002).

The detected structure for ecological traits was clearly related to the longitudinal distribution and local habitat preferences of genera in agreement with their current velocity preferences, which coincides with findings from previous studies (Usseglio-Polatera et al. 2000; Mellado et al. 2008). According to these traits, Elmidae genera (inhabiting lotic, cold and oligotrophic waters), which demonstrated a highly homogeneous ecological response, were opposed to *Noterus*, *Hygrobia* and some Dytiscidae genera (typical of lentic, warm and eutrophic waters). The absence of clear groupings in terms of ecological traits reflects the need to combine trait studies with other works using the species level when analysing ecological aspects of hyperdiverse and widespread groups like water beetles.

Relationships between biological and ecological traits

These results confirm that habitat (inferred from ecological traits) acts as a templet for the biological traits of water beetles in accordance with several previous studies that attempted to test the River Habitat Templet (Williams & Feltmate 1992; Scarsbrook & Townsend 1993; Resh et al. 1994; Muotka & Virtanen 1995; Statzner et al. 1997; Townsend et al. 1997). The significant relationship between biological and ecological traits demonstrates that those water beetles having a certain combination of biological traits (mainly in terms of respiration, dispersal and food) use particular habitats (above all according to substrate preferences, longitudinal distribution and current velocity preferences). However, the relationship between biological and ecological traits varied by family. For instance, the degree of congruence for Elmidae was very high, that is, the ecological strategies almost perfectly matched their biological traits. Thus, most of their genera displayed very similar biological traits and occupied quite comparable

habitats in headwater streams, which suggest they represent a good example of phylogenetic clustering (Cavender-Bares et al. 2004), that is, associated to taxa from a single ancestor found to be more clustered (coexisting) than expected by chance. Other families, such as Hydraenidae, had a low match and demonstrated great similarity in terms of biological traits, but a high diversity of ecological traits, suggesting that niche differentiation was a strong driver of their speciation.

Two different patterns were observed in those genera for which biological and ecological traits were far from matching. On one hand, several Dytiscidae genera (*Deronectes*, *Oreodytes*, *Scarodytes* and *Stictonectes*), whose locomotion types, feeding habits, respiration types and dispersal behaviour rather fit still waters, predominate in streams with strong flows. On the other hand, the biological traits of a few genera cannot explain their great ecological diversity. *Stictonectes*, *Gyrinus*, *Dryops*, *Helophorus*, *Helochares*, *Paracymus* and *Ochthebius* inhabit lotic and lentic waters and *Nebrioporus*, *Paracymus* and *Ochthebius* inhabit saline and fresh waters. A potential reason for such lack of congruence may come from some deficiency in the information on biological trait categories (as indicated above for respiration trait states in some Dytiscidae typical of headwater streams). Another example concerns the salinity preference trait, which does not accurately catch the differences among taxa. Specifically, the osmoregulation and osmotolerance capacities of genera comprising saline species need to be assessed in order to develop multiple trait-based approaches in the Mediterranean area (Millán et al. 2011). One important contribution of this study was to adapt the trait affinities of genera (based on the species they include) to salinity preferences in the study area. Due to the huge salinity differences in Iberian aquatic ecosystems compared with the rest of Europe, most taxa that prefer saline waters in a European context (Tachet et al. 2010) can be considered typical of fresh waters in the Iberian river network, where meso- and hypersaline species that do not exist in the rest of Europe are common (Bonada & Dolédec 2011; Millán et al. 2011). Therefore, further research is needed to improve biological trait knowledge on such physiological aspects.

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SUPPORTING INFORMATION: CHAPTER 3

Table S1: Checklist of water beetle taxa in south eastern Iberia.

Table S2: Taxa affinity scores for each biological trait category.

Table S3 Taxa affinity scores for each ecological trait category.

Table S1

Checklist of water beetle taxa in south eastern Iberia. Modifications regarding trait dabase by Tachet et al. (2010): 1, current name for ancient genus *Copelatus* Erichson, 1832; 2, current name which includes ancient genus *Coelambus* C.G. Thomson, 1860; 3 and 4, taxa not included in Tachet et al. 2010; 5 and 6, previously included in genus *Ochthebius*.

Suborder	**Superfamily**	**Family**	**Genera**
Adephaga	Caraboidea	Gyrinidae	*Gyrinus*O.F. Müller, 1764
			Aulonogyrus Motschulsky, 1853
			*Orectochilus*Dejean, 1833
		Haliplidae	*Peltodytes*Régimbart, 1878
			*Haliplus*Latreille, 1802
		Noteridae	*Noterus*Clairville, 1806
		Hygrobiidae	*Hygrobia*Latreille, 1804
		Dytiscidae	*Liopterus*[1]
			*Laccophilus*Leach, 1817
			*Hyphydrus*Illiger, 1802
			*Hydrovatus*Motschulsky, 1853
			*Yola*Gozis, 1886
			*Bidessus*Sharp, 1882
			*Hydroglyphus*Motschulsky, 1853
			Hygrotus[2] Stephens, 1828
			Herophydrus[3] Sharp, 1882
			*Hydroporus*Clairville, 1806
			*Graptodytes*Seidlitz, 1887
			*Metaporus*Guignot, 1945
			*Scarodytes*Gozis, 1914
			Stictonectes Brinck, 1943
			*Deronectes*Sharp, 1882
			*Stictotarsus*Zimmermann, 1919
			Nebrioporus Régimbart, 1906
			Oreodytes Seidlitz, 1887
			Platambus C.G. Thomson, 1859
			Agabus Leach, 1817
			Ilybius Erichson, 1832
			Rhantus Dejean, 1833
			Colymbetes Clairville, 1806
			Meladema Laporte de Castelnau, 1834
			Eretes Laporte de Castelnau, 1833
			Hydaticus Leach, 1817
			Graphoderus Dejean, 1833
			Acilius Leach, 1817
			Dytiscus Linnaeus, 1758
			Cybister Curtis, 1827

Suborder	Superfamily	Family	Genera
Polyphaga	Hydrophiloidea	Helophoridae	*Helophorus* Fabricius, 1775
		Hydrochidae	*Hydrochus* Leach, 1817
		Hydrophilidae	*Berosus* Leach, 1817
			Hemisphaera Pandellé in Uhagón, 1876
			Chaetarthria Stephens, 1835
			Paracymus C.G. Thomson, 1867
			Anacaena C.G. Thomson, 1859
			Laccobius Erichson, 1837
			Helochares Mulsant, 1844
			Enochrus C.G. Thomson, 1859
			Hydrobius Leach, 1815
			Limnoxenus Motschulsky, 1853
			Hydrochara Berthold, 1827
			Hydrophilus O.F. Müller, 1764
			Coelostoma[4] Brullé, 1835
	Staphilinoidea	Hydraenidae	*Hydraena* Kugelann, 1794
			Limnebius Leach, 1815
			Aulacochthebius[5] Kuwert, 1887
			Calobius[6] Wollaston, 1854
			Ochthebius Leach, 1815
	Byrrhoidea	Elmidae	*Potamophilus* Germar, 1811
			Dupophilus Mulsant & Rey, 1872
			Stenelmis Dufour, 1835
			Elmis Latreille, 1798
			Esolus Mulsant & Rey, 1872
			Oulimnius Gozis, 1886
			Limnius Illiger, 1802
			Normandia Pic, 1900
			Riolus Mulsant & Rey, 1872
		Dryopidae	*Dryops* Olivier, 1791
			Pomatinus Sturm, 1853

Table S2

Taxa affinity scores for each biological trait category (see codes in table 1).

Traits	A				B		C		D			E			F			G		H					I				J								K			
Categories	A1	A2	A3	A4	B1	B2	C1	C2	D1	D2	D3	E1	E2	E3	F1	F2	F3	G1	G2	H1	H2	H3	H4	H5	I1	I2	I3	I4	J1	J2	J3	J4	J5	J6	J7	J8	K1	K2	K3	K4
Gyrinus	0	1	3	0	1	3	3	2	1	2	3	3	0	0	0	2	3	1	3	1	3	0	3	0	1	4	1	0	0	0	0	0	0	1	3	0	0	0	1	3
Aulonogyrus	0	0	3	0	1	3	0	3	1	2	3	3	0	0	0	2	3	1	3	0	2	0	3	0	1	4	1	0	0	0	0	0	0	1	3	0	0	0	1	3
Orectochilus	0	1	3	0	1	3	3	2	1	3	3	3	0	0	1	3	0	1	3	1	3	0	3	0	1	4	1	0	0	0	0	0	0	1	3	0	0	0	1	3
Peltodytes	0	3	0	0	1	3	1	3	1	2	3	0	3	0	0	1	3	0	3	0	2	0	3	0	0	3	2	0	0	0	2	3	0	1	0	0	0	3	2	1
Haliplus	0	3	0	0	1	3	1	3	1	2	3	0	3	0	0	3	2	1	3	0	2	0	3	0	0	2	3	0	0	0	2	3	0	1	0	0	0	3	2	1
Noterus	0	3	0	0	0	3	3	0	0	1	3	0	3	0	0	3	1	0	3	0	0	0	1	3	0	2	3	0	0	1	0	0	0	0	3	0	1	0	0	3
Hygrobia	0	0	3	0	0	3	3	0	1	3	3	0	3	0	0	0	3	0	3	0	0	0	3	3	0	3	2	0	0	3	0	0	0	0	3	0	0	0	0	3
Liopterus	0	0	3	0	0	3	3	1	1	1	3	0	3	0	0	1	3	1	3	1	0	0	1	3	0	3	2	0	0	0	0	0	0	1	3	0	1	0	0	3
Laccophilus	0	3	0	0	0	3	1	3	1	2	3	3	0	0	1	1	3	0	3	1	0	0	2	3	1	3	2	0	0	0	0	0	0	2	3	0	0	0	2	3
Hyphydrus	0	3	1	0	1	3	1	3	1	2	3	3	0	0	0	0	3	0	3	0	0	0	2	3	1	3	2	0	0	0	0	0	0	2	3	0	0	0	2	3
Hydrovatus	0	3	0	0	1	3	1	3	1	2	3	3	0	0	0	0	3	0	3	1	0	0	2	3	0	3	2	0	0	0	0	0	1	2	3	0	0	0	2	3
Yola	3	1	0	0	1	3	1	3	1	2	3	3	0	0	1	1	3	0	3	1	0	0	2	3	1	3	2	0	0	0	0	0	1	3	2	0	0	0	2	3
Bidessus	3	0	0	0	1	3	1	3	1	2	3	3	0	0	1	1	3	0	3	1	0	0	2	3	1	3	2	0	0	0	0	0	1	3	2	0	0	0	2	3
Hydroglyphus	3	0	0	0	0	3	0	3	1	2	3	3	0	0	0	1	3	0	3	0	0	0	2	3	1	3	2	0	0	0	0	0	1	3	2	0	0	0	2	3
Hygrotus	0	2	2	0	1	3	1	3	1	2	3	3	0	0	0	0	3	0	3	0	0	0	2	3	0	3	2	0	0	1	0	0	0	2	3	0	0	0	2	3
Herophydrus	0	3	0	0	1	3	1	3	1	2	3	3	0	0	0	0	3	0	3	0	0	0	2	3	0	3	2	0	0	1	0	0	0	2	3	0	0	0	2	3
Hydroporus	0	3	1	0	1	3	2	3	1	2	3	3	0	0	0	1	3	1	3	1	0	0	2	3	1	3	2	0	0	1	0	0	0	2	3	0	0	0	2	3
Graptodytes	0	3	0	0	1	3	1	3	1	2	3	3	0	0	1	1	3	0	3	1	0	0	2	3	1	3	2	0	1	0	0	0	0	2	3	0	0	0	2	3
Metaporus	0	3	0	0	1	3	1	3	1	2	3	3	0	0	0	1	3	0	3	0	0	0	2	3	0	3	2	0	1	0	0	0	0	2	3	0	0	0	2	3
Scarodytes	0	3	0	0	1	3	1	3	1	2	3	3	0	0	0	2	3	0	3	1	0	0	2	3	0	3	2	0	0	0	0	0	0	2	3	0	0	0	2	3
Stictonectes	0	3	1	0	1	3	1	3	1	2	3	3	0	0	1	2	3	1	3	1	0	0	2	3	0	3	2	0	0	0	0	0	0	2	3	0	0	0	2	3
Deronectes	0	1	3	0	1	3	1	3	1	2	3	3	0	0	2	1	3	1	3	1	0	0	2	3	0	3	2	0	0	0	0	0	0	2	3	0	0	0	2	3
Stictotarsus	0	0	3	0	1	3	1	3	1	2	3	3	0	0	0	1	3	0	3	0	0	0	2	3	1	3	2	0	0	0	0	0	0	2	3	0	0	0	2	3
Nebrioporus	0	0	3	0	1	3	1	3	1	2	3	3	0	0	1	1	3	1	3	1	0	0	2	3	1	3	2	0	0	1	0	0	0	2	3	0	0	0	2	3
Oreodytes	0	3	0	0	1	3	3	1	1	2	3	3	0	0	2	1	3	1	3	1	0	0	2	3	1	3	2	0	0	0	0	0	0	2	3	0	0	0	2	3
Platambus	0	0	3	0	0	3	3	1	1	2	3	3	0	0	2	1	3	1	3	1	0	0	2	3	1	3	2	0	0	0	0	0	0	1	3	1	0	0	2	3
Agabus	0	0	3	1	0	3	3	1	1	2	3	3	1	0	1	1	3	1	3	1	0	0	2	3	1	3	2	0	0	0	0	0	0	1	3	1	0	0	2	3
Ilybius	0	0	3	1	0	3	3	1	1	2	3	0	3	0	0	1	3	0	3	0	0	0	2	3	1	3	2	0	0	0	0	0	1	1	3	1	0	0	2	3
Rhantus	0	0	3	1	0	3	3	1	1	2	3	3	0	0	0	1	3	0	3	0	0	0	2	3	1	3	2	0	0	0	0	0	1	1	3	1	0	0	2	3
Colymbetes	0	0	0	3	0	3	3	1	1	2	3	3	0	0	0	1	3	0	3	0	0	0	2	3	1	3	1	0	0	0	0	0	1	1	3	1	0	0	2	3

Traits	**A**				**B**		**C**		**D**			**E**			**F**			**G**		**H**					**I**				**J**								**K**			
Categories	**A1**	**A2**	**A3**	**A4**	**B1**	**B2**	**C1**	**C2**	**D1**	**D2**	**D3**	**E1**	**E2**	**E3**	**F1**	**F2**	**F3**	**G1**	**G2**	**H1**	**H2**	**H3**	**H4**	**H5**	**I1**	**I2**	**I3**	**I4**	**J1**	**J2**	**J3**	**J4**	**J5**	**J6**	**J7**	**J8**	**K1**	**K2**	**K3**	**K4**
Meladema	0	0	0	3	0	3	3	0	1	2	3	3	0	0	0	1	3	0	3	0	0	0	2	3	1	3	1	0	0	0	0	0	1	1	3	1	0	0	2	3
Eretes	0	0	0	3	0	3	3	0	1	2	3	3	0	0	0	0	3	0	3	0	0	0	2	3	1	3	1	0	0	0	0	0	1	1	3	1	0	0	2	3
Hydaticus	0	0	1	3	0	3	3	0	1	2	3	0	3	0	0	1	3	0	3	0	0	0	2	3	1	3	1	0	0	0	0	0	1	1	3	1	0	0	2	3
Graphoderus	0	0	0	3	0	3	3	0	1	2	3	0	3	0	0	1	3	0	3	0	0	0	2	3	1	3	1	0	0	0	0	0	1	1	3	1	0	0	2	3
Acilius	0	0	0	3	0	3	3	0	1	2	3	3	0	0	0	1	3	0	3	0	0	0	2	3	1	3	1	0	0	0	0	0	1	1	3	1	0	0	2	3
Dytiscus	0	0	0	3	0	3	3	0	1	3	2	0	3	0	0	1	3	0	3	0	0	0	2	3	1	3	1	0	0	0	0	0	0	0	3	3	0	0	3	2
Cybister	0	0	0	3	0	3	3	0	1	3	2	0	3	0	0	1	3	0	3	0	0	0	3	2	1	3	1	0	0	0	0	0	0	0	3	3	0	0	3	2
Helophorus	1	3	3	1	2	2	3	0	0	0	3	0	0	3	1	0	3	0	3	0	0	3	1	0	0	0	4	2	1	0	3	0	0	0	0	0	1	3	0	0
Hydrochus	0	3	0	0	1	3	3	1	0	0	3	0	0	3	1	0	3	0	3	0	0	3	1	0	0	0	4	2	1	0	3	0	0	0	0	0	1	3	0	0
Berosus	0	3	1	0	1	3	1	3	1	3	3	0	3	0	1	1	3	0	3	0	0	3	1	0	1	2	3	0	0	0	3	1	0	3	1	0	1	3	0	2
Hemisphaera	3	0	0	0	1	3	3	1	0	0	3	3	0	0	1	0	3	1	3	0	0	3	1	0	0	0	3	2	2	0	3	0	0	1	0	0	3	1	0	1
Chaetarthria	3	1	0	0	1	3	3	1	0	0	3	3	0	0	1	0	3	1	3	0	0	3	1	0	0	0	2	3	3	0	2	0	0	1	0	0	3	1	0	1
Paracymus	1	3	0	0	1	3	2	2	1	2	3	3	0	0	1	0	3	1	3	0	0	3	1	0	0	1	3	2	0	2	3	2	0	2	0	0	3	1	0	1
Anacaena	0	3	0	0	1	3	3	1	1	1	3	3	0	0	1	0	3	0	3	1	0	3	1	0	1	1	3	2	1	0	3	0	0	1	0	0	3	1	0	1
Laccobius	0	3	0	0	1	3	2	2	1	2	3	3	0	0	1	0	3	0	3	0	0	3	1	0	1	1	3	2	1	1	3	0	0	2	0	0	3	1	0	2
Helochares	0	3	0	0	1	3	1	3	2	2	3	3	0	0	1	0	3	0	3	0	0	3	1	0	0	1	3	2	0	1	1	3	0	0	2	0	1	3	0	2
Enochrus	0	1	3	0	1	3	1	3	1	2	3	3	0	0	1	0	3	0	3	0	0	3	2	0	0	1	3	1	0	1	1	3	0	0	2	0	1	3	0	2
Hydrobius	0	0	2	2	1	3	1	3	1	2	3	3	0	0	1	0	3	0	3	0	0	3	1	0	0	1	3	1	0	1	0	3	0	0	2	0	1	3	0	2
Limnoxenus	0	0	3	1	1	3	1	3	1	2	3	3	0	0	1	0	3	0	3	0	0	3	1	0	0	1	3	1	0	1	0	3	0	0	2	0	1	3	0	2
Hydrochara	0	0	0	3	1	3	1	3	1	2	3	3	0	0	1	0	3	0	3	0	0	3	1	0	0	3	2	0	0	1	0	3	0	0	2	0	0	3	0	2
Hydrophilus	0	0	0	3	1	3	1	3	1	2	3	3	0	0	1	1	3	0	3	0	0	3	1	0	0	3	1	0	0	1	0	3	0	0	2	0	0	3	0	2
Coelostoma	0	3	1	0	1	3	1	3	0	1	3	3	0	0	1	0	3	0	3	0	0	3	1	0	0	0	1	3	0	3	1	0	0	0	0	0	1	3	0	0
Hydraena	3	1	0	0	1	3	3	1	0	0	3	0	0	3	2	1	2	0	3	0	0	3	0	0	0	0	2	3	1	0	3	0	0	0	0	0	2	3	0	0
Limnebius	3	1	0	0	1	3	3	1	0	0	3	0	0	3	2	1	3	0	3	0	0	3	0	0	0	0	2	3	1	0	3	1	0	0	0	0	2	3	0	0
Aulacochthebius	3	0	0	0	1	3	1	3	0	1	3	0	0	3	1	0	3	0	3	0	0	3	0	0	0	0	2	3	2	1	3	0	0	0	0	0	2	3	0	0
Calobius	3	0	0	0	1	3	0	3	0	1	3	0	0	3	0	0	3	0	3	0	0	3	0	0	2	0	3	1	1	1	3	0	0	0	0	0	2	3	0	0
Ochthebius	3	1	0	0	1	3	2	2	0	1	3	0	0	3	2	1	3	0	3	0	0	3	0	0	1	0	2	3	2	1	3	0	0	0	0	0	2	3	0	0
Potamophilus	0	0	3	0	1	3	3	0	0	3	0	0	3	0	1	0	3	1	3	1	3	1	0	0	1	0	3	1	0	3	3	0	0	0	0	0	3	1	0	0
Dupohilus	0	3	0	0	1	3	3	0	0	2	3	3	0	0	2	1	2	0	3	1	3	3	0	0	0	0	3	2	1	0	3	0	0	0	0	0	3	1	0	0
Stenelmis	0	1	3	0	1	3	3	0	0	2	3	3	0	0	2	1	2	0	3	1	3	3	0	0	0	0	2	3	1	0	3	0	0	0	0	0	2	3	0	0
Elmis	0	3	0	0	1	3	3	0	0	2	3	3	0	0	2	1	2	0	3	1	3	3	0	0	0	0	3	1	1	0	3	0	0	0	0	0	1	3	0	0
Esolus	1	3	0	0	1	3	3	0	0	3	2	3	0	0	2	1	2	0	3	1	3	3	0	0	0	0	3	1	1	0	3	0	0	0	0	0	1	3	0	0
Oulimnius	0	3	0	0	1	3	3	0	0	3	2	3	0	0	2	1	2	0	3	1	3	3	0	0	0	0	3	1	1	0	3	0	0	0	0	0	1	3	0	0

Traits	**A**				**B**		**C**		**D**			**E**			**F**			**G**		**H**					**I**				**J**								**K**			
Categories	**A1**	**A2**	**A3**	**A4**	**B1**	**B2**	**C1**	**C2**	**D1**	**D2**	**D3**	**E1**	**E2**	**E3**	**F1**	**F2**	**F3**	**G1**	**G2**	**H1**	**H2**	**H3**	**H4**	**H5**	**I1**	**I2**	**I3**	**I4**	**J1**	**J2**	**J3**	**J4**	**J5**	**J6**	**J7**	**J8**	**K1**	**K2**	**K3**	**K4**
Limnius	0	3	0	0	1	3	3	0	0	2	3	3	0	0	2	1	2	0	3	1	3	3	0	0	1	0	3	1	1	0	3	0	0	0	0	0	1	3	0	0
Normandia	0	3	0	0	1	3	3	0	0	2	3	3	0	0	2	1	2	0	3	1	3	3	0	0	1	0	3	1	1	0	3	0	0	0	0	0	1	3	0	0
Riolus	0	3	0	0	1	3	3	0	0	2	3	3	0	0	2	1	2	0	3	1	3	3	0	0	1	0	3	1	1	0	3	0	0	0	0	0	1	3	0	0
Dryops	0	3	1	0	1	3	3	0	0	2	3	0	1	3	1	1	3	0	3	3	0	3	3	0	2	0	3	1	0	3	3	0	0	0	0	0	3	1	0	0
Pomatinus	0	0	3	0	0	3	3	0	0	1	3	0	0	3	0	1	3	0	3	3	0	3	3	0	0	0	3	2	0	0	3	3	0	0	0	0	3	3	0	0

Table S3

Taxa affinity scores for each ecological trait category (see codes in table 2).

Traits	a							b								c			d					e									f				g			h			i			j					k			
Modalities	a1	a2	a3	a4	a5	a6	a7	b1	b2	b3	b4	b5	b6	b7	b8	c1	c2	c3	d1	d2	d3	d4	d5	e1	e2	e3	e4	e5	e6	e7	e8	e9	f1	f2	f3	f4	g1	g2	g3	h1	h2	h3	i1	i2	i3	j1	j2	j3	j4	j5	k1	k2	k3	k4
Gyrinus	0	2	3	3	0	1	0	0	1	2	2	1	1	0	1	2	3	1	3	1	0	1	0	0	1	3	1	1	0	0	1	0	1	2	3	0	2	3	1	3	1	0	0	2	3	0	2	3	0	0	0	3	3	0
Aulonogyrus	0	2	3	0	0	0	0	0	0	0	1	3	1	1	1	3	1	0	3	0	0	0	0	0	0	3	0	1	0	0	1	0	0	3	2	0	0	0	3	3	1	0	0	0	3	0	0	3	0	0	0	0	3	0
Orectochilus	0	2	3	0	0	0	0	0	0	0	4	2	0	0	0	2	3	1	3	0	0	0	0	0	2	3	0	1	0	0	0	0	0	2	3	0	2	3	0	3	0	0	1	1	3	0	2	3	0	0	0	1	3	0
Peltodytes	0	3	2	2	0	0	0	0	0	0	4	2	0	0	0	1	3	0	3	0	0	0	0	0	0	0	0	4	0	0	1	0	0	3	1	0	0	3	0	3	1	0	0	1	3	0	3	2	0	0	0	0	3	0
Haliplus	0	1	3	1	0	1	0	0	0	3	1	1	0	0	2	2	3	0	3	0	0	0	0	0	0	1	1	4	0	0	0	0	2	2	0	0	0	3	1	3	1	0	0	0	3	1	3	1	0	0	0	0	3	1
Noterus	0	1	2	0	0	3	0	0	0	0	0	0	2	1	3	3	0	0	3	0	0	0	0	0	0	0	0	1	0	0	3	3	3	1	0	0	0	1	3	3	1	0	0	0	3	0	0	0	3	0	0	0	3	1
Hygrobia	0	0	3	1	0	3	0	0	0	0	0	0	0	0	5	3	1	0	3	0	0	0	0	0	0	0	0	0	0	0	3	3	3	0	0	0	0	1	3	3	0	0	0	0	3	0	0	0	3	0	0	0	3	1
Liopterus	0	0	1	3	0	2	0	0	0	0	0	0	0	0	5	3	2	0	3	0	0	0	0	0	0	0	0	3	0	0	3	3	3	0	0	0	0	1	3	3	1	0	0	0	3	0	1	3	1	0	1	1	3	0
Laccophilus	2	1	3	1	1	1	0	0	0	1	1	2	2	0	3	3	1	0	3	0	0	0	0	0	0	0	2	3	0	0	1	1	2	1	1	0	0	2	3	3	1	0	0	2	3	0	1	3	1	0	0	1	3	1
Hyphydrus	0	0	3	2	0	2	0	0	0	0	0	0	0	0	5	3	1	0	3	0	0	0	0	0	0	0	1	3	0	0	2	2	3	0	0	0	0	1	3	3	1	0	0	0	3	0	0	2	3	0	0	0	3	1
Hydrovatus	0	1	3	2	0	2	0	0	0	0	0	0	0	0	5	3	1	0	3	0	0	0	0	0	0	0	0	3	0	0	2	2	3	0	0	0	0	2	3	3	1	0	0	2	2	0	1	3	2	0	0	2	2	1
Yola	0	2	3	0	1	1	0	0	0	0	0	1	3	0	3	3	0	0	3	0	0	0	0	0	0	2	1	2	0	0	2	1	1	3	0	0	0	3	1	3	1	0	0	0	3	0	1	3	1	0	0	0	3	0
Bidessus	1	2	3	0	2	2	0	0	0	0	0	1	3	0	3	3	1	0	2	0	0	2	0	0	0	2	1	2	0	0	2	1	2	2	1	0	1	3	2	3	1	0	0	2	2	0	1	3	2	0	0	2	3	1
Hydroglyphus	1	1	3	1	3	1	0	0	0	0	1	1	1	0	4	3	0	0	2	0	0	2	0	0	0	1	3	0	0	0	1	1	3	1	0	0	0	1	3	3	1	0	0	2	2	0	0	3	3	1	0	1	3	1
Hygrotus	0	1	3	2	1	1	0	0	0	0	0	0	0	0	5	3	1	0	3	0	0	1	1	0	0	0	0	2	0	0	3	2	3	0	0	0	0	1	3	3	1	1	0	1	3	0	1	2	2	0	0	3	2	1
Herophydrus	0	0	4	1	0	1	0	0	0	0	0	0	0	1	4	3	0	0	0	0	0	3	0	0	0	0	0	2	0	0	3	2	3	0	0	0	0	1	3	3	1	0	0	3	1	0	0	2	2	1	0	0	3	1
Hydroporus	0	1	2	2	0	2	0	0	1	2	1	0	0	1	3	3	1	1	3	1	1	0	1	0	1	1	1	3	0	0	3	1	2	2	0	0	1	3	1	3	1	1	1	1	3	1	3	2	1	0	1	3	2	0
Graptodytes	1	2	2	2	0	1	1	0	0	1	1	0	0	0	3	2	2	1	3	0	1	0	1	0	0	1	0	3	0	0	2	1	2	2	0	0	1	3	0	3	0	0	1	0	3	0	1	3	0	0	0	1	3	0
Metaporus	0	0	3	1	0	0	0	0	0	0	0	0	0	0	5	3	0	0	0	0	0	3	0	0	0	0	0	3	0	0	3	2	3	0	0	0	0	0	3	3	1	0	0	0	3	0	0	3	2	0	0	1	3	1
Scarodytes	3	2	1	0	0	0	0	0	1	3	1	0	0	0	0	1	3	0	3	0	0	0	0	0	2	3	0	2	0	0	1	0	0	2	2	0	3	1	0	3	0	0	3	0	0	0	3	3	0	0	1	3	1	0
Stictonectes	2	2	1	1	0	0	0	0	1	3	1	1	0	0	0	3	1	1	2	0	0	0	1	0	1	2	0	2	0	0	2	0	0	2	2	0	1	3	0	3	0	0	1	0	3	0	1	3	0	0	1	3	1	0
Deronectes	4	2	1	0	0	0	0	1	2	3	2	1	0	0	0	1	3	2	1	0	0	1	3	2	1	1	0	1	0	0	1	0	0	2	3	0	3	2	0	3	0	0	3	0	1	1	3	2	1	0	1	3	1	0
Stictotarsus	1	1	2	1	0	1	0	0	0	1	1	0	0	0	3	1	1	2	1	0	0	0	2	0	0	1	1	2	0	0	2	1	2	1	1	0	1	3	1	3	0	0	0	1	3	0	1	3	1	0	0	1	2	0
Nebrioporus	3	1	1	0	0	0	0	0	1	3	3	1	0	0	0	3	2	1	1	1	0	2	1	1	1	2	1	1	0	0	1	1	1	3	1	0	2	2	1	3	1	1	1	1	3	0	1	3	1	0	0	1	3	1
Oreodytes	4	1	0	0	0	0	0	3	2	2	2	1	0	0	0	1	2	3	3	0	0	0	0	1	2	2	1	0	0	0	1	0	0	2	3	0	3	1	0	3	0	0	3	0	1	1	3	2	0	0	0	3	1	0
Platambus	1	3	0	0	0	0	0	0	0	1	3	3	1	0	0	3	1	0	3	0	0	0	0	0	1	1	1	2	0	0	1	0	3	3	0	0	0	3	1	3	0	0	0	0	3	0	1	2	3	0	1	3	1	0
Agabus	0	1	2	2	1	2	0	0	1	2	3	2	1	0	3	3	2	1	3	0	0	0	1	0	1	1	1	3	0	0	3	1	2	3	0	0	1	3	2	3	1	0	0	0	3	0	3	3	2	0	1	1	3	0
Ilybius	0	1	3	2	0	1	0	0	0	0	0	0	0	0	5	1	3	1	3	0	0	0	0	0	0	0	0	3	0	0	3	1	3	0	0	0	0	3	1	3	0	0	0	0	3	0	1	3	1	0	1	3	1	0

Traits	a							b								c			d					e									f				g			h			i			j					k			
Modalities	a1	a2	a3	a4	a5	a6	a7	b1	b2	b3	b4	b5	b6	b7	b8	c1	c2	c3	d1	d2	d3	d4	d5	e1	e2	e3	e4	e5	e6	e7	e8	e9	f1	f2	f3	f4	g1	g2	g3	h1	h2	h3	i1	i2	i3	j1	j2	j3	j4	j5	k1	k2	k3	k4
Rhantus	0	1	3	0	0	1	0	0	0	0	0	0	0	0	5	3	1	0	3	0	0	0	0	0	0	0	0	3	0	0	3	1	3	1	0	0	0	2	2	3	0	0	0	0	3	0	0	3	2	0	0	0	3	0
Colymbetes	0	1	3	1	0	1	0	0	0	0	0	0	0	0	5	3	1	0	2	0	0	2	0	0	0	1	0	3	0	0	2	1	3	1	0	0	0	3	2	3	0	0	0	0	3	0	0	3	2	0	0	1	3	0
Meladema	0	1	3	0	2	0	0	0	0	0	1	2	0	0	3	3	0	0	3	0	0	0	0	3	1	1	0	2	0	0	1	0	3	1	0	0	1	3	0	3	0	0	0	0	3	0	1	3	0	0	0	1	3	0
Eretes	0	0	2	0	4	0	0	0	0	0	0	0	0	0	5	3	0	0	0	0	0	3	0	0	0	0	3	1	0	0	3	3	3	0	0	0	0	1	3	3	1	0	0	1	3	0	0	1	3	2	0	0	3	1
Hydaticus	0	0	3	3	0	1	0	0	0	0	0	0	0	0	5	0	3	0	2	2	0	0	0	0	0	0	0	3	0	0	3	1	3	0	0	0	0	3	1	3	0	0	0	0	3	0	0	3	1	0	0	1	3	0
Graphoderus	0	0	3	3	0	1	0	0	0	0	0	0	0	0	5	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	3	1	3	0	0	0	0	3	1	3	0	0	0	0	3	0	0	3	1	0	0	3	1	0
Acilius	0	0	3	3	0	1	0	0	0	0	0	0	0	0	5	0	3	0	3	0	0	0	0	0	0	0	0	3	0	0	3	1	3	0	0	0	0	3	1	3	0	0	0	0	3	0	0	3	1	0	0	3	1	0
Dytiscus	1	1	2	1	0	2	0	0	1	1	1	0	0	0	2	3	1	1	3	0	1	0	0	0	1	1	0	3	0	0	3	1	2	2	0	0	0	3	2	3	0	0	0	0	3	0	1	2	3	0	0	3	0	0
Cybister	0	0	3	3	0	1	0	0	0	0	0	0	0	0	5	3	1	0	3	0	0	0	0	0	0	0	0	3	0	0	3	2	3	0	0	0	0	1	3	3	0	0	0	0	3	0	0	1	3	0	0	3	0	0
Helophorus	0	1	2	3	2	1	0	0	1	1	1	0	0	0	3	2	2	1	3	0	1	0	0	0	0	0	0	1	3	0	3	1	3	1	0	0	1	3	1	3	1	1	1	0	3	0	1	3	2	0	1	1	3	1
Hydrochus	0	1	2	3	0	0	0	0	2	2	2	0	0	0	3	1	3	1	1	1	1	0	2	0	0	0	0	2	3	0	3	1	2	3	0	0	1	3	0	3	0	0	1	0	3	0	3	2	0	0	0	3	2	0
Berosus	0	1	3	3	1	0	0	0	0	0	0	1	1	1	3	3	0	0	3	1	1	0	0	0	0	0	1	3	3	0	3	1	3	1	0	0	0	1	3	2	3	1	0	0	3	0	0	1	3	0	0	0	3	1
Hemisphaera	0	0	3	1	1	0	0	0	0	3	3	3	0	0	1	3	1	0	0	3	0	0	0	0	1	3	0	1	0	0	2	0	1	3	0	0	1	3	1	3	0	0	0	0	3	0	3	0	0	0	0	3	0	0
Chaetarthria	0	0	3	3	0	0	0	0	0	3	3	3	0	0	1	2	3	0	3	0	0	0	0	0	1	3	0	2	1	0	2	1	1	3	0	0	1	3	2	3	1	0	0	0	3	0	1	3	2	0	0	3	1	0
Paracymus	0	0	4	1	0	0	0	0	0	0	0	0	0	1	4	3	1	1	3	0	0	0	0	0	0	2	1	3	1	0	1	1	3	1	0	0	0	2	1	2	1	1	0	0	3	0	3	1	1	0	0	2	3	1
Anacaena	0	2	3	3	0	0	0	0	2	3	2	1	0	0	3	3	1	0	3	1	0	0	0	0	0	2	0	3	3	0	3	1	3	2	0	0	2	3	1	3	1	0	0	0	3	0	1	2	1	0	0	1	2	0
Laccobius	0	1	3	2	0	0	0	0	2	3	2	1	0	0	3	3	1	0	3	0	1	1	0	0	0	1	3	2	1	0	2	1	2	1	1	0	1	3	1	3	1	0	0	1	3	0	2	3	1	0	0	2	3	1
Helochares	0	1	3	1	1	1	0	0	0	1	1	1	3	1	3	3	1	0	2	2	0	0	0	0	0	1	3	3	1	0	2	1	3	1	0	0	0	1	3	3	1	0	0	2	2	0	0	2	3	0	0	1	3	1
Enochrus	0	1	3	1	1	1	0	0	0	1	1	2	1	1	3	3	1	0	3	1	0	1	0	0	0	1	3	3	1	0	3	2	3	1	1	0	0	3	1	3	2	1	0	1	3	0	1	3	2	0	0	1	3	1
Hydrobius	0	1	3	1	0	0	0	0	0	0	2	2	0	0	3	3	1	0	3	0	0	0	0	0	0	1	3	3	1	0	2	1	3	1	0	0	0	3	1	3	0	0	0	0	3	0	0	3	1	0	0	0	3	0
Limnoxenus	0	1	3	0	0	0	0	0	0	0	2	1	0	0	3	3	1	0	3	0	0	0	0	0	0	1	3	3	1	0	2	1	3	1	0	0	0	3	1	3	0	0	0	0	3	0	0	3	1	0	0	0	3	0
Hydrochara	0	1	3	1	0	0	0	0	0	0	1	2	0	0	3	3	1	0	3	0	0	0	0	0	0	1	3	3	1	0	2	1	3	1	0	0	0	3	2	3	0	0	0	0	3	0	0	3	1	0	0	0	3	0
Hydrophilus	0	2	3	0	0	0	0	0	0	0	2	2	2	0	3	3	1	0	3	0	0	0	0	0	0	1	3	3	1	0	2	1	3	1	0	0	0	3	2	3	1	0	0	0	3	0	0	3	1	0	0	0	3	0
Coelostoma	0	2	2	1	0	0	0	0	0	0	2	2	2	0	3	2	2	0	3	0	0	0	0	0	1	3	0	0	0	0	0	0	1	3	0	0	0	3	1	3	1	0	0	0	3	0	0	3	0	0	0	0	3	0
Hydraena	3	2	1	1	0	0	0	1	3	3	3	3	0	0	1	1	3	2	2	1	0	0	3	1	3	1	0	3	1	0	0	0	0	2	3	2	2	3	1	3	0	0	1	0	3	0	3	1	0	0	0	3	2	0
Limnebius	1	2	1	1	0	0	0	2	3	3	3	0	0	0	0	2	3	1	2	1	1	0	3	0	1	3	0	2	2	0	0	0	1	3	2	0	1	3	0	3	0	0	1	0	3	1	3	1	0	0	0	2	3	0
Aulacochthebius	0	0	3	1	0	0	0	0	0	0	1	1	1	0	3	3	1	0	3	0	0	0	0	0	0	1	2	2	2	0	2	1	1	3	0	0	0	1	3	3	1	0	0	0	3	0	1	3	0	0	0	1	3	0
Calobius	0	0	0	0	5	0	0	0	0	0	0	0	0	0	5	3	0	0	0	0	0	3	0	0	0	1	3	0	3	0	0	0	3	0	0	0	0	1	3	0	1	3	0	3	0	0	0	3	0	0	0	3	0	0
Ochthebius	0	1	2	1	1	0	0	1	2	2	2	2	0	1	3	3	1	1	2	1	2	1	3	0	1	1	2	2	2	0	1	1	1	3	0	0	0	1	3	3	2	2	0	1	3	1	2	2	1	0	0	1	3	1
Potamophilus	3	3	0	0	0	0	0	0	0	1	4	4	0	0	0	3	0	0	3	0	0	0	0	0	3	1	0	1	0	3	0	0	0	3	2	0	0	3	0	3	0	0	0	0	3	0	2	3	0	0	0	0	3	0
Dupohilus	3	2	0	0	0	0	0	1	3	3	1	0	0	0	0	2	3	1	0	3	0	0	0	0	3	1	0	2	0	0	0	0	0	3	3	1	2	3	0	3	0	0	1	0	3	0	3	0	0	0	0	3	2	0
Stenelmis	3	2	0	0	0	0	0	0	1	2	3	3	0	0	0	3	1	0	3	0	0	0	0	0	2	1	0	1	0	2	0	0	0	3	3	1	2	3	0	3	0	0	0	0	3	0	2	3	0	0	0	2	3	0

Traits	a							b								c			d					e									f				g			h			i			j					k			
Modalities	a1	a2	a3	a4	a5	a6	a7	b1	b2	b3	b4	b5	b6	b7	b8	c1	c2	c3	d1	d2	d3	d4	d5	e1	e2	e3	e4	e5	e6	e7	e8	e9	f1	f2	f3	f4	g1	g2	g3	h1	h2	h3	i1	i2	i3	j1	j2	j3	j4	j5	k1	k2	k3	k4
Elmis	3	2	0	0	0	0	0	1	3	3	3	1	0	0	0	3	1	1	3	1	0	0	0	3	3	1	0	3	0	0	0	0	0	3	3	3	3	2	0	3	0	0	1	0	3	1	3	2	0	0	1	2	3	0
Esolus	3	2	0	0	0	0	0	1	3	3	3	0	0	0	0	3	1	0	3	0	0	0	0	1	3	3	1	2	0	0	0	0	0	3	2	1	3	2	0	3	0	0	1	0	3	1	3	2	0	0	0	2	3	0
Oulimnius	2	3	0	0	0	0	0	1	3	3	3	1	0	0	0	3	1	0	1	0	0	0	2	1	3	3	1	2	0	0	0	0	1	3	2	1	3	2	0	3	0	0	0	0	3	0	1	3	0	0	0	2	3	0
Limnius	3	2	0	0	0	0	0	1	3	3	3	1	0	0	0	3	1	1	3	0	0	0	1	2	3	3	1	3	0	0	0	0	0	3	3	2	2	3	0	3	0	0	1	0	3	0	3	3	0	0	0	2	3	0
Normandia	3	2	0	0	0	0	0	1	3	3	3	1	0	0	0	3	1	0	2	2	0	0	0	3	3	1	0	2	0	0	0	0	0	3	3	3	2	3	0	3	0	0	0	0	3	0	2	3	0	0	0	1	3	0
Riolus	3	2	0	0	0	0	0	1	3	3	3	1	0	0	0	3	1	0	3	1	0	0	0	3	3	1	0	2	0	0	0	0	0	3	3	3	2	3	0	3	0	0	0	0	3	0	2	3	0	0	0	1	3	0
Dryops	0	1	2	2	0	0	0	0	0	1	1	1	0	0	3	3	1	0	3	1	0	0	0	1	2	0	0	1	1	3	3	1	2	1	1	0	0	3	2	3	1	0	0	0	3	0	0	3	2	0	0	0	3	1
Pomatinus	0	2	3	0	0	0	0	0	0	1	3	3	1	0	0	3	1	0	3	0	0	0	0	0	1	3	1	0	1	0	3	0	0	0	1	2	1	3	2	3	0	0	0	0	3	0	0	3	2	0	0	0	3	1

Chapter 4

Stictonectes abellani sp. n. (Coleoptera: Dytiscidae: Hydroporinae) from the Iberian Peninsula, with notes on the phylogeny, ecology and distribution of the Iberian species of the genus

‘Arroyo de los pescados’ stream (Parque Nacional de Cabañeros)

Author: Ecología Acuática

Introduction

The genus *Stictonectes* Brinck, 1943 consists of 12 species (including the one described here), all of which are restricted to the western Mediterranean and Macaronesian regions (Bilton 2011; Nilsson & Hájek 2013). The Iberian Peninsula harbours eight of these species, three of which are endemic. *Stictonectes epipleuricus* (Seidlitz, 1887)—mainly distributed in the Iberian Peninsula—is also recorded from the south of France and therefore cannot be considered as a true Iberian endemic. Species of the genus are rather similar externally and even the shape of the male genitalia is of little help if it is not very accurately studied—this all making a reliable identification difficult. In order to identify individual specimens it is mainly necessary to study the dorsal colour pattern, the dorsal and ventral punctation and the shape of the male parameres. In general, *Stictonectes* species have similar habitat preferences, for which reason it is common to find more than one species of this genus living together in the same locality, something that can additionally complicate their identification.

In this work we describe a new species which, surprisingly, shows a wide distribution across the south-western part of the Iberian Peninsula. It has probably remained undetected due to its external similarity to *S. optatus* (Seidlitz, 1887), which often co-occurs with the new species. In addition, we include a molecular phylogeny showing the relationships between the new species and all other members of the genus. Finally, based on known species occurrences, we estimate the environmental preferences and potential distributions of all three endemic Iberian *Stictonectes*, including *S. abellani* sp. n.

Material and methods

Specimens were studied using a Leica M165C and an Olympus SZX16 stereomicroscope. Genitalia were studied wet. Photographs of habitus and other external features were taken with a Nikon Coolpix 995 camera fitted to the Olympus stereomicroscope. Image stacks were treated using CombineZP image stacking software. The holotype and most paratypes are mounted on glue-cards with the dissected genitalia glued behind the specimens, but parts of the material stored in the "Ecología Acuática" group collection are kept in pure ethanol for eventual further studies. Abbreviations used in the description are: TL – total length from front of the head to the elytral apex; TW – maximum width of body measured at right angles to TL. Details of analyses of phylogenetic relationships and general distribution of the Iberian *Stictonectes*, as well as climatic suitability and potential distributions of the Iberian endemic *Stictonectes*, are explained in the respective sections below. The following acronyms are used in the text for collections where specimens are deposited:

CAM	Collection Andrés Mellado (Madrid, Spain).
CCREA	Collection Centro Regional de Estudios del Agua (Universidad de Castilla-La Mancha, Albacete, Spain).
CDTB	Collection David T. Bilton (Plymouth, UK).
CHF	Collection Hans Fery (Berlin, Germany); property of the NMW.
CIE	Collection Íñigo Esteban (Zaragoza, Spain).
EAM	Collection Ecología Acuática (Universidad de Murcia, Spain).
IBE	Collection Institut de Biologia Evolutiva (UPF-CSIC, Barcelona, Spain).
MNCN	Museo Nacional de Ciencias Naturales (Madrid, Spain).
NMW	Naturhistorisches Museum Wien (Austria).

Taxonomy

Stictionectes abellani Millán, Picazo & Fery sp. n.

Stictonectes optatus (Seidlitz, 1887); Guignot 1959: 420 (partim); Ribera et al. 1999: 60 (partim); Fery & Fresneda 2007: 140, 147 (partim).

Type locality: Spain, Cáceres province, ca. 15 km S Coria, ca. 39.9N 6.5W.

Type material. Holotype: ♂, "27.5.1990 (E) Cáceres, ca. 15 km S Coria, ca. 320 m, ca. 39.9N 6.5W, pond in brook, Fery leg.", "Holotype, Stictonectes abellani sp. n., Millán, Picazo & Fery det. 2013" [red, printed] (NMW). **Paratypes:** Spain: 48 ♂♂, 100 ♀♀, same data as the holotype (EAM, CHF). 3 ♂♂, 4 ♀♀ "3.7.1988 (E) Cáceres, S Coria, ca. 5 km SW Cañaveral, ca. 220 m, ca. 39.76N 6.43W, brook, Fery leg." (CHF). 2 ♂♂, "9.08.1984 (E) Cáceres, ca. 10 km N Moraleja, ca. 2 km N Perales del Puerto, ca. 390 m", "Sra de St. Olalla, affl. riv. de Acebo, small brook, Fery leg., 40.167412N 6.679499W" (CHF). 5 ♀♀, "6.9.2010, Spain, Cáceres, Serradilla, Arroyo Trasierra (Garganta Fraile). PN Monfragüe, 330 m, 39.83538N 6.10076W, Sánchez-Fernández & Abellán leg. " (EAM). 2 ♂♂, "7.9.2010, Spain, Cáceres, Embalse de Torrejón, Toril, Arroyo Gargantilla. PN Monfragüe, 250 m, 39.82727N 5.91855W, Sánchez-Fernández & Abellán leg." (EAM). 1 ♂, "7.9.2010, Spain, Cáceres, Villarreal de San Carlos, Serradilla, Arroyo de Malvecino. PN Monfragüe, 307 m, 39.8520097N 6.03968W, Sánchez-Fernández & Abellán leg." (EAM). 1 ♂, 1 ♀, "7.9.2010, Spain, Cáceres, Salto de Torrejón, Toril, Charca, arroyo de las Cansinas. PN Monfragüe, 256 m, 39.83866N 5.93890W, Sánchez-Fernández & Abellán leg." (CIE). 1 ♀, "7.9.2010, Spain, Cáceres, Villarreal de San Carlos, Serradilla, Charca, Villarreal de San Carlos, PN Monfragüe, 292 m, 39.84529N 6.02824W, Sánchez-Fernández & Abellán leg." (EAM). 3 ♂♂, "23.7.2011, Spain, Cáceres, Alía, Arroyo de la Jarigüela en Alía, 650 m, 39.48993N 5.24888W, Millán & col leg." (EAM). 2 ♀♀, "27.5.1990 (E) Ciudad Real, Montes de Toledo, W Retuerta del Bullaque, brook, ca. 750 m, ca. 39.46N 4.48W, Fery leg." (CHF). 1 ♂, "1.7.1992 (E) Ciudad Real, NW Malagón, brook, ca. 39.21N 3.89W, ca. 650 m, Fery leg." (CHF). 1 ♀, "28.10.2002, Spain, Ciudad Real, Abenójar, Río Tirteafuera, 560 m, 38.88837N 4.40569W, Moreno & col leg." (EAM). 1 ♂, "12.6.2008, Spain, Ciudad Real, Salto de Torrejón, Toril, Arroyo de las Cansinas. PN Monfragüe, 228 m, 39.84039N 5.95241W, Ribera & Abellán leg." (CDTB). 2 ♀♀, "7.7.2008, Spain, Ciudad Real, Alcoba, Arroyo de los Pescados, PN Cabañeros, 657 m, 39.32006N 4.51300W, Millán & col leg." (IBE, DNA of one female extracted, voucher number IBE-PA312). 5 ♀♀, "11.6.2009, Spain, Ciudad Real, San Lorenzo de Calatrava, Río Rigüelo, 532 m, 38.45744N 3.87100W, Moreno & Picazo leg." (IBE). 7 ♂♂, 9 ♀♀, "27.7.2012, Spain, Ciudad Real, San Lorenzo de Calatrava, Río Rigüelo, 532 m, 38.45744N 3.87100W, Picazo & Millán leg." (EAM). 1 ♂, 7 ♀♀, "8.6.2009, Spain, Ciudad Real, Villamanrrique, Río Dañador, 772 m, 38.44770N 2.99503W, Moreno & col leg." (EAM). 1 ♂, 2 ♀♀, "9.6.2009, Spain, Ciudad Real, Huertezuelas, Arroyo de la Nava del Rey, 578 m, 38.52618N 3.80816W, Moreno & Picazo leg." (2 ♀♀ EAM; 1 ♂ IBE,

DNA extracted, voucher number IBE-PA313). 1 ♀, "10.6.2009, Spain, Ciudad Real, Puerto de Niefla, Brazatortas, Arroyo de los Caballeros del Escorial, 742 m, 38.51053N 4.39842W, Moreno & Picazo leg." (EAM). 2 ♀♀, "11.6.2009, Spain, Ciudad Real, Ventillas, Fuencaliente, Arroyo de la Aliseda, 705 m, 38.48957N 4.28841W, Moreno & Picazo leg." (EAM). 3 ♂♂, 1 ♀, "27.7.2012, Spain, Ciudad Real, Ventillas, Fuencaliente, Caño de Ventillas, 685 m, 38.49660N 4.29358W, Picazo & Millán leg." (EAM). 3 ♂♂, 5 ♀♀, "4.8.2009, Spain, Ciudad Real, Ventillas, Fuencaliente, Caño de Ventillas, 685 m, 38.49660N 4.29358W, Millán & col leg." (EAM). 1 ♀, "26.5.1990 (E) Córdoba, N Villa del Río, pond in brook, ca. 38.05N 4.29W, ca. 400 m, Fery leg." (CHF). 16 ♂♂, 14 ♀♀, "16.3.1997 (E) Jaén, ca. 60 km N Andújar, ca. 38.32N 4.083W, ca. 630 m, brook, Fery leg." (CHF). Portugal: 1 ♀, "20.7.1987 (P), N Odemira, S São Luíz/Cercal, pond, 37.682N 8.656W, Fery leg." (CHF). 2 ♂♂, 2 ♀♀, "29.7.1989 (P) NE Vilanova de Milfontes, Brunheiras-Cercal, brooklet/reservoir, ca. 190 m, 37.784N 8.712W, Fery leg." (CHF). 1 ♂, 3 ♀♀, "25.5.2010, Portugal, Baixo Alentejo, Vale de Vargo, Serpa, Río Enxoé (1.2), 223 m, 37.96288N 7.38505W, A. Mellado leg." (CHF). 1 ♀, "26.5.2010, Portugal, Baixo Alentejo, Vale de Vargo, Serpa, Río Enxoé (7.3), 201 m, 37.96268N 7.39905W, A. Mellado leg." (EAM). 2 ♀♀, "26.5.2010, Portugal, Baixo Alentejo, Vale de Vargo, Serpa, Río Enxoé (6.3), 195 m, 37.99003N 7.4200973W, A. Mellado leg." (EAM). 2 ♂♂, 5 ♀♀, "26.5.2010, Portugal, Baixo Alentejo, Vale de Vargo, Serpa, Río Enxoé (2.1), 238 m, 36.16817N 7.41633W, A. Mellado leg." (CAM). 1 ♂, "27.5.2010, Portugal, Baixo Alentejo, Vale de Vargo, Serpa, Río Enxoé (7.2), 198 m, 37.98270N 7.42572W, A. Mellado leg." (MNCN). 2 ♀♀, "27.5.2010, Portugal, Baixo Alentejo, Vale de Vargo, Serpa, Río Enxoé 3, 219 m, 37.97423N 7.3920095W, A. Mellado leg." (EAM). Notes: All paratypes are provided with the respective red printed labels.

Description

The following description relates chiefly to the male holotype. Variations of characters in the paratypes are given in a separate section at the end of the description.

- Habitus: Oval in dorsal view (figure 1), broadest near middle of elytra, apex pointed; rather vaulted in lateral view. Upper surface black with brownish pronotal margin and yellowish elytral pattern; surface appearing silky matt although reticulation almost totally absent; this being due to rather dense punctation, in particular with stellate punctures (see figures 2A and 2B in Bilton 2011 for a detailed view of stellate punctures).

Figure 1 Habitus of *Stictonectes abellani* sp. n.

- Head: Mainly black; clypeus anteriorly dark brownish; anterior part of clypeus with dark brownish distinct rim, medially rim shallower (figures 2a, b). Clypeal grooves shallow; alongside inner margin of eyes with strongly impressed groove. Vertex reticulated, rest smooth. Head provided with (normal) punctures, these becoming larger and denser posteriad, particularly coarse and dense in mid of frons and in shallow clypeal grooves. On vertex punctures again smaller. Except rim and vertex entire surface between normal punctures with numerous stellate punctures. Setae absent, except very few in grooves on clypeus and alongside eyes.

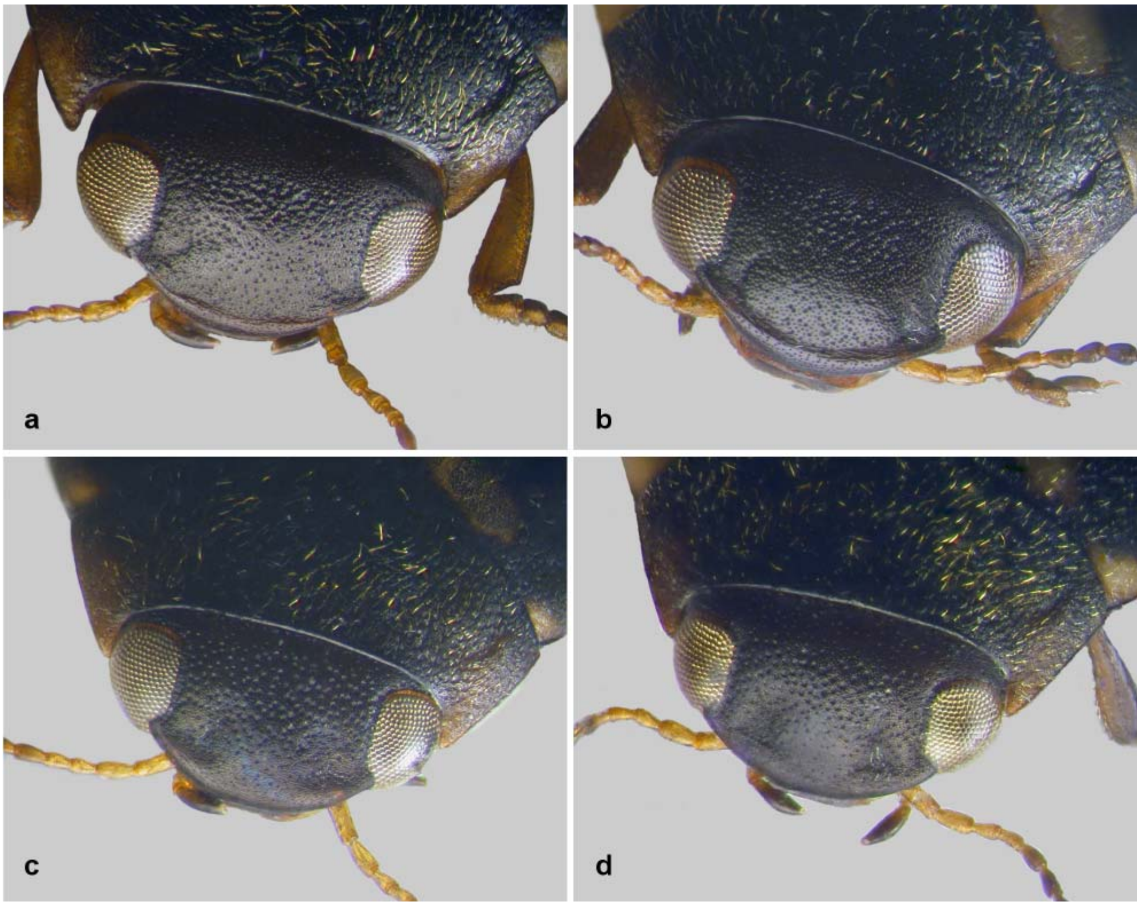

Figure 2 Details of clypeus. *Stictonectes abellani* sp. n.: (a) male, (b) female; *S. optatus*: (c) male, (d) female.

- Pronotum: black with sides between sublateral stria and pronotal margin brownish, lighter yellowish brown in anterior half (figure 1). Sides almost straight in posterior two thirds, before slightly curved inwards. Sides with narrow rim, anteriorly somewhat broader. Short sublateral striae present (figures 2a, b), but scarcely recognisable if inappropriately illuminated. Disk weakly impressed. Surface without reticulation, densely covered with normal punctures, these smaller on disk, coarser anteriad and laterally intern of striae, especially coarse before posterior margin. Between stria and margin punctation very dense and appearing rugose. Entire surface between normal punctures with numerous stellate punctures. Setation rather dense and prominent because most normal punctures provided with one seta.

- Elytra: Mostly black with rather small yellowish brown spots (figure 1). Sides in dorsal view almost evenly curved; elytra at apex not conjointly rounded, but pointed. Elytron and epipleuron separated by fine rim of equal width. Rim in lateral view moderately ascending to humeral angle and epipleuron not visible up to humeral angle. Discal and sutural puncture lines absent. Surface mostly covered with larger normal punctures (diameter similar to that of punctures on pronotal disc); most punctures "horseshoe-like" with anterior border rather sharp and posterior border weak or absent. Near elytral apex punctation denser, rather rugose. As on head and pronotum, entire surface between normal punctures with numerous stellate punctures. Setation rather dense, similar to that of pronotum.

- Ventral side: Black to large extent; general appearance matt due to mostly rugose sculpture; simple reticulation largely absent. Underside of head—including mouthparts—reddish brown, genae and gula of same colour. Without crease behind eye; wrinkles beside inner margin of eye at most very indistinctly indicated anteriorly. Surface of genae with small and flat, but distinctly vaulted cells of meshes; gula similarly structured, but cells smaller; provided with a few coarse punctures.

More lateral parts of underside of prothorax somewhat lighter reddish brown than head; prosternum strongly raised in middle, here blackish brown; between procoxae dark brown, same as prosternal process (behind procoxae). Large parts of surface covered with small protuberances; raised part of prosternum very rugosely structured; between procoxae with very distinct peak-like elevation (no transverse ridge), behind longitudinally carinate; prosternal process lanceolate, strongly carinate, sides only in anterior half flattened, without coarse punctures laterally; tip of process pointed, slightly curved upwards (if specimen studied with underside turned upwards); reaching far backwards between mesocoxae and onto anteromedial metaventral process; latter provided with shallow furrow for reception of prosternal process.

Mesepisternum and mesepimeron provided with relatively flat, but distinct protuberances. Metepisternum, metaventrite in large part, and metacoxal plates with distinct, almost conical protuberances. Metaventrite medially more shiny because protuberances reduced to almost simple reticulation. Metaventrite medially very dark brownish; metacoxal interlinear space, metacoxal processes and second to fifth abdominal ventrites medially diffusely limited brownish; hind margin of third to fifth ventrites brownish translucent. Epipleura yellowish brown. Metaventrite right and left of midline with line of some punctures, lines diverging weakly posteriad. A very few additional punctures in posterior part of metaventrite. Metacoxal plates with sparse and rather shallow, but well perceptible larger punctures. Metacoxal interlinear space smooth and shiny, provided with several punctures. Epipleuron with very small protuberances and without oblique humeral carina. Protuberances on first four abdominal ventrites somewhat unequally raised, thus, surface appearing as if provided with impressions or larger punctures. Only fifth and sixth ventrites with more distinct punctures. Anteromedial metaventral process reaching far forward and distinctly in contact with mesoventral fork. Metepisternum behind anterior margin distinctly excavated; behind with a few rather large but shallow impressions. Metaventrite in mid vaulted, especially in anterior half; in central part with distinctly impressed narrow longitudinal groove. Lateral lobe of metaventrite ("wing") relatively narrow; ratio of width of wing and width of metacoxal plate (WS:WC) ca. 1:3 (cf. figure 1 in Larson et al. 2000: 35). Metacoxal lines weakly diverging anteriad (almost parallel), reaching hind margin of metaventrite. Metacoxal processes deeply incised, interlaminary bridge totally concealed; lobes of metacoxal processes evenly rounded, outline more or less elliptical in part. Last ventrite short before hind margin strongly raised, then abruptly descending before hind margin and here provided with short but very distinct and sharp keel, running until somewhat pointed apex.

Setation on underside—except on legs and epipleuron—not very prominent and sparse, much finer than on upper surface; more or less only perceptible if adequately illuminated; present mainly on prosternum, interlinear space of metacoxa and mid of second to fourth abdominal ventrites; very few setae on sides of prosternal process; epipleuron with distinct setae; last abdominal ventrite with a few setae at apical margin and short setae on end of raised part.

- Appendages: Antennomeres 1–4 pale reddish brown, fifth darkened in distal half, 6–11 more or less uniformly dark brown. Fourth antennomere shorter than third and fifth, latter both almost equal in length, second antennomere almost as long as third and fourth together. Palpomeres reddish brown, last ones somewhat darkened distally. Pro- and mesoleg as well as entire metafemur and knee of metatibia reddish brown; else metatibia black; metatarsomeres black. First three protarsomeres somewhat broadened, mesotarsomeres less so. First pro- and mesotarsomeres provided with sucker cups (difficult to observe). Claws of pro-and mesotarsi equal in size and shape, evenly curved and not particularly prolonged.

- Aedeagus: Median lobe in ventral and lateral view as in figures 3c, d; parameres with characteristic long finger-like projection (figures 3a, b in oblique lateral and frontal views). For comparison median lobe and parameres of *S. optatus* given in figures 3e–h (specimen from near Mogón, Sierra de Cazorla, Jaén, Spain).

- Measurements: Holotype TL 3.6 mm, MW 2.0 mm; paratypes TL 3.4–3.9 mm, MW 1.8–2.1 mm. Females generally slightly larger than males. Females cannot be separated externally from males, except by less broadened pro- and mesotarsomeres and lack of sucker cups on first tarsomeres (both difficult to observe and to assess without males for comparison). Gonocoxosternum and gonocoxa are not illustrated because they are similar to those of other species of the genus and, consequently, they are not helpful for diagnostic purposes (cf. figures 6–7 in Fresneda & Fery 1990 and figure 7 in Bilton 2011).

- Variability: Generally the variation of most features is weak. However, specimens vary both within and between localities in the extent of the yellowish elytral spots (cf. spectrum of elytral pattern in Fig. 4a–d, upper row of specimens), and the brownish parts of the abdominal ventrites can be more or less extended; in some specimens the ventrites are entirely black except for the translucent hind margins.

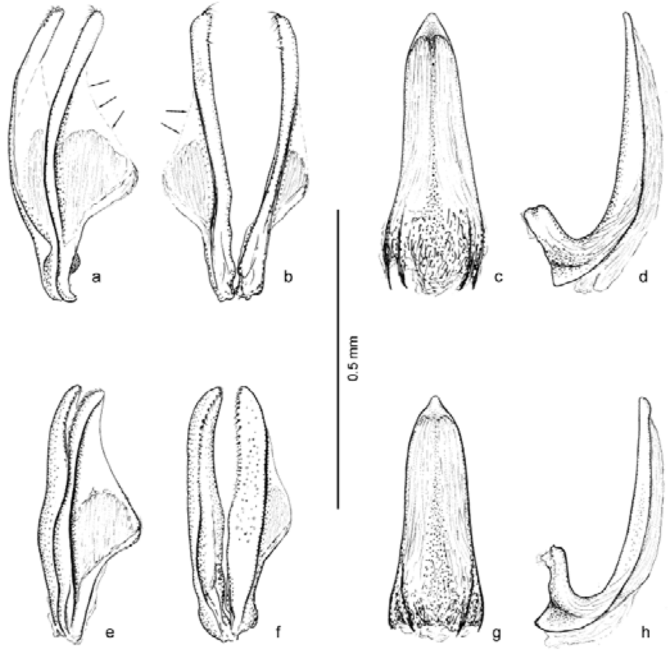

Figure 3 Genitalia of: (a-d) Stictonectes abellani sp. n.: paremeres (a) in oblique lateral and (b) in frontal view (the arrows indicate the indistinct margin of the very transparent medio-lateral part of the parameres); median lobe (c) in ventral and (d) in lateral view; (e-h) S. optatus: parameres (e) in oblique lateral and (f) in frontal view; median lobe (g) in ventral and (h) in lateral view.

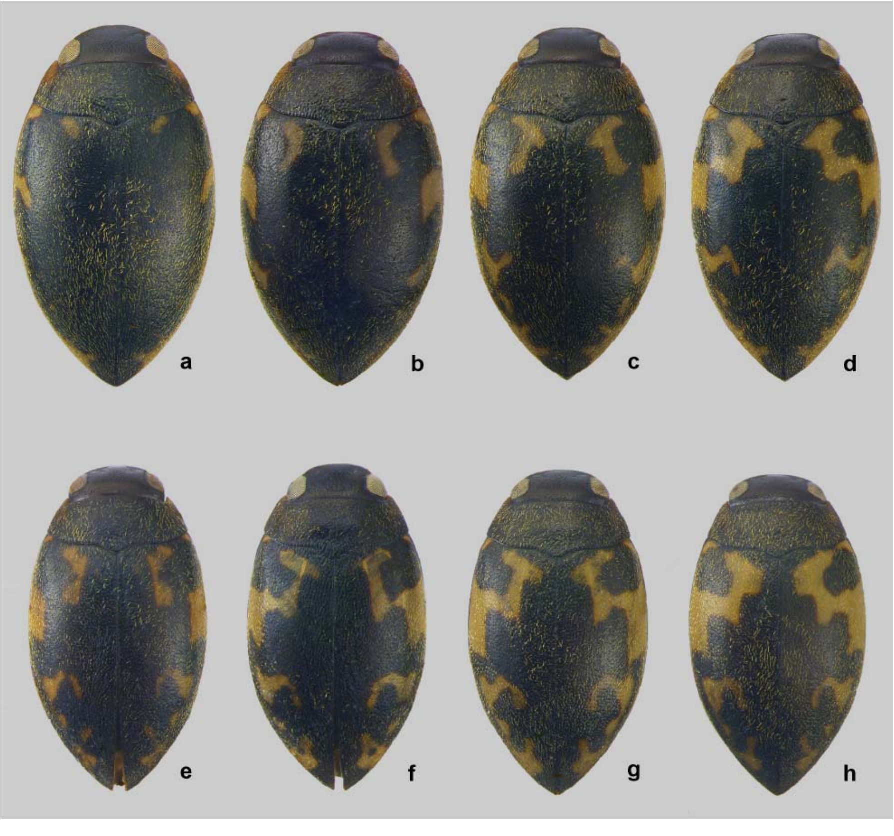

Figure 4 Colour pattern variability in (a-d) *Stictonectes abellani* sp. n. and (e-h) in *S. optatus*.

- Distribution: So far only known from central-southwest Iberia, mainly in the Guadiana basin, from the Sierra Morena range (Spain) to the Baixo Alentejo region (Beja district, Portugal).

- Etymology: Named after our friend and colleague Pedro Abellán. The specific epithet is a noun in the genitive case.

- Ecology: The new species seems to prefer depositional microhabitats in temporary siliceous streams with a substrate mainly composed of gravel and large boulders, and coarse organic matter. Figure 5 shows the Río Rigüelo near San Lorenzo de Calatrava (Ciudad Real). In some cases the species was collected in very eutrophic waters remaining in residual stream pools. The pH values in the more recently studied sites range from 7 to 8, conductivity from 30 to 900 µS/cm, nitrates from 0.01 to 0.6 mg/l and phosphates from 0 to 0.5 mg/l. The new species has been found three times together with *S. occidentalis*, and several times with *S. epipleuricus*, *S. optatus* and especially *S. lepidus*. It is remarkable that at "Vilanova de Milfontes" the new species could be found together with three other *Stictonectes*: *S. lepidus*, *S. occidentalis* and *S. optatus*. In the type locality the new species was found together with Agabus didymus (Olivier, 1795), *Bidessus coxalis* Sharp, 1882, *B. minutissimus* (Germar, 1824), *Colymbetes schildknechti* Dettner, 1983, *Deronectes opatrinus* (Germar, 1824), *Graptodytes flavipes* (Olivier, 1795), *G. ignotus* (Mulsant & Rey, 1861), *Hydroglyphus geminus* (Fabricius, 1792), *Hydroporus decipiens* Sharp, 1878, *Laccophilus hyalinus* (De Geer, 1774), *Scarodytes halensis* (Fabricius, 1787), *Stictonectes lepidus* (Olivier, 1795), *Stictotarsus duodecimpustulatus* (Fabricius, 1792) and *Yola bicarinata* (Latreille, 1804).

Phylogenetic position of *Stictonectes abellani* sp. n.

Sequences of the mitochondrial genes COI, 16SrRNA, tRNA-Leu and NAD1 extracted from all described species of *Stictonectes* were obtained from Bilton (2011) and Abellán et al. (2013). An additional specimen of *S. abellani* sp. n. was extracted (voucher numbers IBE-PA313) and the same gene fragments sequenced, following the methods described in Abellán et al. (2013) (see table 1 for the specimen data and EMBL accession numbers). The genus *Porhydrus* Guignot, 1945, sister to *Stictonectes* (Ribera 2003), was used as outgroup. Species of this genus

and of *Stictonectes* are the only Dytiscidae which possess stellate punctures on their upper and ventral surface.

Figure 5 Rigüelo stream at San Lorenzo de Calatrava, collecting site of *Stictonectes abellani* sp. n. (Spain, Ciudad Real, Sierra Morena, ca. 532 m. Photo F. Picazo).

To estimate the phylogenetic relationships of the species we conducted maximum-likelihood (ML) searches in the parallel version of RA X ML 7.0.4 (Stamatakis et al. 2008), with an estimated GTR+I+G model and partition by sequenced fragment. We chose the best of 100 replicates as our preferred topology. Node support was measured with 1,000 fast bootstrap replicates using the CAT approximation (Stamatakis et al. 2008).

Phylogenetic relationships between all known *Stictonectes* species, based on the ML algorithm, are shown in figure 6. Although some of the basal nodes within *Stictonectes* remain poorly supported, *S. abellani* sp. n. is one of the four main lineages within the genus, the other three being *S. lepidus*, *S. formosus* plus *S. escheri*, and the remaining species.

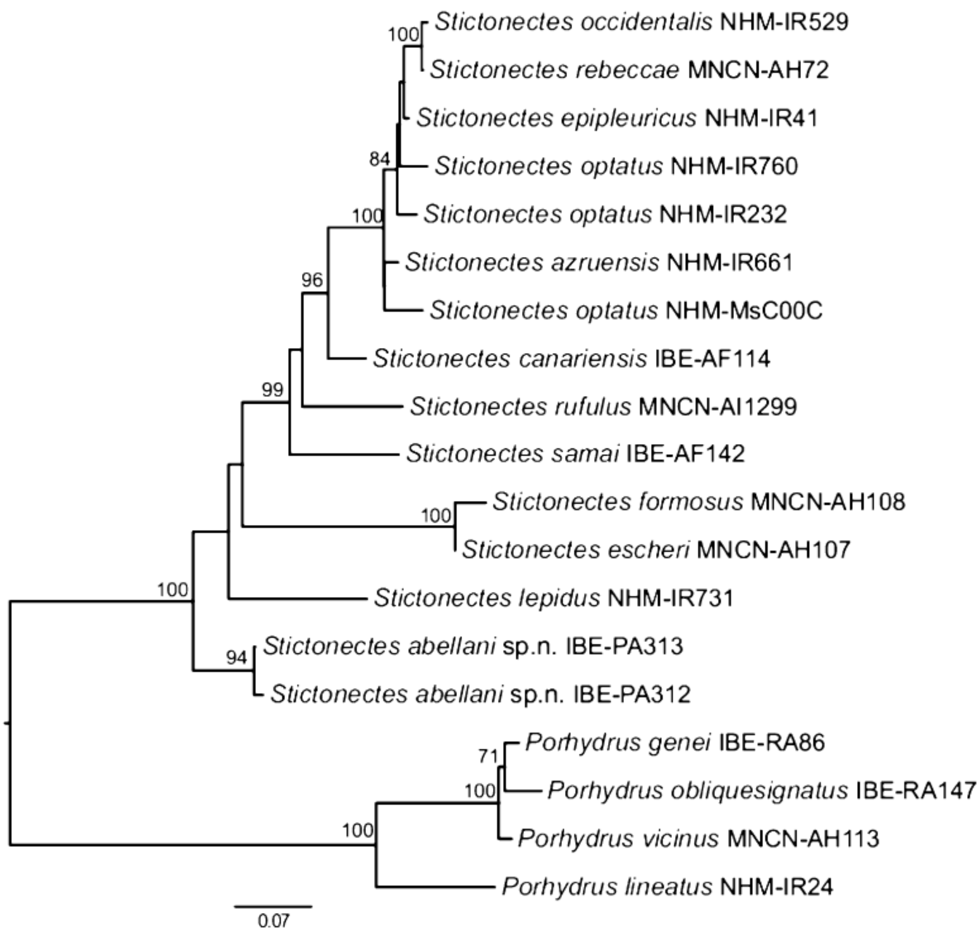

Figure 6 Phylogram of *Stictonectes* species obtained in RA x ML. Numbers on nodes indicate bootstrap support (> 70%). See table 1 for details of specimens.

Known distribution of the eight Iberian *Stictonectes*

Distributional data for Iberian *Stictonectes* species were obtained from the ESACIB database (Sánchez-Fernández et al. 2008a), which represents the most complete information available for water beetles in the Iberian Peninsula and Balearic Islands. This database includes all available geographical and biological data from the literature as well as from museum and private collections, PhD theses and other unpublished sources. For the eight species considered in the present study, ESACIB currently contains 1,385 records with associated location data at a resolution of 10 km x 10 km UTM cells (last update September 2013).

Table 1 Material used in the molecular study, with locality data, voucher and EMBL accesing numbers. See text for detailed locality of type material. (NP = National Park, col. = collaborators).

Species	DNA voucher	Country	Locality	Collector	cox1	16S (rrnL+trnL+nad1)
Porhydrus genei	IBE-RA86	Algeria	Ben-Azzouz, Garaet Aïn Nechma	S. Bouzid	HF931320	HF931543
P. lineatus	NHM-IR24	UK	Somerset Levels, Chilton Trinity	I. Ribera	AY250973	AY250933
P. obliquesignatus	IBE-RA147	Italy	Umbria, Piano di Castelluccio	M. Toledo	HF931305	–
P. vicinus	MNCN-AH113	Portugal	Setubal, Cercal	I. Ribera	HF931132	HF931350
Stictonectes abellani sp. n.	IBE-PA312	Spain	A^{yo} Pescados, Alcoba (Cabañeros NP)	Millán & col.	HF931298	HF931530
S. abellani sp. n.	IBE-PA313	Spain	Huertezuelas, A^{yo} de la Nava del Rey	Moreno & Picazo.	(still missing)	(still missing)
S. azruensis	NHM-IR661	Morocco	Azrou, Col du Zad	Pellecchia & Pizzetti	AY250979	AY250940
S. canariensis	IBE-AF114	Spain	El Risco, Barranco Güigüi grande	J. Hájek & K. Kaliková	HF931113	HF931330
S. epipleuricus	NHM-IR41	Spain	Burgos, Pineda de la Sierra, Río Arlanzon	I. Ribera	AF518285	AF518255
S. escheri	MNCN-AH107	Morocco	Asilah	I. Ribera & col.	HF931130	HF931349
S. formosus	MNCN-AH108	Morocco	Asilah	I. Ribera & col.	HF931131	–
S. lepidus	NHM-IR731	Spain	Avila, Sierra de Gredos, nr P^{to} de Menga	H. Fery	FR851845	AY250941
S. occidentalis	NHM-IR529	Portugal	Algarve	P. Aguilera	AY250980	AY250942
S. optatus	NHM-IR232	Morocco	Ait-Iftene, oued Ait-Baha	I. Ribera & A. Cieslak	FR851844	AY250945
S. optatus	NHM-IR760	Tunisia	Aïn-Draham	I. Ribera & A. Cieslak	FR851844	AY250941
S. optatus	NHM-MsC00C	France	Corsica, Porto-Vecchio, l'Ospedale	I. Ribera	AY250982	AY250944
S. rebeccae	MNCN-AH72	Portugal	Serra da Estrela, Sabugueiro	I. Ribera	FR851207	FR851208
S. rufulus	MNCN-AI1299	Italy	Sardinia, Mount Limbara	G.N. Foster	HF931179	HF931400
S. samai	IBE-AF142	Algeria	Oued Bagrat	S. Bouzid	HF931119	HF931336

Concerning the non-endemic Iberian *Stictonectes*, *S. epipleuricus*, *S. lepidus* and *S. optatus* are widespread across the Iberian Peninsula, whilst *S. escheri* (Aubé, 1838) and *S. formosus* (Aubé, 1838) have a narrow distribution in the south and south-west extremes of the region (figure 7). Of the three endemic Iberian species, *S. rebeccae* is restricted to the centre and north-west of the Iberian Peninsula, *S. occidentalis* is located in the middle and low areas of the Guadiana Basin, and *S. abellani* sp. n. is mainly placed in the western part of the Iberian "Meseta Sur". The latter two were the only endemic *Stictonectes* found to coexist (Caño de Ventillas in Ciudad Real and Vilanova de Milfontes in Baixo Alentejo).

Estimating the potential distribution of the endemic Iberian *Stictonectes*

Since it is well known that species distribution models which do not incorporate global data could misrepresent potential distributions (Sánchez-Fernández et al. 2011a), we have only considered in this work those species for which we have good faunistic knowledge on their entire distributional ranges, i.e. the three Iberian endemic species of the genus (*S. abellani* sp. n., *S. occidentalis* and *S. rebeccae*). Below we describe the data sources and methods used for the estimation of the potential distributions more in detail, before discussing the results of our investigations.

Climatic data

Current climatic data were obtained from WORLDCLIM version 1.3 (http://www.worldclim.org; Hijmans et al. 2005). These data were obtained by interpolation of climate station records from the years 1950–2000. In the present study, 19 bioclimatic variables were used as predictors: Annual Mean Temperature, Mean Diurnal Range, Isothermality, Temperature Seasonality, Maximum Temperature of Warmest Month, Minimum Temperature of Coldest Month, Temperature Annual Range, Mean Temperature of Wettest Quarter, Mean Temperature of Driest Quarter, Mean Temperature of Warmest Quarter, Mean Temperature of Coldest Quarter, Annual Precipitation, Precipitation of Wettest Month, Precipitation of Driest Month, Precipitation Seasonality (Coefficient of Variation), Precipitation of Wettest Quarter, Precipitation of Driest Quarter, Precipitation of Warmest Quarter, Precipitation of Coldest Quarter. Data concerning all of the referred environmental variables were extracted at the same resolution as biological data (10 km x 10 km UTM cells).

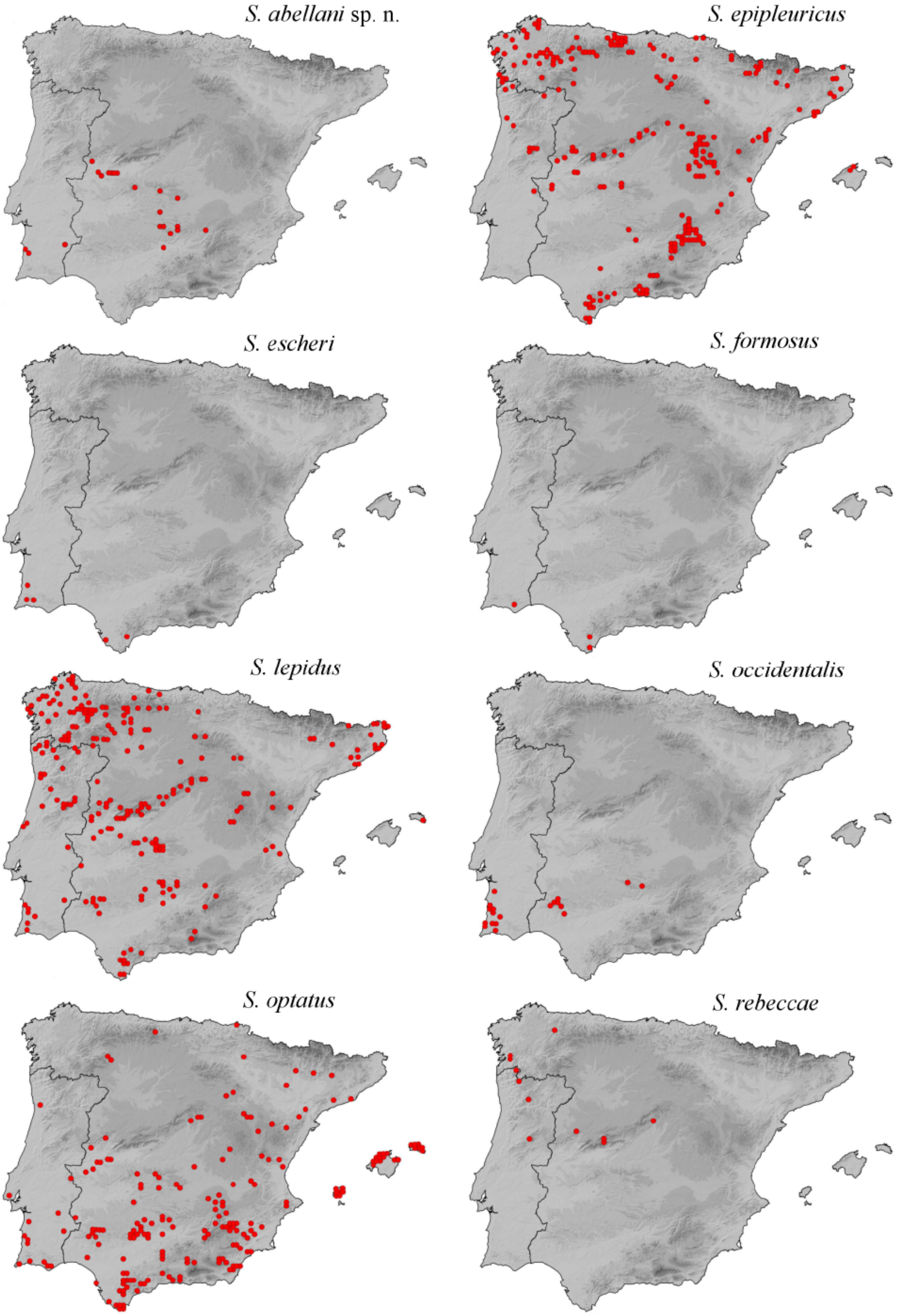

Figure 7 Known distribution of all *Stictonectes* species recorded from the Iberian Peninsula.

In order to compare the climatic conditions which each of the three endemic species prefers, we represented the location of the occurrence cells of each species across the climatic space of the Iberian Peninsula. To achieve this, values of all the 19 bioclimatic variables mentioned above were summarized using a principal component analysis (PCA) in order to obtain uncorrelated environmental factors (Varimax rotation). Values of the first two PCA factors were used to plot the occurrences of these three species in the climatic space (e.g. Sánchez-Fernández et al. 2011b).

The principal component analysis was used to explore environmental differences between the climatic conditions of the occurrences of the three species (see figure 8). Two initial factors were selected, which jointly accounted for 79.26% of the total variability and can be associated with 'aridity' and 'climatic stability' gradients, respectively. The variable F1 is positively related with Precipitation of the Driest Month and Precipitation of the Driest Quarter, and negatively with Maximum Temperature of the Warmest Month and Mean Temperature of the Warmest Quarter. The variable F2 is positively related with Temperature Seasonality and negatively with Precipitation of the Coldest Quarter.

Modelling procedure

We estimated the potential distribution of a species using an established procedure, which maximizes the capacity to represent its entire distribution by using available presence data (Jiménez- Valverde et al. 2008; 2011; Aragón et al. 2010). This method employs a multidimensional envelope procedure (MDE) to obtain a map with the potential distribution of each one of the three endemic species.

Firstly, because distributional simulations obtained by MDE procedures are highly dependent on the number of selected predictors (Beaumont et al. 2005), the minimum set of climatic variables needed to explain the occurrence of each species was estimated using ecological-niche factor analysis (ENFA; Hirzel et al. 2002; Basille et al. 2008) with the Iberian Peninsula as the background area. Factors were retained or discarded based on their eigenvalues relative to a broken-stick distribution (Hirzel et al. 2002). Climatic variables selected as predictors were those showing the highest correlation values (factor scores > 0.30) with the retained ENFA factors. The number of climatic predictors ranged from 2 to 6, depending on the species.

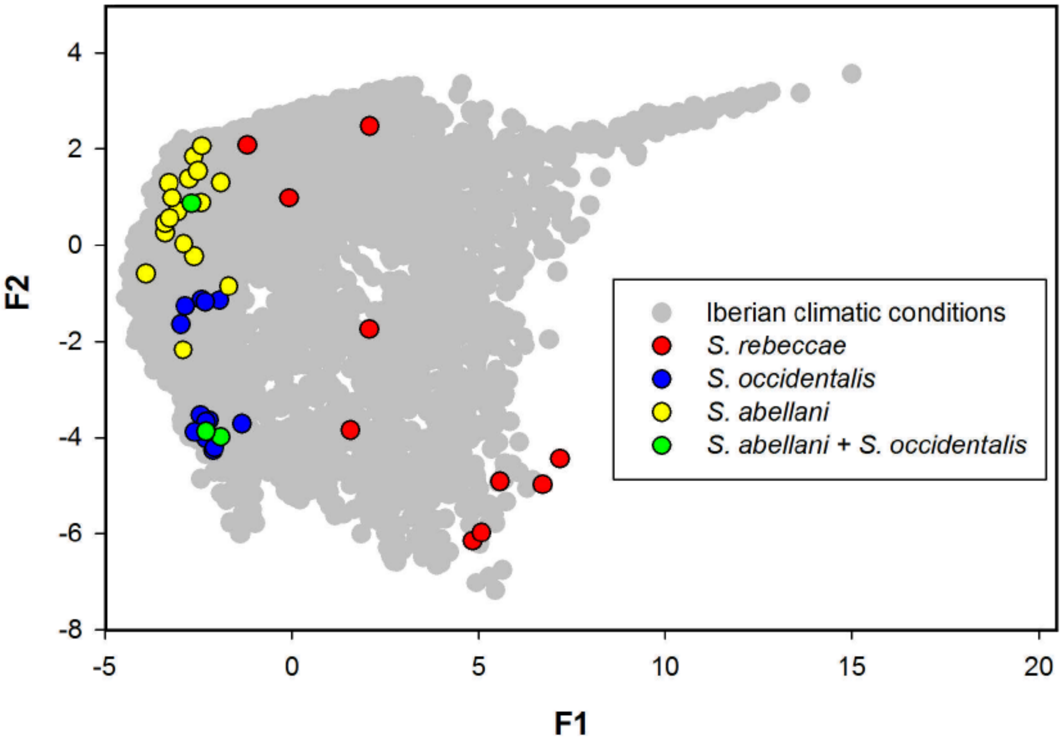

Figure 8 Known presence of the Iberian endemic *Stictonectes* species in relation to climatic conditions (circles represent 10 km x 10 km grid cells).

Maximum and minimum scores (extreme values) for all relevant climatic variables in all observed presence cells were calculated for each species, selecting as suitable grid cells all those which showed climatic values falling within the mentioned range and designating as unsuitable all cells outside it. 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.

However, the nature of the substratum influences the conductivity and pH of running waters, and therefore it may fundamentally affect the presence and abundance of aquatic species (Velasco et al. 2006). As endemic *Stictonectes* species mostly inhabit water bodies associated with siliceous substrates, we considered one geological variable; the percentage of each grid cell with an acidic surface geology (i.e. both acidic bedrock and/or surface deposits). These data were obtained from the Geological Survey of Spain (Instituto Geológico y Minero de España; IGME). We removed all areas (grid cells) from the potential climatic distribution map which contained a percentage of acid surface geology lower than the lowest percentage at which the species has been detected. We thus obtained a final binary potential distribution map showing the climatic and geologically suitable areas for each of the three endemic Iberian *Stictonectes* species.

In order to obtain continuous values of climatic suitability within the binary potential distribution, Mahalanobis distances (a measure of multidimensional non-Euclidean distance widely used in studies of spatial ecology; e.g. Farber & Kadmon 2003; Etherington et al. 2009) from each cell to the mean of the hypervolume formed by the selected variables were calculated, with reference to species presence records. Thus, the potential distribution of each of the three species is illustrated in a map of the Iberian Peninsula by dots which represent different favourability values (a measure of climatic suitability) ranging from 0 (low suitability) to 100 (high suitability) (see figure 9).

Results

S. rebeccae occupies colder and wetter areas than the other two species (see figure 8). On the other hand, *S. abellani* sp. n. and *S. occidentalis* seem to have very similar climatic preferences, with some overlapping areas. However, *S. abellani* sp. n. is more frequent in areas with higher climatic seasonality (seasonal fluctuations in temperature and/or rainfall) than *S. occidentalis* (see figure 8).

Potential distribution maps of the Iberian endemic *Stictonectes* are shown in figure 9. The most favourable areas for the new species are located in the foothills of the Montes de Toledo and the Sierra Morena, in the south of the Hercynian region. On the other hand, the most favourable areas for *S. rebeccae* are located in the Sistema Central range and northern Portuguese mountains, and for *S. occidentalis*, the Sierra de Beja and other small southern Portuguese ranges. Interestingly, we found little geographical overlap between the most potential suitable climatic conditions for these species.

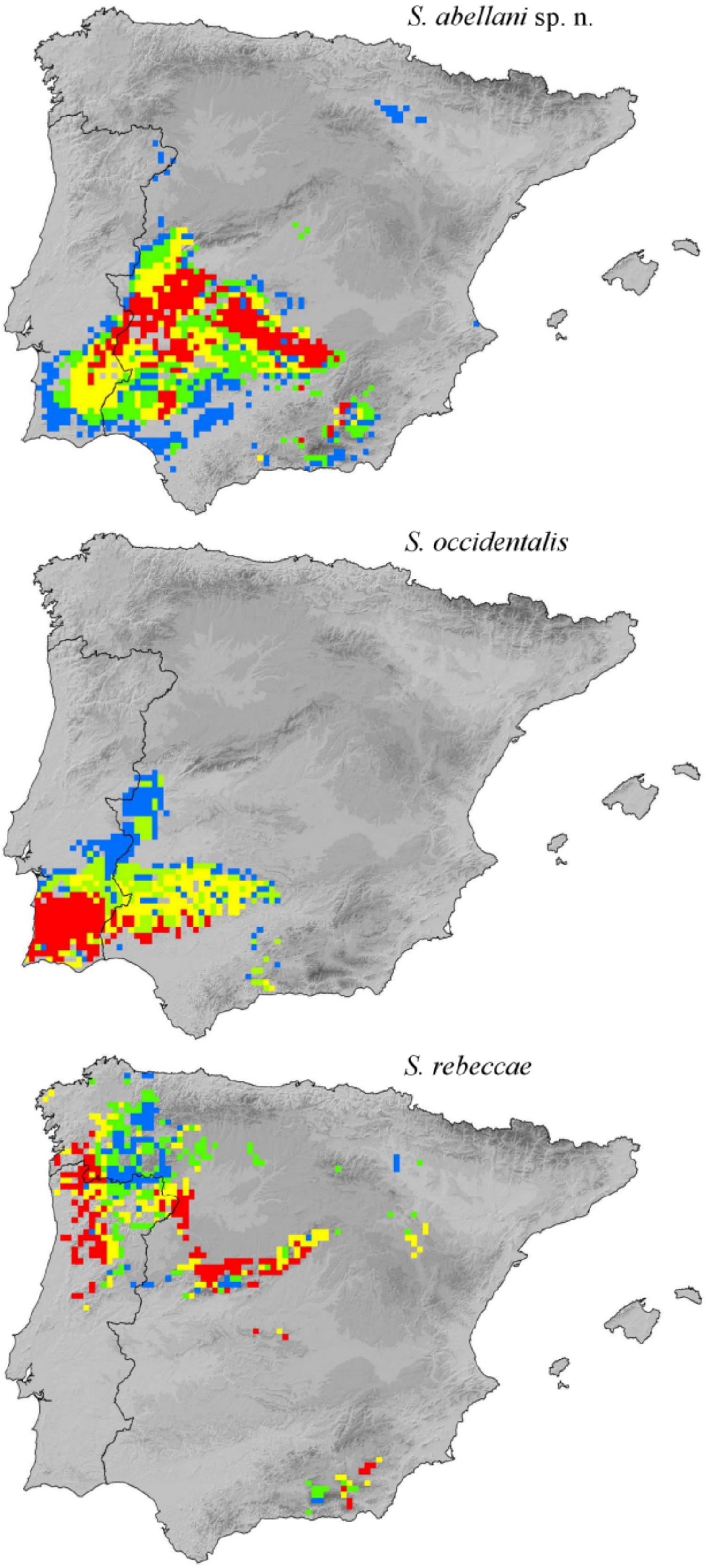

Figure 9 Estimated presences, together with potential climatic and geological favourability for Iberian endemic *Stictonectes* species. Colurs range from red (very high suitability) to blue (very low suitability).

Discussion

Despite the fact that the Dytiscidae of the Iberian Peninsula are relatively well known (Ribera, 2000; Fery & Fresneda 2007; Sánchez-Fernández et al. 2008b and b), this new species has been found to be not uncommon across a relatively wide distributional range, making it all the more surprising that this rather distinctive species had been overlooked to date. However, all *Stictonectes* species are externally rather similar and can easily be confounded on first glance if the relevant characters are not studied carefully. Even the shape of the male median lobe cannot be used for a reliable identification. Additionally, many species vary rather strongly in elytral pattern— in particular if non-European specimens are involved—and different species can show more or less the same pattern in some cases.

We refrain from constructing a key to species, because it seems to us to be practically impossible to construct one which is entirely reliable and straightforward to use. Existing keys provided by Zimmermann (1932: 89; under the generic name *Stictonotus* Zimmermann, 1932), Guignot (1947: 129), Franciscolo (1979: 421), or genitalia descriptions and illustrations of several *Stictonectes* by Grasso (1983), may be useful, but will not work with all specimens.

In the following paragraphs we provide characters which will assist in distinguishing the Iberian species. However, we are aware that in some cases a reliable determination—in particular of females—is impossible.

- *Stictonectes escheri* and *S. formosus* are rather easily to separate from all other species because of the somewhat more elongate body shape, the greater total length (which is similar to that of *S. abellani* sp. n.), the relatively shiny upper surface, and the elytral pattern (cf. figure 1182 in Franciscolo 1979). The females of *S. formosus* have a very prominent foveola (small but deep round groove) in the anterior part of each clypeal groove, whilst these foveolae are indistinct or absent in *S. escheri*. Males of *S. escheri* have the fifth to seventh antennomeres broadened.

- *Stictonectes lepidus* is externally much more similar to the other five species, nevertheless, it can be easily separated due to the characteristic elytral pattern (useless, however, in colour forms with strongly reduced black parts, e.g. ab. *oberthueri* Guignot 1931): the anterior margin of the black central transverse stripe has three forward projecting teeth, the inner one distinctly separated from the black sutural stripe (cf. figure 56 in Guignot 1947 and figure 1185 in Franciscolo 1979). The females of *S. lepidus* have each clypeal groove provide with a very prominent foveola (as in *S. formosus*).

- *Stictonectes optatus* has an elytral pattern (cf. spectrum of elytral pattern in lower row of figure 4 and figure 56 'bis' in Guignot 1947 or figure 1186 in Franciscolo 1979) in which the anterior margin of the black central transverse stripe has three forward projecting teeth, the inner one, however, is connected over its entire length with the black sutural stripe—in contrast to *S. lepidus*. Lighter forms of *S. abellani* sp. n. (figures 4c, d) have a similar elytral pattern to darker forms of *S. optatus* (figures 4e, f) and this is why both species can be confounded at first glance (and, possibly, why the new species has so far not been detected). In general, the new species is larger than *S. optatus*, although there is a small overlap in length.

Both sexes of the new species and *S. optatus*, however, can be relatively reliably separated by the shape of the anterior margin of the clypeus: this margin is vaulted in *S. abellani* sp. n. over its entire length and can be also slightly vaulted before the clypeal grooves in *S. optatus*; the hind margin of this rim is, however relatively abruptly descending to the level of the clypeus, either side of the centre, in the new species, whilst it is evenly sloping into the posterior clypeal area in *S. optatus* (cf. figures 2a–d). Males of both species can be clearly separated by the shape of the distal part of their parameres—in lateral view finger-like in the new species (figures 3a, b), more or less triangular in *S. optatus* (figures 3e, d).

- *Stictonectes epipleuricus*, *S. occidentalis* and *S. rebeccae* have an elytral pattern (cf. figure 1 in Bilton 2011) which in some individuals can be similar to that of *S. optatus* and the new species. However, the relatively large punctures on the elytra, metaventrite and metacoxae separate them clearly from these latter two species. Additionally, the shape of the distal part of the male parameres of the former three species is very characteristic (cf. figure 7 in Bilton 2011) and totally different of that of *S. optatus* and the new species. Females of *Stictonectes epipleuricus*, *S. occidentalis* and *S. rebeccae* have a foveola behind the anterior clypeal margin, a feature which is absent in *S. abellani* sp. n. and *S. optatus*.

- The new species has the middle of the second to fifth abdominal ventrites diffusely darkly brownish coloured. Brownish abdominal ventrites can also be frequently found in *S. occidentalis* and *S. epipleuricus*, but very rarely in the other members of the genus.

- Except for *S. escheri* and *S. formosus*, the new species is on average the largest of all other six Iberian species. Some populations of *S. abellani* sp. n. contain individuals of more moderate size (e.g. TL = 3.4–3.5 mm in Río Rigüelo), however, others contain considerably larger ones (until TL = 3.9 mm), resulting in an average TL of ca. 3.7 mm.

As mentioned above, the new species has been found together with *S. epipleuricus*, *S. lepidus*, *S. occidentalis* and *S. optatus*. Nevertheless, they all seem to have somewhat different habitat preferences. *S. occidentalis* appears to prefer partially similar, but more permanent and oligotrophic water bodies than *S. abellani* sp. n. The rest of the Iberian *Stictonectes* seem to prefer (1) pools in more permanent siliceous streams in mid and high altitude mountains (*S. lepidus* and *S. rebeccae* respectively), (2) pools in calcareous streams in mid and high altitude mountains (*S. optatus* and *S. epipleuricus* respectively), or (3) relatively eutrophic pools in calcareous streams in mid or low altitude (*S. escheri* and *S. formosus*).

S. abellani sp. n. occurs in areas having mild continental climate, i.e. mild and wet winters, but hot summers. Its optimum climatic conditions seem to be in Sierra Morena, whilst other northern (Monfragüe) or western populations (Río Enxoé, Portugal) seem to be more marginal. Species distribution models, like those employed in the present work, can be useful for directing new surveys in poorly recorded areas in order to confirm the occurrence of the species in places where it is likely to be found due to its established environmental suitability (Hernández et al. 2008; Sánchez-Fernández et al. 2011b).

In a conservation framework, *S. abellani* sp. n. shows (1) high phylogenetic uniqueness within the genus (sensu Abellán et al. 2013), (2) a relatively small geographical range size (only Hercynian Iberian biogeographic region), and (3) high preference for one of the most impacted habitats in the Iberian Peninsula, i.e. streams and rivers at mid and low altitudes (Sánchez-Fernández et al. 2008b). As a consequence it can be considered as a highly threatened species, and direct conservation actions would be desirable to minimize and reduce human impact on its habitats and catchments, to guarantee its long-term survival. It is also important to carefully revise existing *Stictonectes* material, especially from populations located in the Sierra Morena and adjacent areas, to better understand the distribution of the species of this genus, particularly the one described here. Nevertheless, it is worth noting that, for water beetles, the least surveyed areas in the Iberian Peninsula are located in central Spain (with the exception of the Sierra de Guadarrama and Sierra de Gredos) and south-central Portugal (Sánchez-Fernández et al. 2008a). In this sense, future sampling efforts in these areas will also help to improve our knowledge on the general distribution of the new species and other members of the genus in order to get more accurate information about their degree of vulnerability.

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Chapter 5

Habitat stability determines latitudinal gradients of diversity in Western Palaearctic water beetles

‘Laguna de Aguas Verdes’ lagoon (Parque Nacional de Sierra Nevada)

Author: Ecología Acuática

Introduction

The general trend of decreasing richness from the equator to the poles is considered the oldest known macroecological pattern (Hawkins 2001). The debate about its causes and how they interact has been intense in the last two decades (Currie 1991; Rohde 1997; Rosenzweig & Sandlin 1997; Willig et al. 2003), and multiple hypotheses have been proposed to explain the diversity latitudinal gradients (see Pianka 1966 and Willig et al. 2003 for reviews). Most prevalent among them are those related to energy and water availability (Currie 1991; Allen et al. 2002), area size (Rosenzweig 1995), biological interactions (Pianka 1966), and effective evolutionary time (Rohde 1992).

Most of the studies on diversity gradients have been based on the comparison of regional species pools (gamma diversity), with less attention to local richness (alpha diversity) or gradients in community composition shifts (beta diversity) (Hillebrand 2004; Heino 2011). While gamma diversity is a well established, non-controversial measure, beta diversity has recently become the subject of much theoretical and methodological discussions (Baselga 2012; Carvalho et al. 2012), and its use in studies of latitudinal diversity gradients has greatly increased in recent years (e.g. Hof et al. 2008; Hortal et al. 2011; Baselga et al. 2012; Boyero et al. 2012). In addition, the discrimination between its nestedness and turnover components is a useful tool to explore the role of dispersal and recolonization processes after the last glacial maximum (LGM) (Hof et al. 2008; Baselga 2010; Dobrovolski et al. 2011; Hortal et al 2011; Baselga et al. 2012; Villéger el at. 2013).

Macroecological patterns in alpha diversity have received much less attention. The few published studies usually rely on information from databases containing high taxonomic levels and narrow latitudinal extents (see some examples in Heino 2011). Latitudinal gradients for alpha diversity are normally shallower than those for gamma diversity (Hillebrand 2004), as local richness is generally considered to be the result of the combined influence of the regional species pool, local abiotic factors and biotic interactions (Cornell & Lawton 1992). Among the factors influencing alpha diversity, the most prominent is its dependence on regional richness (Cornell & Lawton 1992; see some recent examples in Heino 2011), usually studied in the context of biotic interactions and

the possibility of detecting saturation of communities (Caley & Schluter 1997). A linear relationship between alpha and gamma diversities would suggest that local communities are just a subsample of the available regional pool. On the contrary, an asymptotic curve would suggest the existence of other (abiotic and/or biotic) factors operating at local scale (Cornell & Lawton 1992).

In this study we aim to determine the role of long-term habitat stability, with the constraints it imposes on species dispersal abilities, in shaping latitudinal gamma, beta and alpha diversity gradients. We focus on inland aquatic ecosystems as they can be readily classified into two main habitat types, lotic (running) or lentic (standing), with contrasting habitat permanence over geological timescales. Standing water bodies, particularly the smaller ones, are generally short-lived and discontinuous in time and space. Once a location vanish there may be no physical connection with similar habitats, and individuals are thus forced to look for a new locality. In contrast, running water bodies are more permanent at geological scales, and remain connected to other similar systems by means of the drainage network. As a consequence of these constraints it has been hypothesized that habitat type, as a surrogate of long-term habitat persistence, is a good predictor of species dispersal ability (Ribera, 2008). The relationship between habitat stability and dispersal is asymmetric: while there may be good and poor dispersers among lotic specialists, among lentic specialists there can be only good dispersers, since poor dispersers would be already extinct. It should thus be possible to detect differences in the latitudinal diversity gradients of lentic and lotic species, as lotic species will be more dependent on historical factors (e.g. distance to glacial refugia), whereas lentic species will be closer to equilibrium with current environmental conditions (Ribera 2008; Sánchez-Fernández et al. 2012).

We tested the predictions derived from these contrasting patterns with a comprehensive dataset of aquatic Coleoptera, covering the whole latitudinal gradient of the Western Palaearctic. Aquatic Coleoptera are a well known and hyperdiverse group, with over 1000 species in the study area occurring in almost all types of inland waters (Ribera et al. 2003). Among them there are many species with restricted ranges, but also widespread species with continental scale distributions (Jäch & Balke 2008).

The occurrence of lotic and lentic species among closely related groups in multiple lineages allows to test the effect of habitat stability independently of other confounding factors, which are assumed to affect species in both habitats equally (Ribera et al. 2003). Our initial hypotheses are that:

i) The latitudinal gradient of regional (gamma) diversity should be stronger for the poor dispersers (lotic) than that for the good dispersers (lentic species), as the former are likely to be scarcely represented in recently deglaciated northern regions.

ii) The accumulation of lotic specialists in southern glacial refuge areas will result in a stronger beta-diversity gradient than in the lentic pool. We also expect a predominance of the turnover component among regions in the south, with a high presence of species evolved in situ (especially for lotic specialist), and a dominant nestedness component in the north (again, more pronounced in lotic specialist) as only the subset of strongest dispersers would have been able to colonize deglaciated areas.

iii) Local assemblages of lentic species should include a higher percentage of the regional diversity than lotic ones. In consequence, the latitudinal variation in alpha diversity should be steeper and be a closer reflect to that obtained for gamma diversity in lentic than in lotic assemblages. However, it is also more likely that lentic assemblages show signs of saturation as gamma diversity increases, resulting in the loss of the correlation between the latitudinal trends of both metrics.

Material and methods

Regional inventories of species and regionalization

We compiled a dataset of water beetles based on published Palaearctic catalogues (Löbl & Smetana 2003; 2004; 2006), which provide species distributions by administrative-political entities. Whenever possible we updated and completed these distributions at finer geographical scales based on published and unpublished data. We also compiled data from some neighbouring areas used in the iterative process of establishing the regional species lists and the biogeographic regions (see appendixes S1 and S2 for details). All species of "true aquatic beetles" (Jäch & Balke 2008) belonging to families Gyrinidae, Haliplidae, Noteridae, Hygrobiidae, Dytiscidae, Helophoridae, Hydrochidae, Hydrophilidae, Hydraenidae, Elmidae and Dryopidae, were included in the database, with details on their distribution in the regions studied. We assigned each species to one main habitat category (lotic, lentic or generalist) based on literature (Ribera et al. 2003) and our own observations (see appendix S1 for details). For each region we obtained the total number of species, the number of lotic and lentic species, and the percentage of both lotic and lentic specialist above each total regional pool (table 1).

The Western Palaearctic approximately comprises Europe, North Africa, northern and central areas of the Arabian Peninsula and part of temperate Asia until the Ural Mountains. It is well delimited by oceans to the west and the north and the Sahara desert to the south, but it is relatively open to the east due to the lack of strong physical barriers, not being possible to establish a clear natural frontier between the western and eastern Palaearctic regions (Masseti & Bruner 2008). We divided the whole latitudinal gradient, which spans from approximately 27º N to 70º N, in ten biogeographic regions: Northern Europe, Southern Sweden, Northern Germany-Denmark, Southern Germany, French Massif Central, Pyrenean, Hercynian Iberia, Southeastern Iberia, Northern Morocco and Southern Morocco (figure 1; table 1; see appendix S2 for methodological details). Once regions were delimited, we measured their area and calculated the latitude of the centroid for each polygon using ArcGIS 9.2 software (Environmental Systems Research Institute Inc., Redlands, CA).

Local inventories of species

The initial dataset compiled richness data for 748 localities from the 10 studied regions, 391 lotic and 357 lentic. Our final selection included 250 localities (133 lotic and 117 lentic), evenly distributed across regions with the only exception of the absence of lentic sites in Southern Morocco (see the Discussion below) (table 1; figure 1). We compiled species lists for 15 lotic and 15 lentic (whenever possible) sites in each region. Only well-inventoried sites which could be clearly assigned to one main habitat category (lotic or lentic) were selected, mixed or complex sites

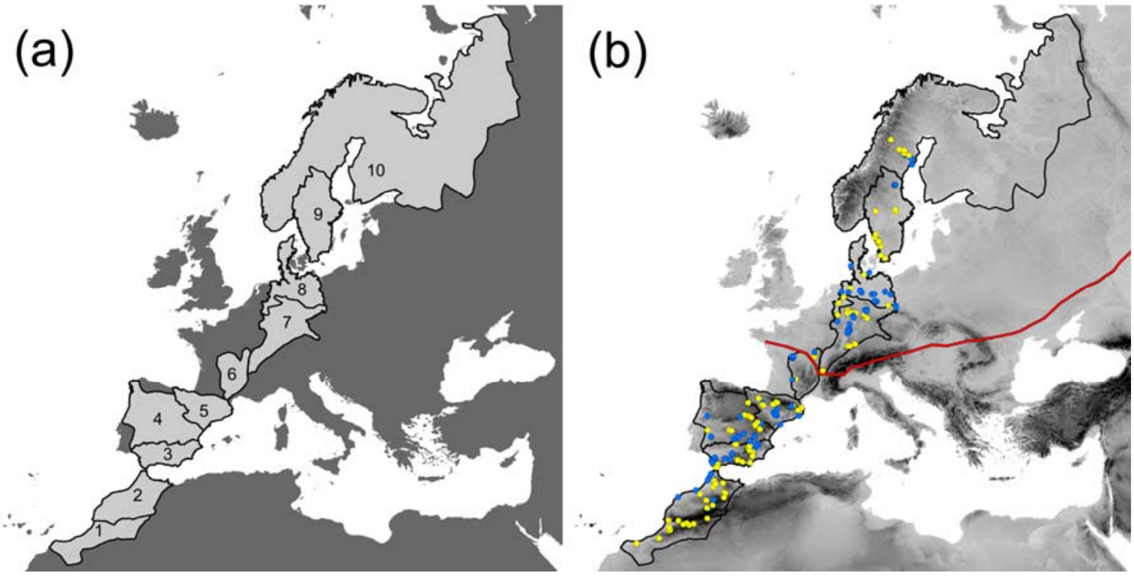

Figure 1 Study area, (a) regions established and (b) site location (lotic sites, yellow circles; lentic sites, blue circles). The 0º C isotherm during the last glacial maximum is shown (red line). Regions: 1, Southern Morocco; 2, Northern Morocco; 3, Southeastern Iberia; 4, Hercynian Iberia; 5, Pyrenean; 6, French Massif Central; 7, Southern Germany; 8, Northern Germany-Denmark; 9, Southern Sweden; 10, Northern Europe.

being discarded. In the final set of sites we only included those with the most complete inventories, but taking into account the variability exhibited by lotic and lentic habitats in each region. Thus, sites with low species richness in natural conditions (such as saline streams in Iberia and Morocco) were represented, whereas some outliers showing extraordinarily high richness were removed as their data was likely the result of pooling several localities. Coastal rock-pools was the only excluded habitat type, as these extreme systems are inhabited exclusively by a very low number of species (see appendix S1). We used unpublished data for regions in Morocco, Iberia, France and Germany, and different published sources for regions in France and Sweden (see appendix S3 for details).

Data analyses

We considered gamma and alpha diversity as the regional and local richness respectively. Beta diversity and its turnover and nestedness components were calculated as the pairwise value average between each region and their closest northern and southern neighbour regions following the methodology proposed by Baselga (2010). For each dataset (total, lotic and lentic pools of species), three different dissimilarity matrices were computed as follows: (1) total pairwise beta diversity, equal to the Sørensen dissimilarity between two regional pools (ßsor); (2) species turnover, measured using the Simpson dissimilarity index (ßsim); and (3) species nestedness-resultant dissimilarity (ßnes), which is the result of subtracting the turnover effect from the total beta diversity (ßnes = ßsor - ßsim). We also calculated the nestedness/total beta diversity ratio to assess the contribution of the nestedness component to beta diversity. It provides an intuitive measure of turnover, equal to 1 – (nestedness/beta diversity).

Table 1 Regions studied and main statistics. * Percentage above the total regional pool.

Region	Acronym	Surface (km2)	Latitude (centroid)	N sites (lotic/lentic)	Total richness	Lotic richness*	Lentic richness*	N endemics (lotic/lentic)
Northern Europe	NEU	2,227,231	64.6º N	5/15	278	34 (12)	187 (67)	0/2
Southern Sweden	SSW	256,404	59.7º N	15/15	262	27 (10)	181 (69)	0/0
Northern Germany-Denmark	NGD	172,054	53.5º N	15/15	297	47 (16)	183 (62)	0/0
Southern Germany	SGE	226,614	49.6º N	15/15	317	77 (24)	160 (50)	0/0
French Massif Central	FCR	88,508	45.3º N	11/10	291	80 (27)	127 (44)	1/0
Pyrenean-Ebro Valley	PEV	128,394	42.2º N	15/10	321	122 (38)	113 (35)	12/0
Hercynian Iberia	HEI	295,220	40.5º N	15/15	380	175 (46)	109 (29)	21/1
Southeastern Iberia	SEI	115,795	37.7º N	15/15	319	144 (45)	94 (29)	13/1
Northern Morocco	NMO	193,980	33.0º N	15/7	269	111 (41)	88 (33)	19/3
Southern Morocco	SMO	166,638	29.2º N	12/0	106	47 (44)	26 (24)	3/0

We first studied the relationship between gamma diversity and area (measured as the natural logarithm of the total surface) by means of general linear models (GLM). Similarly, the relationship between latitude and both gamma diversity, the percentage of exclusive lotic *vs*. lentic species in each region, beta diversity (in all its components) and alpha diversity was assessed by using GLM. In all the cases we assumed a Poisson error distribution of the dependent variable. We assessed the significance of linear and quadratic coefficients for every diversity measure by means of a forward stepwise procedure, finally selecting the model that minimized the Akaike information criterion (AIC) after testing for overdispersion. All statistical analyses were carried out using the statistical computing software R (R Development Core Team, 2012) and the libraries betapart (Baselga & Orme 2012), ecodist (Lichstein 2007) and vegan (Oksanen et al. 2015).

Results

Gamma diversity

The final dataset included information on habitat preference and their distribution across the ten established biogeographic regions for a total of 755 species, 309 lotic, 300 lentic and 146 generalists (see appendix S1 for details). The richest region was Hercynian Iberia and the poorest Southern Morocco, with 308 and 106 species respectively (table 1). By habitat, the richest region in lotic species was again Hercynian Iberia (175) and the poorest Southern Sweden (27). This gradient was reversed for lentic species, with a maximum in Northern Europe and a minimum in Southern Morocco (187 and 26 species respectively) (table 1).

Total gamma diversity was significantly related to latitude but not to area, this relationship being stronger for lentic than for lotic species (table 2). Our results showed a clear latitudinal gradient with peak values at intermediate latitudes: just south of the Ebro Valley-Pyrenees barrier (EV-P barrier hereafter) in the case of both total and lotic species, and just north of the 0 ºC isotherm band during the last glacial maximum (0º-LGM band hereafter) in the case of lentic species (figure 2a-c). Differences between the lotic and lentic gamma diversity were remarkably larger north of the 0º-LGM band.

Table 2 Simple GLM results: Gamma, alpha and beta diversity (including turnover, nestedness and ratio nestedness/beta-diversity) vs Latitude. Only best models are shown (linear, linear+quadratic or quadratic): lowest AIC. ED: explained deviance of the GLM. NA: the term does not exist for this model. Signification level: * = p<0.05; ** = p<0.01; *** = p<0.001; n.s.= non significant.

	Intercept	**Linear coefficient**	**Quadratic coefficient**	**ED**
Regional richness vs. Area				
Total pool	5.6**	n.s.	NA	0.0
Lotic pool	n.s.	n.s.	n.s.	15.4
Lentic pool	n.s.	n.s.	NA	16.5
Regional richness vs. Latitude				
Total pool	n.s.	0.2*	0.0*	53.3
Lotic pool	n.s.	0.3*	0.0*	70.6
Lentic pool	n.s.	0.2**	0.0*	90.9
% Specialist *vs.* Latitude				
Lotic	83.1***	-1.2***	NA	86.0
Lentic	-19.4*	1.4***	NA	90.4
Beta diversity *vs.* Latitude				
Total pool	1.3**	0.0*	0.0*	88.3
Lotic pool	1.2**	0.0*	0.0*	86.3
Lentic pool	0.7***	-0.0**	NA	65.1
Turnover				
Total pool	n.s.	n.s.	n.s.	46.3
Lotic pool	0.4***	0.0*	NA	53.2
Lentic pool	0.2**	NA	n.s.	12.6
Nestedness				
Total pool	1.6***	-0.1**	0.0**	90.3
Lotic pool	n.s.	n.s.	n.s.	30.1
Lentic pool	1.9**	-0.1**	0.0*	81.1
Ratio Nestedness/Total beta diversity *vs.* Latitude				
Total pool	3.0**	-0.1**	0.0**	83.5
Lotic pool	n.s.	n.s.	n.s.	11.2
Lentic pool	1.0**	0.0*	NA	44.7
Local richness *vs.* Latitude				
Total pool	3.3***	NA	0.0***	6.6
Lotic pool	n.s.	0.2***	0.0***	42.1
Lentic pool	n.s.	0.2**	0.0**	26.1
% Local richness over Regional richness *vs.* Latitude				
Lotic pool	57.6***	-2.0***	0.0**	9.4
Lentic pool	n.s.	n.s.	n.s.	0.4
Local richness *vs.* regional richness				
Lotic pool	1.3***	0.0***	NA	49.6
Lentic pool	1.5***	0.1***	NA	34.4

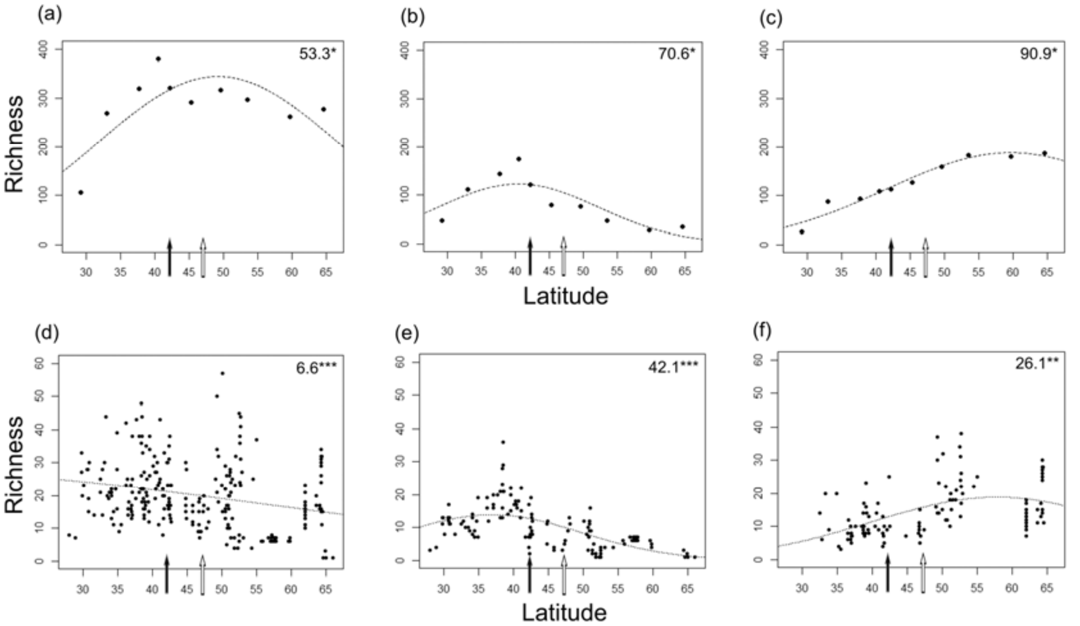

Figure 2 Regional (up) and local (down) richness *vs.* latitude for the whole dataset (left), the lotic pool (centre) and the lentic pool (right). ED: explained deviance of the GLM. * $p<0.05$; ** $p<0.01$; *** $p<0.001$. Black and white arrows represent the latitude where the Ebro valley-Pyrenees barrier (EV-P) and the 0º C isotherm during the last glacial maximum (0º LGM) are located, respectively.

The percentage of lotic and lentic specialist in every region showed a clear and opposite latitudinal gradient, with both trends crossing around the EV-P barrier (figure 3). Lotic specialist predominated in the south (with a maximum of 46% in Hercynian Iberia), and lentic in the north (up to 69% of the regional pool in Southern Sweden). The largest differences between the two groups were found in the north part of the gradient (figure 3; table 1).

Beta diversity and its partitioning in turnover and nestedness components

Total beta diversity significantly decreased from lower to higher latitudes, more pronouncedly for the lentic than for the lotic pool (table 2; figure 4a-c). For the whole dataset most of the beta diversity was found associated with the turnover component, with nestedness predominating only in both Moroccan regions. We found no significant relationship between latitude and turnover both for the whole dataset and the lentic pool, with very uniform values except for a strong peak at mid latitudes (Pyrenean and French Massif Central regions, figure 4d and f). However, the turnover of lotic species decreased linearly as latitude increased (figure 4e). We also found a clear relationship between nestedness and latitude for the whole dataset and the lentic pool (figure 4g and 4i), but not for the lotic species pool (figure 4h). Nestedness was in general low, except for the southernmost regions (Morocco) (figure 4g and 4i).

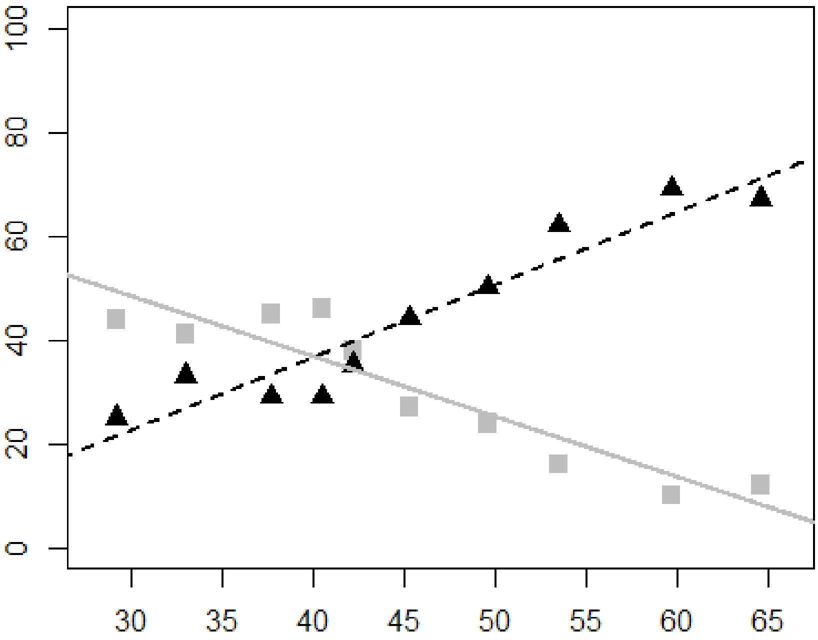

Figure 3 Percentage of specialist in regional faunas (lotic: squares; lentic: triangles) *vs*. latitude. ED: explained deviance of the GLM. * p<0.05; ** p<0.01; *** p<0.001. Black and white arrows represent the latitude where the Ebro valley-Pyrenees barrier (EV-P) and the 0º C isotherm during the last glacial maximum (0º LGM) are located, respectively.

Alfa diversity and its relationship with gamma diversity

A total of 514 species, 193 lotic, 208 lentic and 111 generalists, were recorded from the 250 sites selected. Although there was a large variation in the number of species per site, the global trend displayed a weak but significant decrease with latitude (table 2; figure 2d). When separated by habitat, lotic species richness peaked south beyond the EV-P barrier, with a gentle decrease towards the south and a more pronounced one towards the north (figure 2e). Lentic species had a similar but opposed pattern (figure 2f). Local richness of lotic and lentic species thus closely followed the general trend observed for their respective regional richness.

The percentage of the lotic regional pool present in lotic sites was slightly higher in both extremes of the latitudinal gradient (figure 5a). For lentic species this percentage did not show any significant pattern (figure 5b). In both cases the relationship between local and regional richness was increasing approximately linearly, with no sign of saturation (figure 5c and d). All these relationships were significant (table 2).

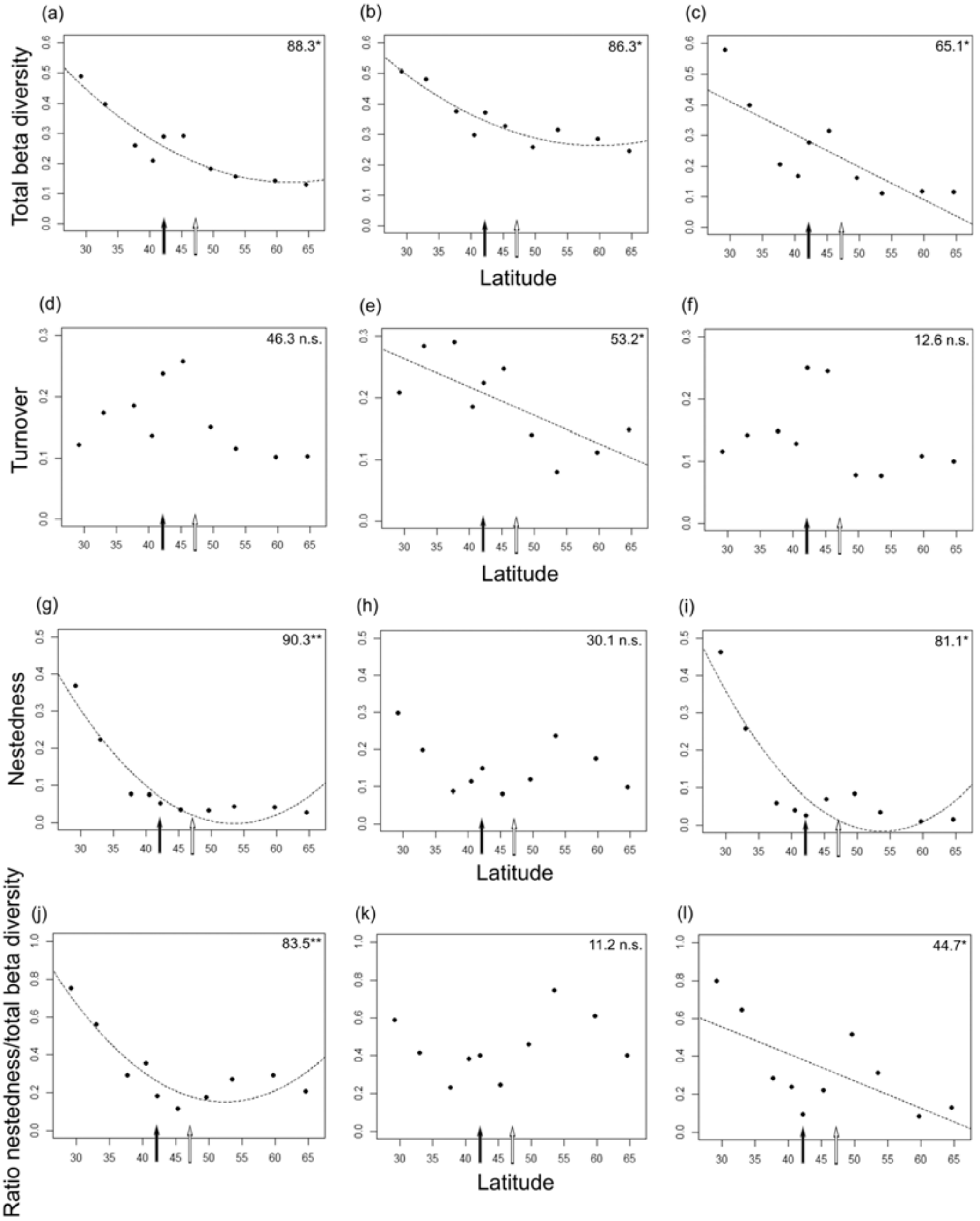

Figure 4 Total beta-diversity, turnover, nestedness and ratio nestedness/beta-diversity *vs*. latitude for the total (left), lotic (centre) and lentic (right) pools of species. ED: explained deviance of the GLM. * p<0.05; ** p<0.01; *** p<0.001. Only significant trends are shown. Black and white arrows represent the latitude where the Ebro valley-Pyrenees barrier (EV-P) and the 0º C isotherm during the last glacial maximum (0º LGM) are located, respectively.

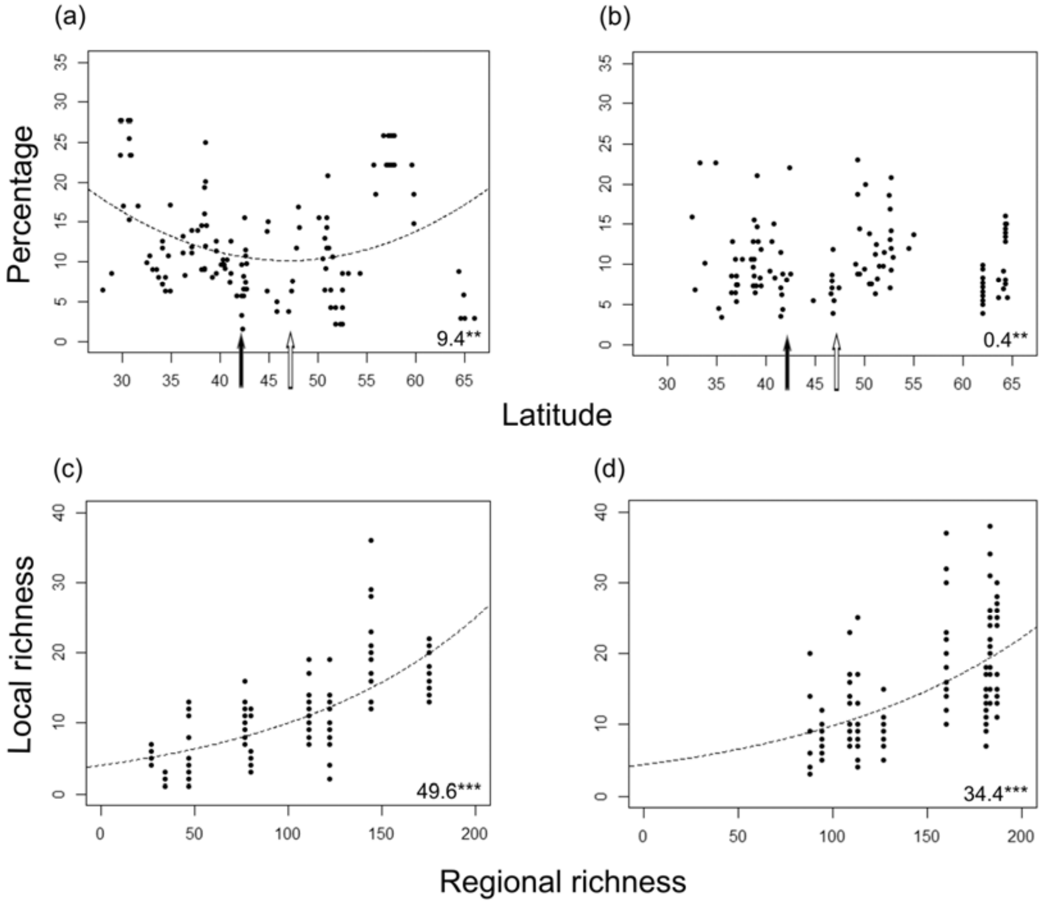

Figure 5 Contribution of local richness to regional richness (up) and relationship between local and regional richness (down) for the lotic pool (left) and the lentic pool (right). ED: explained deviance of the GLM. * $p<0.05$; ** $p<0.01$; *** $p<0.001$. Black and white arrows represent the latitude where the Ebro valley-Pyrenees barrier (EV-P) and the 0º C isotherm during the last glacial maximum (0º LGM) are located, respectively.

Discussion

Gamma diversity

The gamma diversity of the total species pool followed the general pattern of decreasing richness from the equator to the poles, except for the south extreme of the gradient likely due to the severe environmental filter imposed by the proximity of the Sahara desert. This general pattern was also found for the lotic, but not the lentic species pool, which showed the opposite trend. Our results are not completely in agreement with those obtained for other groups of aquatic insects. Thus, Boyero et al. (2012) did not found any global latitudinal trend for gamma diversity of stream detritivores, i.e. for exclusively lotic taxa. Meanwhile, for all

European freshwater animals Hof et al. (2008) found a monotonic decline for total and lotic taxa and a hump-shaped trend for lentic taxa, but the gradient of their study did not span the southern part of the Palaearctic region. The higher values of lotic gamma diversity at latitudes south of the EV-P barrier (peaking in the Hercynian region of Iberia) may be explained by the high climatic stability of these areas during the Pleistocene. Hence, these areas are considered as centres of diversification, providing stable conditions over long evolutionary times and thus ample opportunities for the taxa to evolve and radiate (Pianka 1966; Ribera & Vogler 2004). This is particularly the case for lotic taxa with limited dispersal, most of them showing restricted ranges, as for instance species of the genera *Hydraena* (Trizzino et al. 2013) or *Deronectes* (Ribera & Vogler 2004).

The abrupt decrease of gamma diversity towards the southern extreme of the gradient can be associated with two different factors. First, a pure edge effect due to the south boundary of the Palaearctic region (the Sahara desert), in agreement with the mid-domain effect (Colwell & Lees 2000). But also to the fact that it is not a hard boundary but a gradient extending over a large territory that imposes stringent climatic conditions, likely limiting the number of species able to stand them.

In the regions north of the Pyrenees lotic gamma diversity decreased sharply. The lotic fauna of these regions is mainly composed by a few good disperser species, able to reach more or less far north depending on their dispersal abilities (Hewitt 1999). During the ice shelf retreat after the LGM there must have been an ephemeral (at geological time scale) but very extended front of available lotic habitats as ice melted, which may have allowed the best lotic dispersers to recolonize Central and North Europe from their southern glacial refuges. Displacement towards the north from southern peninsulas would have been limited due to the presence of important geographic barriers with West-East orientation, in our case the Pyrenean mountains but also the arid area of the Ebro Valley, something that has frequently been overlooked. Longitudinal movements in the south part of the gradient would have been limited by the Mediterranean Sea, confining species to the southern peninsulas. After this post-glacial habitat window was closed, the dispersal from eastern and southern glacial refuges could have

been more difficult due to the decreased availability of suitable habitat, increasing the isolation among populations due to habitat discontinuity or fragmentation (Ribera et al. 2011).

The scarcity of lentic species in the extreme south of the latitudinal gradient can be clearly linked to lack of available habitat. The few lentic habitats in South Morocco are normally linked to permanent ground water or springs (considered to be lotic under our criteria), whereas isolated lentic water bodies are usually so ephemeral that they can be only colonized by a few specialised opportunistic species. However, and with the exclusion of the extreme south, there is no evidence of differences in habitat availability for lotic or lentic species across Europe (Dehling et al. 2010). The fact that many lentic species have northern distributions with their southern range limit around the Pyrenees must then be explained by the existence of some biogeographic barrier, preventing the spread within the Iberian Peninsula of species from glacial refugia in Eastern Europe and Asia, as it has been demonstrated for other groups (e.g. Bilton et al. 1998). More than the Pyrenees, such barrier could be the arid zone of the central Ebro Valley, with very few and mostly highly saline water bodies. The special role of the arid central Ebro Valley as a barrier isolating the Iberian Peninsula would be supported by the fact that in the Italian Peninsula, which lacks arid areas in the north but has an important mountainous barrier with West-East orientation (the Alps), many of the typical European lentic species missing from Iberia can be found through the Apennines up to Sicily (Löbl & Smetana 2003).

The higher richness of lentic species in the north extreme of the gradient could be the result of recolonization during the current interglacial period of species from multiple glacial refuges, likely in Eastern Europe and Asia (it should be remembered here that, geographically, Western Europe is basically a peninsula of mainland Eurasia). The absence of important biogeographic barriers across Central Europe unquestionably played an important role in this process. Such fact has been demonstrated for a number of taxa belonging to different groups of organisms, as in the case of the key role played by the Ponto-Caspian glacial refuge as a source for the postglacial recolonization process of European freshwater fishes (Griffiths 2006).

Beta diversity and its partitioning in the turnover and nestedness components

Confirming our expectations, beta diversity was higher in the south both for lotic and lentic species (figure 3a-c). Our results are in agreement with Hof et al. (2008), although in our case lotic species presented higher values, especially at high latitudes (north the 0º-LGM band). Surprisingly, and contrary to our predictions, the lentic pool showed a steeper gradient in beta diversity (figure 4 c). This could be due to the inclusion of the whole latitudinal gradient of the Palaearctic region, as the highest values of beta diversity were obtained for the southernmost regions in Morocco, not examined in previous studies (Hof et al. 2008; Hortal et al. 2011; Baselga et al. 2012). But it should be also noted that such studies analysed intra-, not inter-regional beta diversity, as was our case.

The analysis of the nestedness and turnover components revealed further differences between the lotic and lentic species. For the lotic pool, the significant decrease experienced by the turnover component as latitude increased is in agreement with the high proportion of endemics reported for the Moroccan (mainly in the north) and Iberian faunas (Ribera 2000; Millán et al. 2014). For the lentic pool, the importance of the nestedness component in southern regions was probably related to the loss of the less warm/arid-adapted taxa due to the strong filter imposed by the extreme climatic conditions. To interpret these differences is necessary to consider the highest values of beta diversity found in southern regions, as well as the different sizes of the regional pools (larger in the south for lotic species, and in the north for lentic). Thus, depending on the interplay of these variables the loss or replacement of species between regional faunas will result in a higher or lower beta diversity.

Despite the lack of a significant trend in the turnover of lentic species, it is remarkable the substitution of species between the Pyrenean and the French Massif Central regions. The EV-P area seems to be a clear biogeographical barrier between two different faunas. Many northern species have around this area their southern limit of their distributional ranges, and southern species their northern limit. Lentic species have normally broad range sizes (Ribera 2008), so it can be expected that the replacement of faunas would mainly occur through latitudinal bands and based on species climatic tolerances. Contrary to Hortal et al. (2011), who argued that some southern generalists could have adapted to cold conditions and subsequently colonized more northern regions, our results suggest that central and northern Europe was recolonized by cold adapted taxa arriving from continental glacial refugia in the east. The steeper climatic gradients towards the north may result in narrower faunal latitudinal bands, with a replacement of species increasingly adapted to colder conditions until the appearance of arctic specialists (such as e.g. *Agabus arcticus, A. confinis, A. elongatus, A. zetterstedti, A. serricornis, Ilybius opacus, I. picipes*, etc.).

For lotic species the observed patterns were more complex. The nestedness component was especially relevant north of the 0º-LGM band due to the absence of poor dispersers from southern glacial refugia. The small rise of turnover in the northern extreme of the gradient can be attributable to the presence of some cold adapted lotic species that have nonetheless wide geographical distributions (e.g. *Agabus discolor, A. pseudoclypealis, A. setulosus* or *A. adpressus*; Lölb & Smetana 2003), but all of them absent from the Mediterranean peninsulas. These species, probably with an origin in eastern refugia, took advantage of the post-glacial habitat window referred previously.

Alpha diversity and its relationship with gamma diversity

We found that local richness of water beetles is largely dependent on regional richness, showing no sings of saturation. However, the strong variability of alpha diversity shows that it can also be influenced to some degree by local factors. There are well preserved localities with either high or low richness within every region, demonstrating the overriding effect of local conditions over large scale factors in at least some cases (Hillebrand 2004; Heino 2011). But despite the potential influence of local factors, the overall parallelism between the latitudinal gradients of local and regional richness, both for the lotic and lentic pools, would indicate that local richness of aquatic Coleoptera greatly depends on the available regional species pool (Gaston & Blackburn 2000). This is in agreement with most of the results reported in the literature (see Hillebrand 2004 for a review), although for instance Boyero et al. (2012) found that alpha diversity of stream detritivores increased with latitude even if there was no change in gamma diversity, suggesting that in this group local factors were the dominant effect to determine alpha diversity.

Contrary to our expectations, lentic local assemblages did not contain on average a higher percentage of the regional pool than lotic ones. It could be expected that when the regional richness is low local faunas would contain most of the species of the regional pools, especially for taxa displaying strong dispersal abilities and wide ecological niches. This is the case of lotic species in the north and lentic species in the south, but we found evidence to support only the former, i.e. a slight increase of the local/regional ratio in northern lotic sites. There were no latitudinal differences in the proportion of local/regional species in the lentic sites, pointing to the limiting role of local factors such as biotic interactions (Cornell & Lawton 2000).

We found that lotic local assemblages tended to contain a slightly higher percentage of the regional pools at both extremes of the latitudinal gradient. In northern regions this may be due to both the small size of their regional pools and the wider range size of the northern lotic species (Sánchez-Fernández et al. 2012). A similar pattern was observed in the southern extreme of the gradient, in this case likely due to the high ecological instability of lotic habitats, which in this area may be more similar than lentic ones in terms of the constraints they pose on the dispersal abilities of their species.

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SUPPORTING INFORMATION: CHAPTER 5

Appendix S1: Species occurrence across the ten biogeographical regions established.

Appendix S2: Regionalization process.

Appendix S3: Local checklist compilation.

Appendix S1

All the species belonging to the *Empleurus* subgenus (Helophoridae: *Helophorus*) were not taken into account due to their mainly terrestrial habits. We dismissed 3 species for which was not possible to obtain any information about their habitat preferences (*Yola alluaudi*, *Helophorus bergrothi* and *Ochthebius maroccanus*). We also dismissed 3 species which are considered groundwater dwellers (*Graptodytes eremitus*, *Iberoporus cermenius* and *Limnius stygius*). Species which occur in sites belonging to extreme habitats such as rock-pools were also discarded because of they are species having wide range size but exclusive for such habitat type (*O. quadricollis*, *O. lejolisi* and *O. subinteger*). See table 1 for explanation of the established regions acronyms. HABITAT: habitat preferences of species (0, lotic specialist; 1, generalist; 2, lentic specialist).

FAMILY	SPECIES	HABITAT	NEU	SSW	NGD	SGE	FCR	PEV	HEI	SEI	NMO	SMO
HYDROSCAPHIDAE	*Hydroscapha complex*	0	0	0	0	0	0	0	1	1	1	0
SPHAERIUSIDAE	*Sphaerius acaroides-hispanicus*	1	1	1	1	1	1	1	0	1	1	1
GYRINADE	*Aulonogyrus concinnus*	1	0	0	1	1	0	1	1	1	1	0
	Aulonogyrus striatus	0	0	0	0	0	0	1	1	1	1	1
	Gyrinus minutus	2	1	1	1	1	1	1	1	0	0	0
	Gyrinus aeratus	1	1	1	1	0	0	0	0	0	0	0
	Gyrinus caspius	2	1	1	1	1	1	1	1	1	1	0
	Gyrinus colymbus	2	0	0	1	0	1	0	0	0	0	0
	Gyrinus dejeani	1	0	0	0	1	1	1	1	1	1	1
	Gyrinus distinctus	2	1	1	1	1	1	1	1	1	0	0
	Gyrinus marinus	1	1	1	1	1	1	0	0	0	0	0
	Gyrinus natator	2	1	1	1	0	0	0	0	0	0	0
	Gyrinus opacus	2	1	1	0	0	0	0	0	0	0	0
	Gyrinus paykulli	2	1	1	1	1	0	0	0	0	0	0
	Gyrinus pullatus	1	1	0	0	0	0	0	0	0	0	0
	Gyrinus substriatus	1	1	1	1	1	1	1	1	1	1	0
	Gyrinus suffriani	2	1	1	1	1	1	0	1	0	0	0
	Gyrinus urinator	1	0	0	1	0	1	1	1	1	1	0
	Orectochilus villosus	0	1	1	1	1	1	1	1	1	1	0
	Brychius elevatus	0	1	1	1	1	1	1	1	0	0	0
HALIPLIDAE	*Haliplus confinis*	2	1	1	1	1	0	0	0	0	0	0
	Haliplus obliquus	2	1	1	1	1	1	1	1	1	1	0
	Haliplus varius	2	1	0	1	1	0	0	0	0	0	0
	Haliplus apicalis	2	1	1	1	0	0	0	0	0	0	0
	Haliplus fluviatilis	1	1	1	1	1	1	0	0	0	0	0
	Haliplus fulvicollis	2	1	1	1	0	0	0	0	0	0	0
	Haliplus furcatus	2	1	1	1	1	0	0	0	0	0	0

FAMILY	SPECIES	HABITAT	NEU	SSW	NGD	SGE	FCR	PEV	HEI	SEI	NMO	SMO
HALIPLIDAE	*Haliplus heydeni*	1	1	1	1	1	1	1	1	0	0	0
	Haliplus immaculatus	2	1	1	1	1	1	0	0	0	0	0
	Haliplus interjectus	1	1	0	0	0	0	0	0	0	0	0
	Haliplus lineolatus	1	1	1	1	1	0	0	0	0	0	0
	Haliplus ruficollis	2	1	1	1	1	1	1	0	1	0	0
	Haliplus sibiricus	1	1	1	1	1	1	0	0	0	0	0
	Haliplus andalusicus	2	0	0	0	0	0	1	1	1	1	0
	Haliplus flavicollis	1	1	1	1	1	1	0	0	0	0	0
	Haliplus fulvus	2	1	1	1	1	1	1	1	0	1	0
	Haliplus guttatus	2	0	0	0	0	1	1	1	1	1	0
	Haliplus laminatus	1	0	1	1	1	1	0	0	0	0	0
	Haliplus mucronatus	1	0	0	0	1	1	1	1	1	1	1
	Haliplus rubidus	2	0	0	0	0	0	1	1	1	1	0
	Haliplus variegatus	2	1	1	1	1	1	1	1	0	0	0
	Haliplus lineatocollis	1	0	1	1	1	1	1	1	1	1	1
	Peltodytes caesus	2	0	1	1	1	1	1	1	1	1	0
	Peltodytes rotundatus	2	0	0	0	1	1	1	1	1	1	1
NOTERIDAE	*Canthydrus diophthalmus*	2	0	0	0	0	0	0	0	1	1	1
	Noterus clavicornis	2	1	1	1	1	1	1	1	1	0	0
	Noterus crassicornis	2	1	1	1	1	1	0	0	0	0	0
	Noterus laevis	2	0	0	0	0	1	1	1	1	1	1
HYGROBIIDAE	*Hygrobia hermanni*	2	0	0	1	1	1	1	1	1	1	0
DYTISCIDAE	*Agabus arcticus arcticus*	2	1	1	0	0	0	0	0	0	0	0
	Agabus clypealis	2	1	1	1	0	0	0	0	0	0	0
	Agabus confinis	2	1	1	0	0	0	0	0	0	0	0
	Agabus congener	2	1	1	1	1	1	0	0	0	0	0
	Agabus coxalis	2	1	0	0	0	0	0	0	0	0	0
	Agabus discolor	0	1	0	0	0	0	0	0	0	0	0
	Agabus elongatus	2	1	1	0	0	0	0	0	0	0	0
	Agabus fuscipennis	2	1	1	1	1	0	0	0	0	0	0
	Agabus infuscatus	2	1	0	0	0	0	0	0	0	0	0
	Agabus lapponicus	2	1	1	0	0	0	1	1	0	0	0
	Agabus moestus	2	1	0	0	0	0	0	0	0	0	0
	Agabus pseudoclypealis	0	1	0	0	0	0	0	0	0	0	0
	Agabus setulosus	0	1	0	0	0	0	0	0	0	0	0
	Agabus sturmii	2	1	1	1	1	1	1	0	0	0	0
	Agabus thomsoni	1	1	0	0	0	0	0	0	0	0	0
	Agabus zetterstedti	2	1	0	0	0	0	0	0	0	0	0
	Agabus bifarius	2	1	0	0	0	0	0	0	0	0	0
	Agabus jacobsoni	2	1	0	0	0	0	0	0	0	0	0
	Agabus labiatus	2	1	1	1	1	1	1	1	0	0	0
	Agabus luteaster	2	1	0	0	0	0	0	0	0	0	0
	Agabus pallens	2	1	0	0	0	0	0	0	0	0	0
	Agabus serricornis	2	1	1	0	0	0	0	0	0	0	0
	Agabus uliginosus	2	1	1	1	1	1	0	1	0	0	0

FAMILY	SPECIES	HABITAT	NEU	SSW	NGD	SGE	FCR	PEV	HEI	SEI	NMO	SMO
DYTISCIDAE	*Agabus undulatus*	2	1	1	1	1	1	0	0	0	0	0
	Agabus adpressus	0	1	0	0	0	0	0	0	0	0	0
	Agabus affinis	2	1	1	1	1	1	0	0	0	0	0
	Agabus alexandrae	0	0	0	0	0	0	0	0	0	1	0
	Agabus biguttatus	0	0	0	1	1	1	1	1	1	1	1
	Agabus biguttulus	1	1	1	0	0	0	0	0	0	0	0
	Agabus bipustulatus	1	1	1	1	1	1	1	1	1	1	1
	Agabus brunneus	0	0	0	1	1	1	1	1	1	1	1
	Agabus conspersus	2	0	1	1	0	0	1	1	1	1	0
	Agabus didymus	0	0	1	1	1	1	1	1	1	1	1
	Agabus guttatus	0	1	1	1	1	1	1	1	1	0	0
	Agabus heydeni	0	0	0	0	0	0	1	1	1	1	0
	Agabus melanarius	1	1	1	1	1	1	0	0	0	0	0
	Agabus nebulosus	2	1	1	1	1	1	1	1	1	1	1
	Agabus nevadensis	1	0	0	0	0	0	0	0	1	0	0
	Agabus paludosus	0	1	1	1	1	1	1	1	1	0	0
	Agabus ramblae	0	0	0	0	0	0	1	1	1	1	1
	Agabus striolatus	2	1	1	1	0	0	0	0	0	0	0
	Agabus tristis	1	1	0	0	0	0	0	0	0	0	0
	Agabus unguicularis	2	1	1	1	1	0	0	0	0	0	0
	Ilybius aenescens	2	1	1	1	1	1	0	0	0	0	0
	Ilybius albarracinensis	1	0	0	0	0	0	1	1	0	0	0
	Ilybius angustior	2	1	1	1	0	0	0	0	0	0	0
	Ilybius ater	2	1	1	1	1	1	0	1	0	0	0
	Ilybius chalconatus	2	1	1	1	1	1	1	1	1	1	1
	Ilybius crassus	2	1	1	1	1	0	0	0	0	0	0
	Ilybius dettneri	0	0	0	0	0	0	0	1	0	0	0
	Ilybius erichsoni	2	1	1	1	0	0	0	0	0	0	0
	Ilybius fenestratus	2	1	1	1	1	1	0	0	0	0	0
	Ilybius fuliginosus	1	1	1	1	1	1	1	0	0	0	0
	Ilybius guttiger	2	1	1	1	1	1	0	0	0	0	0
	Ilybius hozgargantae	0	0	0	0	0	0	0	0	1	1	0
	Ilybius meridionalis	1	0	0	0	0	0	1	1	1	1	0
	Ilybius montanus	2	0	0	1	1	1	1	1	1	1	0
	Ilybius neglectus	2	1	1	1	1	1	0	0	0	0	0
	Ilybius opacus	2	1	1	0	0	0	0	0	0	0	0
	Ilybius picipes	2	1	0	0	0	0	0	0	0	0	0
	Ilybius quadriguttatus	2	1	1	1	1	1	1	0	0	0	0
	Ilybius similis	2	1	1	1	1	1	0	0	0	0	0
	Ilybius subaeneus	2	1	1	1	1	1	0	0	0	0	0
	Ilybius subtilis	2	1	1	1	1	0	0	0	0	0	0
	Ilybius vittiger	2	1	1	0	0	0	0	0	0	0	0
	Ilybius wasastjernae	2	1	1	1	1	0	0	0	0	0	0
	Platambus maculatus	0	1	1	1	1	1	1	1	0	0	0
	Colymbetes dolabratus	2	1	1	0	0	0	0	0	0	0	0

FAMILY	SPECIES	HABITAT	NEU	SSW	NGD	SGE	FCR	PEV	HEI	SEI	NMO	SMO
DYISCIDAE	*Colymbetes fuscus*	2	1	1	1	1	1	1	1	1	1	0
	Colymbetes paykulli	2	1	1	1	0	0	0	0	0	0	0
	Colymbetes schildknechti	1	0	0	0	0	0	0	1	1	1	0
	Colymbetes striatus	2	1	1	1	0	0	0	0	0	0	0
	Meladema coriacea	0	0	0	0	0	1	1	1	1	1	1
	Rhantus grapii	2	1	1	1	1	1	0	0	0	0	0
	Rhantus bistriatus	2	1	1	1	1	1	0	0	0	0	0
	Rhantus consputus	2	0	0	1	1	0	0	0	0	0	0
	Rhantus exsoletus	2	1	1	1	1	1	0	0	0	0	0
	Rhantus fennicus	2	1	0	0	0	0	0	0	0	0	0
	Rhantus frontalis	2	1	1	1	1	1	0	0	0	0	0
	Rhantus hispanicus	2	0	0	0	0	1	1	1	1	1	0
	Rhantus incognitus	0	1	0	1	0	0	0	0	0	0	0
	Rhantus latitans	2	0	0	1	1	0	0	0	0	0	0
	Rhantus notaticollis	2	1	1	1	1	0	0	0	0	0	0
	Rhantus suturalis	2	1	1	1	1	1	1	1	1	1	0
	Rhantus suturellus	2	1	1	1	1	1	0	0	0	0	0
	Liopterus atriceps	2	0	0	0	0	0	0	1	1	1	0
	Liopterus haemorrhoidalis	2	1	1	1	1	1	1	1	0	0	0
	Acilius canaliculatus	2	1	1	1	1	1	0	0	0	0	0
	Acilius sulcatus	2	1	1	1	1	1	1	1	0	0	0
	Acilius duvergeri	2	0	0	0	0	0	0	1	1	1	0
	Graphoderus austriacus	2	0	1	1	1	1	0	0	0	0	0
	Graphoderus bilineatus	2	1	1	1	1	0	0	0	0	0	0
	Graphoderus cinereus	2	1	1	1	1	1	1	1	1	0	0
	Graphoderus zonatus verrucifer	2	1	0	0	0	0	0	0	0	0	0
	Graphoderus zonatus zonatus	2	0	1	1	1	0	0	0	0	0	0
	Cybister lateralimarginalis	2	0	1	1	1	1	1	1	1	1	0
	Cybister tripunctatus africanus	2	0	0	0	0	0	1	1	1	1	1
	Cybister vulneratus	2	0	0	0	0	0	0	0	1	1	1
	Dytiscus circumcinctus	2	1	1	1	1	1	0	0	0	0	0
	Dytiscus circumflexus	2	0	1	1	1	1	1	1	1	1	0
	Dytiscus dimidiatus	2	1	1	1	1	1	0	0	0	0	0
	Dytiscus lapponicus	2	1	1	1	0	0	0	0	0	0	0
	Dytiscus latissimus	2	1	1	1	1	0	0	0	0	0	0
	Dytiscus marginalis	1	1	1	1	1	1	1	1	1	0	0
	Dytiscus pisanus	1	0	0	0	1	1	1	1	1	1	1
	Dytiscus semisulcatus	1	1	1	1	1	1	1	1	1	1	0
	Eretes griseus&sticticus	2	0	0	0	0	1	1	1	1	1	1
	Hydaticus aruspex	2	1	1	1	0	0	0	0	0	0	0
	Hydaticus continentalis	2	0	1	1	1	0	0	0	0	0	0
	Hydaticus seminiger	2	1	1	1	1	1	1	1	0	0	0
	Hydaticus transversalis	2	1	1	1	1	1	1	0	0	0	0
	Hydaticus grammicus	2	0	0	0	1	0	0	0	0	0	0
	Hydaticus leander	2	0	0	0	0	0	1	1	1	1	0

FAMILY	**SPECIES**	**HABITAT**	**NEU**	**SSW**	**NGD**	**SGE**	**FCR**	**PEV**	**HEI**	**SEI**	**NMO**	**SMO**
DYTISCIDAE	*Bidessus coxalis*	1	0	0	0	1	1	1	1	1	1	1
	Bidessus delicatulus	1	0	0	0	1	1	0	0	0	0	0
	Bidessus goudotii	1	0	0	0	1	1	1	1	1	1	0
	Bidessus grossepunctatus	2	1	1	1	1	0	0	0	0	0	0
	Bidessus minutissimus	0	0	0	1	1	1	1	1	1	1	1
	Bidessus pumilus	2	0	0	0	0	1	1	1	1	0	0
	Bidessus unistriatus	2	1	1	1	1	1	0	0	0	0	0
	Hydroglyphus angularis	2	0	0	0	0	0	0	0	0	1	0
	Hydroglyphus geminus	1	1	1	1	1	1	1	1	1	1	1
	Hydroglyphus hamulatus	2	1	1	1	0	0	0	0	0	0	0
	Hydroglyphus signatellus	1	0	0	0	0	0	1	1	1	1	1
	Pseuduvarus vitticollis	2	0	0	0	0	0	0	0	0	0	1
	Yola bicarinata	1	0	0	0	1	1	1	1	1	1	1
	Boreonectes griseostriatus	2	1	1	0	0	0	0	0	0	0	0
	Boreonectes ibericus	2	0	0	0	0	0	1	1	1	1	0
	Boreonectes multilineatus	2	1	1	0	0	0	1	0	0	0	0
	Deronectes algibensis	0	0	0	0	0	0	0	0	1	0	0
	Deronectes angusi	0	0	0	0	0	0	0	1	0	0	0
	Deronectes aubei aubei	0	0	0	0	1	0	0	0	0	0	0
	Deronectes aubei sanfilippoi	0	0	0	0	0	1	1	0	0	0	0
	Deronectes bicostatus	0	0	0	0	0	0	0	1	0	0	0
	Deronectes costipennis	0	0	0	0	0	0	0	1	0	0	0
	Deronectes delarouzei	0	0	0	0	0	0	1	0	0	0	0
	Deronectes depressicollis	0	0	0	0	0	0	0	1	1	0	0
	Deronectes fairmairei	0	0	0	0	0	0	1	1	1	1	1
	Deronectes ferrugineus	0	0	0	0	0	0	0	1	0	0	0
	Deronectes fosteri	0	0	0	0	0	0	1	0	0	0	0
	Deronectes hispanicus	0	0	0	0	0	0	1	1	1	1	0
	Deronectes latus	0	1	1	1	1	1	0	0	0	0	0
	Deronectes moestus	0	0	0	0	0	1	1	1	1	1	1
	Deronectes opatrinus	0	0	0	0	0	1	1	1	1	0	0
	Deronectes platynotus	1	0	0	1	1	0	0	0	0	0	0
	Deronectes theryi	0	0	0	0	0	0	0	0	0	1	0
	Deronectes wewalkai	0	0	0	0	0	0	0	1	0	0	0
	Graptodytes aequalis	2	0	0	0	0	0	0	1	1	1	0
	Graptodytes atlantis	1	0	0	0	0	0	0	0	0	1	0
	Graptodytes bilineatus	2	1	1	1	1	1	1	1	0	0	0
	Graptodytes bremondi	0	0	0	0	0	0	0	0	0	1	0
	Graptodytes castilianus	1	0	0	0	0	0	1	1	1	0	0
	Graptodytes flavipes	1	0	0	1	1	1	1	1	1	1	0
	Graptodytes fractus	0	0	0	0	0	1	1	1	1	1	1
	Graptodytes granularis	2	1	1	1	1	1	0	0	0	0	0
	Graptodytes ignotus	0	0	0	0	0	1	1	1	1	1	1
	Graptodytes pictus	1	1	1	1	1	1	0	0	0	0	0
	Graptodytes varius	1	0	0	0	1	1	1	1	1	1	0

FAMILY	SPECIES	HABITAT	NEU	SSW	NGD	SGE	FCR	PEV	HEI	SEI	NMO	SMO
DYTISCIDAE	*Hydrocolus sahlbergi*	2	1	0	0	0	0	0	0	0	0	0
	Hydroporus acutangulus	2	1	1	0	0	0	0	0	0	0	0
	Hydroporus angustatus	2	1	1	1	1	1	0	0	0	0	0
	Hydroporus basinotatus	0	0	0	0	0	0	0	0	1	1	0
	Hydroporus brancoi brancoi	1	0	0	0	0	0	0	1	0	0	0
	Hydroporus brancoi gredensis	1	0	0	0	0	0	0	1	0	0	0
	Hydroporus brancuccii	0	0	0	0	0	0	1	1	0	0	0
	Hydroporus brevis	2	1	1	1	0	0	0	0	0	0	0
	Hydroporus constantini	0	0	0	0	0	0	1	1	0	0	0
	Hydroporus decipiens	1	0	0	0	0	0	1	1	1	0	0
	Hydroporus discretus	0	1	1	1	1	1	1	1	1	1	1
	Hydroporus elongatulus	2	1	1	1	1	0	0	0	0	0	0
	Hydroporus erythrocephalus	2	1	1	1	1	1	0	0	0	0	0
	Hydroporus ferrugineus	0	0	0	1	1	1	0	0	0	0	0
	Hydroporus foveolatus	2	0	0	0	0	0	1	1	0	0	0
	Hydroporus fuscipennis	2	1	1	1	0	0	0	0	0	0	0
	Hydroporus geniculatus	2	1	1	0	0	0	0	0	0	0	0
	Hydroporus glabriusculus	2	1	1	1	0	0	0	0	0	0	0
	Hydroporus gyllenhalii	2	1	1	1	1	1	1	1	1	0	0
	Hydroporus incognitus	2	1	1	1	1	1	1	1	0	0	0
	Hydroporus kraatzii	1	0	0	0	1	0	0	0	0	0	0
	Hydroporus lapponum	2	1	1	0	0	0	0	0	0	0	0
	Hydroporus limbatus	2	0	0	0	0	0	1	1	1	1	0
	Hydroporus longicornis	0	1	1	1	1	1	0	0	0	0	0
	Hydroporus longulus	0	0	0	0	1	1	0	0	0	0	0
	Hydroporus lucasi	1	0	0	0	0	0	1	1	1	1	0
	Hydroporus marginatus	1	0	0	1	1	1	1	1	1	1	0
	Hydroporus melanarius	1	1	1	1	1	1	0	0	0	0	0
	Hydroporus memnonius	1	1	1	1	1	1	1	1	0	1	0
	Hydroporus morio	2	1	1	1	1	1	0	0	0	0	0
	Hydroporus necopinatus necopinatus	2	0	0	0	0	0	1	1	0	0	0
	Hydroporus necopinatus robertorum	2	0	0	0	0	1	0	0	0	0	0
	Hydroporus neglectus	2	1	1	1	1	1	0	0	0	0	0
	Hydroporus nevadensis	1	0	0	0	0	0	1	1	1	0	0
	Hydroporus nigellus	2	1	1	1	0	0	1	0	0	0	0
	Hydroporus nigrita	2	1	1	1	1	1	1	1	1	0	0
	Hydroporus normandi	0	0	0	0	0	0	1	1	1	1	0
	Hydroporus notabilis	1	1	1	0	0	0	0	0	0	0	0
	Hydroporus notatus	2	1	1	1	0	0	0	0	0	0	0
	Hydroporus obscurus	2	1	1	1	1	1	0	0	0	0	0
	Hydroporus obsoletus	0	1	1	1	1	0	1	1	1	1	1
	Hydroporus paganettianus	1	0	0	0	0	0	0	1	0	0	0
	Hydroporus palustris	1	1	1	1	1	1	1	0	0	0	0
	Hydroporus planus	2	1	1	1	1	1	1	1	1	0	0
	Hydroporus puberulus	2	1	1	0	0	0	0	0	0	0	0

FAMILY	SPECIES	HABITAT	NEU	SSW	NGD	SGE	FCR	PEV	HEI	SEI	NMO	SMO
DYTISCIDAE	*Hydroporus pubescens*	2	1	1	1	1	1	1	1	1	1	1
	Hydroporus rifensis	2	0	0	0	0	0	0	0	0	1	0
	Hydroporus rufifrons	2	1	1	1	1	0	0	0	0	0	0
	Hydroporus sabaudus	2	0	0	0	0	0	1	1	1	0	0
	Hydroporus scalesianus	2	1	1	1	1	0	0	0	0	0	0
	Hydroporus semenowi	2	1	1	0	0	0	0	0	0	0	0
	Hydroporus striola	2	1	1	1	1	0	0	0	0	0	0
	Hydroporus submuticus	1	1	1	0	0	0	0	0	0	0	0
	Hydroporus tessellatus	1	0	0	0	1	1	1	1	1	1	0
	Hydroporus toubkal	0	0	0	0	0	0	0	0	0	1	0
	Hydroporus tristis	2	1	1	1	1	1	0	0	0	0	0
	Hydroporus umbrosus	2	1	1	1	1	1	0	0	0	0	0
	Hydroporus vagepictus	1	0	0	0	1	0	1	1	0	0	0
	Hydroporus vespertinus	2	0	0	0	0	0	0	1	0	0	0
	Metaporus meridionalis	2	0	0	0	0	0	1	1	1	1	0
	Nebrioporus assimilis	1	1	1	1	1	0	0	0	0	0	0
	Nebrioporus baeticus	0	0	0	0	0	0	1	1	1	0	0
	Nebrioporus bucheti cazorlensis	0	0	0	0	0	0	1	1	1	0	0
	Nebrioporus canaliculatus	1	0	1	1	1	1	1	1	1	0	0
	Nebrioporus carinatus	0	0	0	0	0	0	0	1	0	0	0
	Nebrioporus ceresyi	2	0	0	0	0	0	1	1	1	1	1
	Nebrioporus clarkii	0	0	0	0	0	0	1	1	1	1	1
	Nebrioporus croceus	0	0	0	0	0	0	0	1	0	0	0
	Nebrioporus depressus	1	1	1	1	0	0	0	0	0	0	0
	Nebrioporus elegans	1	0	0	1	1	1	1	1	0	0	0
	Nebrioporus fabressei	0	0	0	0	0	0	1	1	0	0	0
	Nebrioporus luctuosus	0	0	0	0	0	0	1	1	0	0	0
	Nebrioporus nemethi	0	0	0	0	0	0	0	0	0	1	0
	Nebrioporus sansii	0	0	0	0	0	0	1	1	1	0	0
	Oreodytes alpinus	2	1	1	0	0	0	0	0	0	0	0
	Oreodytes davisii	0	0	0	0	0	1	1	1	1	0	0
	Oreodytes sanmarkii	0	1	1	1	1	1	1	1	0	0	0
	Oreodytes septentrionalis	0	1	0	0	1	1	1	1	1	0	0
	Porhydrus genei	2	0	0	0	0	0	0	0	0	1	0
	Porhydrus lineatus	2	1	1	1	1	1	0	0	0	0	0
	Porhydrus vicinus	2	0	0	0	0	0	0	0	0	1	0
	Rhithrodytes agnus agnus	0	0	0	0	0	0	0	1	0	0	0
	Rhithrodytes agnus argaensis	0	0	0	0	0	0	0	1	0	0	0
	Rhithrodytes bimaculatus	0	0	0	0	0	0	1	0	0	0	0
	Scarodytes halensis halensis	1	1	1	1	1	1	1	1	1	1	0
	Stictonectes abellani	0	0	0	0	0	0	0	1	0	0	0
	Stictonectes azruensis	1	0	0	0	0	0	0	0	0	1	0
	Stictonectes epipleuricus	0	0	0	0	0	0	1	1	1	0	0
	Stictonectes escheri	0	0	0	0	0	0	0	0	1	1	0
	Stictonectes formosus	0	0	0	0	0	0	0	0	1	1	0

FAMILY	**SPECIES**	**HABITAT**	**NEU**	**SSW**	**NGD**	**SGE**	**FCR**	**PEV**	**HEI**	**SEI**	**NMO**	**SMO**
DYTISCIDAE	*Stictonectes lepidus*	1	0	0	0	1	1	1	1	1	1	0
	Stictonectes occidentalis	0	0	0	0	0	0	0	1	0	0	0
	Stictonectes optatus	0	0	0	0	0	0	1	1	1	1	1
	Stictonectes rebeccae	0	0	0	0	0	0	0	1	0	0	0
	Stictotarsus bertrandi	0	0	0	0	0	0	0	1	0	0	0
	Stictotarsus duodecimpustulatus	1	1	1	1	1	1	1	1	1	0	0
	Stictotarsus maghgrebinus	2	0	0	0	0	0	0	0	0	1	1
	Stictotarsus procerus	2	0	0	0	0	0	0	0	0	1	0
	Suphrodytes complex	2	1	1	1	1	1	0	0	0	0	0
	Trichonectes otini	0	0	0	0	0	0	0	0	1	1	0
	Hydrovatus clypealis	2	0	0	0	0	1	1	1	1	1	0
	Hydrovatus cuspidatus	2	0	1	1	1	1	1	1	1	1	1
	Herophydrus musicus	1	0	0	0	0	0	1	1	1	1	1
	Hygrotus confluens	2	1	1	1	1	1	1	1	1	1	1
	Hygrotus enneagrammus	2	0	0	1	0	0	0	0	0	0	0
	Hygrotus flaviventris	2	0	0	1	0	0	0	0	0	0	0
	Hygrotus fresnedai	2	0	0	0	0	0	0	1	0	0	0
	Hygrotus impressopunctatus	2	1	1	1	1	1	1	1	1	0	0
	Hygrotus lagari	2	0	0	0	0	0	1	1	1	1	0
	Hygrotus marklini	2	1	1	1	0	0	1	1	0	0	0
	Hygrotus nigrolineatus	2	1	1	1	1	0	0	0	0	0	0
	Hygrotus novemlineatus	2	1	1	1	0	0	0	0	0	0	0
	Hygrotus pallidulus	2	0	0	0	0	0	1	1	1	1	1
	Hygrotus parallellogramus	2	1	1	1	1	0	1	0	0	0	0
	Hygrotus polonicus	2	1	0	0	0	0	0	0	0	0	0
	Hygrotus unguicularis	2	1	0	0	0	0	0	0	0	0	0
	Hygrotus decoratus	2	1	1	1	1	0	0	0	0	0	0
	Hygrotus inaequalis	1	1	1	1	1	1	1	1	1	1	0
	Hygrotus quinquelineatus	2	1	1	1	1	0	0	0	0	0	0
	Hygrotus versicolor	1	1	1	1	1	1	0	0	0	0	0
	Hyphydrus aubei	2	0	0	0	0	1	1	1	1	1	0
	Hyphydrus ovatus	2	1	1	1	1	1	0	0	0	0	0
	Laccornis oblongus	2	1	1	1	1	0	0	0	0	0	0
	Methles cribatellus	2	0	0	0	0	0	1	0	1	1	1
	Laccophilus biguttatus	2	1	1	0	0	0	0	0	0	0	0
	Laccophilus hyalinus	0	1	1	1	1	1	1	1	1	1	1
	Laccophilus minutus	1	1	1	1	1	1	1	1	1	1	1
	Laccophilus poecilus	2	1	1	1	1	1	1	1	1	1	0
HELOPHORIDAE	*Helophorus oxygonus*	2	0	0	0	0	0	0	0	0	1	0
	Helophorus sibiricus	1	1	0	0	0	0	0	0	0	0	0
	Helophorus aequalis	2	1	1	1	1	1	1	0	0	0	0
	Helophorus aquaticus	2	1	0	1	1	1	1	1	1	0	0
	Helophorus grandis	2	1	1	1	1	1	1	1	1	1	0
	Helophorus maritimus	1	0	0	0	0	0	1	0	0	0	0
	Helophorus occidentalis	1	0	0	0	0	0	0	1	1	1	0

FAMILY	SPECIES	HABITAT	NEU	SSW	NGD	SGE	FCR	PEV	HEI	SEI	NMO	SMO
HELOPHORIDAE	*Helophorus strandi*	2	1	0	0	0	0	0	0	0	0	0
	Helophorus tuberculatus	2	1	1	1	1	0	0	0	0	0	0
	Helophorus algiricus	1	0	0	0	0	0	0	0	0	1	1
	Helophorus arvernicus	0	1	0	1	1	1	0	0	0	0	0
	Helophorus asperatus	2	0	1	1	1	1	0	0	0	0	0
	Helophorus asturiensis	2	0	0	0	0	0	1	1	1	1	0
	Helophorus atlantis	2	0	0	0	0	0	0	0	0	1	0
	Helophorus bameuli	1	0	0	0	0	0	0	1	1	0	0
	Helophorus brevipalpis	1	1	1	1	1	1	1	1	1	0	0
	Helophorus calpensis	2	0	0	0	0	0	0	0	1	0	0
	Helophorus cincticollis	2	0	0	0	0	0	0	0	1	1	0
	Helophorus croaticus	2	0	0	1	1	0	0	0	0	0	0
	Helophorus discrepans	2	1	0	0	1	1	1	1	0	1	0
	Helophorus dorsalis	2	0	0	1	1	0	0	0	0	0	0
	Helophorus elizabethae	1	0	0	0	0	0	0	0	0	1	0
	Helophorus flavipes	2	1	1	1	1	1	1	1	1	0	0
	Helophorus fulgidicollis	2	0	1	1	0	0	1	1	1	1	0
	Helophorus glacialis	2	1	1	0	0	0	1	1	1	0	0
	Helophorus granularis	2	1	1	1	1	1	1	1	0	0	0
	Helophorus gratus	2	0	0	0	0	0	0	0	1	1	0
	Helophorus griseus	1	1	1	1	1	1	1	1	0	0	0
	Helophorus illustris	2	0	0	0	0	0	1	0	0	0	0
	Helophorus jocoteroi	1	0	0	0	0	0	0	1	0	0	0
	Helophorus lapponicus	2	1	1	1	0	0	1	1	0	0	0
	Helophorus laticollis	2	1	1	1	1	1	0	0	0	0	0
	Helophorus leontis	1	0	0	0	0	0	0	1	0	0	0
	Helophorus longitarsis	2	0	0	1	1	1	1	1	1	1	0
	Helophorus minutus	1	1	1	1	1	1	1	1	1	1	0
	Helophorus nanus	2	1	1	1	1	1	0	0	0	0	0
	Helophorus nevadensis	2	0	0	0	0	0	0	1	1	0	0
	Helophorus nivicola	2	0	0	0	0	0	0	0	0	1	0
	Helophorus obscurus	2	0	1	1	1	1	1	1	1	0	0
	Helophorus orientalis	2	1	0	0	0	0	0	0	0	0	0
	Helophorus pallidulus	2	1	0	0	0	0	0	0	0	0	0
	Helophorus paraminutus	2	0	0	1	1	0	0	0	0	0	0
	Helophorus pumilio	1	1	0	1	1	1	0	0	0	0	0
	Helophorus redtenbacheri	2	0	1	1	1	0	0	0	0	0	0
	Helophorus seidlitzii	1	0	0	0	0	0	1	1	1	0	0
	Helophorus strigifrons	1	1	1	1	1	0	0	0	0	0	0
	Helophorus theryi	0	0	0	0	0	0	0	0	0	1	0
	Helophorus villosus	1	0	0	0	1	0	0	0	0	0	0
	Helophorus alternans	2	0	0	0	0	0	1	1	1	1	0
HYDROCHIDAE	*Hydrochus aljibensis*	0	0	0	0	0	0	0	1	1	1	0
	Hydrochus angusi	1	0	0	0	0	0	0	1	0	0	0
	Hydrochus angustatus	2	0	0	1	1	1	1	1	1	1	0

FAMILY	**SPECIES**	**HABITAT**	**NEU**	**SSW**	**NGD**	**SGE**	**FCR**	**PEV**	**HEI**	**SEI**	**NMO**	**SMO**
HYDROCHIDAE	*Hydrochus brevis*	2	1	1	1	1	1	0	0	0	0	0
	Hydrochus crenatus	2	1	1	1	1	1	0	0	0	0	0
	Hydrochus elongatus	2	0	1	1	1	1	0	0	0	0	0
	Hydrochus flavipennis	1	0	0	0	0	1	1	1	1	1	0
	Hydrochus grandicollis	0	0	0	0	0	1	1	1	1	1	1
	Hydrochus ibericus	0	0	0	0	0	0	0	1	1	0	0
	Hydrochus ignicollis	2	1	1	1	1	1	0	0	0	0	0
	Hydrochus interruptus	0	0	0	0	0	0	0	1	0	0	0
	Hydrochus kirgisicus	1	1	0	0	0	0	0	0	0	0	0
	Hydrochus megaphallus	2	1	1	1	1	0	0	0	0	0	0
	Hydrochus nitidicollis	1	0	0	0	1	1	1	1	1	0	0
	Hydrochus nooreinus	0	0	0	0	0	0	0	1	1	0	0
	Hydrochus obtusicollis	1	0	0	0	0	0	0	0	0	1	0
	Hydrochus smaragdineus	1	0	0	0	0	1	1	1	1	1	1
	Hydrochus tariqi	0	0	0	0	0	0	0	0	1	1	0
HYDROPHILIDAE	*Spercheus emarginatus*	2	1	1	1	1	1	0	0	0	0	0
	Anacaena bipustulata	1	0	0	1	1	1	1	1	1	1	1
	Anacaena globulus	0	1	1	1	1	1	1	1	1	1	1
	Anacaena limbata	1	1	1	1	1	1	1	1	1	1	0
	Anacaena lutescens	1	1	1	1	1	1	1	1	1	1	0
	Crenitis punctatostriata	2	0	0	0	1	0	0	0	0	0	0
	Paracymus aeneus	1	1	1	1	1	0	1	1	1	1	1
	Paracymus phalacroides	2	0	0	0	0	0	0	0	1	1	0
	Paracymus scutellaris	1	0	0	1	1	1	1	1	1	1	0
	Berosus affinis	1	0	0	0	1	1	1	1	1	1	0
	Berosus geminus	2	0	0	1	1	0	0	0	0	0	0
	Berosus hispanicus	1	0	0	0	0	1	1	1	1	1	1
	Berosus luridus	2	1	1	1	1	1	0	0	0	0	0
	Berosus signaticollis	2	1	1	1	1	1	1	1	1	1	0
	Berosus frontifoveatus	2	0	0	1	1	0	0	0	0	0	0
	Berosus fulvus	2	0	1	1	0	0	1	0	1	1	0
	Berosus guttalis	2	0	0	0	0	0	1	1	1	1	0
	Berosus jaechi	2	0	0	0	0	0	1	0	0	0	0
	Berosus spinosus	2	1	1	1	1	0	0	0	0	0	0
	Amphiops senegalensis	2	0	0	0	0	0	0	0	0	1	1
	Chaetarthria complex	1	1	1	1	1	1	1	1	1	1	1
	Hemisphaera guignoti	0	0	0	0	0	0	0	1	1	1	1
	Hemisphaera seriatopunctata	0	0	0	0	0	0	0	1	1	0	0
	Chasmogenus livornicus	2	0	0	0	0	0	1	0	0	0	0
	Cymbiodyta marginella	2	1	1	1	1	1	1	1	1	0	0
	Enochrus melanocephalus	2	1	1	1	1	1	1	1	1	0	0
	Enochrus ater	2	0	0	0	0	0	1	1	1	1	0
	Enochrus bicolor	2	1	1	1	1	0	1	1	1	1	1
	Enochrus blazquezae	0	0	0	0	0	0	0	0	0	1	0
	Enochrus halophilus	2	0	1	1	1	1	1	1	1	0	0

FAMILY	SPECIES	HABITAT	NEU	SSW	NGD	SGE	FCR	PEV	HEI	SEI	NMO	SMO
HYDROPHILIDAE	*Enochrus hamifer*	2	0	0	1	0	0	0	0	0	0	0
	Enochrus jesusarribasi	0	0	0	0	0	0	0	1	1	0	0
	Enochrus ochropterus	2	1	1	1	1	1	0	0	0	0	0
	Enochrus politus	0	0	0	0	0	0	1	1	1	1	1
	Enochrus quadripunctatus-fuscipennis	2	1	1	1	1	1	1	1	1	1	0
	Enochrus risii	0	0	0	0	0	0	0	0	0	0	1
	Enochrus salomonis	0	0	0	0	0	0	1	1	1	0	0
	Enochrus segmentinotatus	2	0	0	0	0	0	1	0	1	1	0
	Enochrus testaceus	2	1	1	1	1	1	1	0	1	0	0
	Enochrus affinis	2	1	1	1	1	1	0	0	0	0	0
	Enochrus coarctatus	2	1	1	1	1	1	0	0	0	0	0
	Enochrus morenae	0	0	0	0	0	0	1	1	1	0	0
	Enochrus natalensis	2	0	0	0	0	0	0	0	1	1	1
	Enochrus nigritus	2	0	0	0	1	1	1	1	0	1	0
	Helochares lividus	1	0	0	1	1	1	1	1	1	1	1
	Helochares obscurus	2	1	1	1	1	1	0	0	0	0	0
	Helochares punctatus	2	0	0	1	1	1	0	1	0	0	0
	Hydrobius arcticus	2	1	0	0	0	0	0	0	0	0	0
	Hydrobius convexus	2	0	0	0	0	1	1	1	1	1	0
	Hydrobius fuscipes	2	1	1	1	1	1	1	1	1	1	0
	Limnoxenus niger	2	0	0	1	1	1	1	1	1	0	0
	Limnoxenus olmoi	2	0	0	0	0	0	0	1	0	1	0
	Hydrochara caraboides	2	1	1	1	1	1	1	0	0	0	0
	Hydrochara flavipes	2	0	0	1	1	0	1	1	1	1	0
	Hydrophilus aterrimus	2	1	1	1	1	0	0	0	0	0	0
	Hydrophilus piceus	2	1	1	1	1	1	1	1	0	0	0
	Hydrophilus pistaceus	2	0	0	0	0	1	1	1	1	1	1
	Laccobius decorus	2	1	1	0	0	0	0	0	0	0	0
	Laccobius albescens	1	0	0	0	0	1	0	0	0	0	0
	Laccobius atratus	0	0	0	0	1	1	1	1	1	1	0
	Laccobius atrocephalus atrocephalus	1	0	0	0	0	0	0	1	1	1	1
	Laccobius bipunctatus	1	1	1	1	1	1	1	1	1	1	0
	Laccobius gloriana	0	0	0	0	0	0	0	1	1	0	0
	Laccobius hispanicus	1	0	0	0	0	0	1	1	1	1	1
	Laccobius moraguesi	1	0	0	0	0	0	1	1	1	1	0
	Laccobius neapolitanus	0	0	0	1	1	0	1	1	1	1	0
	Laccobius obscuratus	0	0	0	0	1	0	1	1	1	0	0
	Laccobius sculptus	0	0	0	0	0	0	0	0	0	1	1
	Laccobius simulatrix	1	0	0	0	0	1	0	0	0	0	0
	Laccobius sinuatus	1	1	1	1	1	1	1	1	1	1	0
	Laccobius striatulus	0	1	1	1	1	1	1	1	0	0	0
	Laccobius ytenensis	1	0	0	0	1	1	1	1	1	1	1
	Laccobius femoralis	1	0	0	0	0	1	1	1	1	1	1
	Laccobius revelieri	2	0	0	0	0	0	0	1	1	1	1
	Laccobius albipes	1	0	0	0	0	1	0	0	0	0	0

FAMILY	SPECIES	HABITAT	NEU	SSW	NGD	SGE	FCR	PEV	HEI	SEI	NMO	SMO
HYDROPHILIDAE	*Laccobius colon*	1	1	1	1	1	0	0	0	0	0	0
	Laccobius minutus	1	1	1	1	1	1	0	1	1	0	0
	Laccobius alternus	0	0	0	0	1	1	1	1	0	0	0
	Laccobius gracilis	1	0	0	1	1	1	1	1	1	1	1
	Laccobius pommayi	0	0	0	0	0	0	0	0	0	1	0
	Coelostoma hispanicum	1	0	0	0	0	1	1	1	1	1	1
	Coelostoma orbiculare	2	1	1	1	1	1	1	1	1	0	0
HYDRAENIDAE	*Hydraena exarata*	0	0	0	0	0	0	0	1	1	0	0
	Hydraena marinae	0	0	0	0	0	0	0	1	0	0	0
	Hydraena rugosa	1	0	0	0	0	1	1	1	1	1	0
	Hydraena affusa	0	0	0	0	0	0	1	1	1	0	0
	Hydraena africana	0	0	0	0	0	0	0	0	0	1	0
	Hydraena albai	0	0	0	0	0	0	0	1	1	0	0
	Hydraena alcantarana	0	0	0	0	0	0	0	0	1	0	0
	Hydraena allomorpha	0	0	0	0	0	0	0	0	1	1	0
	Hydraena andalusa	0	0	0	0	0	0	0	0	1	0	0
	Hydraena angulosa	0	0	0	1	1	1	0	0	0	0	0
	Hydraena antiatlantica	0	0	0	0	0	0	0	0	0	0	1
	Hydraena assimilis	0	0	0	1	1	1	0	0	0	0	0
	Hydraena barrosi	0	0	0	0	0	0	1	1	0	0	0
	Hydraena bisulcata	0	0	0	0	0	0	0	1	1	1	1
	Hydraena bolivari	0	0	0	0	0	0	0	1	1	0	0
	Hydraena brachymera	0	0	0	0	0	0	1	1	0	0	0
	Hydraena britteni	1	1	1	1	1	1	0	0	0	0	0
	Hydraena capta	0	0	0	0	0	0	0	1	1	1	0
	Hydraena carbonaria	0	0	0	0	0	0	1	1	1	0	0
	Hydraena cordata	0	0	0	0	0	1	1	1	1	1	0
	Hydraena corinna	0	0	0	0	0	0	1	1	0	0	0
	Hydraena corrugis	0	0	0	0	0	0	1	1	1	0	0
	Hydraena curta	0	0	0	0	0	0	1	0	0	0	0
	Hydraena delia	0	0	0	0	0	0	1	0	0	0	0
	Hydraena egoni	0	0	0	0	1	0	0	0	0	0	0
	Hydraena gavarrensis	0	0	0	0	0	0	1	0	0	0	0
	Hydraena inapicipalpis	0	0	0	0	0	0	1	1	0	0	0
	Hydraena kocheri	0	0	0	0	0	0	0	0	0	1	0
	Hydraena lucasi	0	0	0	0	0	0	1	0	0	0	0
	Hydraena marcosae	0	0	0	0	0	0	0	1	0	0	0
	Hydraena mecai	0	0	0	0	0	0	0	0	1	0	0
	Hydraena melas	1	0	0	1	1	1	0	0	0	0	0
	Hydraena minutissima	0	0	0	0	1	1	1	1	1	0	0
	Hydraena nigrita	0	1	1	1	1	1	1	1	0	0	0
	Hydraena palustris	2	1	1	1	1	0	0	0	0	0	0
	Hydraena pulchella	0	1	1	1	1	1	0	0	0	0	0
	Hydraena pygmaea pygmaea	0	0	0	1	1	1	1	1	1	0	0
	Hydraena quetiae	0	0	0	0	0	0	0	1	0	0	0

FAMILY	SPECIES	HABITAT	NEU	SSW	NGD	SGE	FCR	PEV	HEI	SEI	NMO	SMO
HYDRAENIDAE	*Hydraena quilisi*	0	0	0	0	0	0	1	1	1	0	0
	Hydraena reyi	0	0	0	1	1	1	0	1	0	0	0
	Hydraena riberai	0	0	0	0	0	0	0	0	0	0	1
	Hydraena rigua	0	0	0	0	0	0	0	0	0	1	1
	Hydraena riparia	1	1	1	1	1	1	1	1	1	0	0
	Hydraena rufipennis	0	0	0	0	0	0	1	1	1	0	0
	Hydraena rufipes	0	0	0	0	1	0	0	0	0	0	0
	Hydraena scabrosa	0	0	0	0	0	0	0	0	0	1	0
	Hydraena servilia	0	0	0	0	0	0	0	1	1	0	0
	Hydraena sharpi	0	0	0	0	0	0	1	1	0	0	0
	Hydraena stussineri	0	0	0	0	0	0	1	1	0	0	0
	Hydraena subimpresa	0	0	0	0	1	1	1	1	1	0	0
	Hydraena unca	0	0	0	0	0	0	0	1	1	0	0
	Hydraena altamirensis	0	0	0	0	0	0	0	1	0	0	0
	Hydraena belgica	0	0	0	0	1	0	0	0	0	0	0
	Hydraena bicuspidata	0	0	0	0	0	1	0	0	0	0	0
	Hydraena bitruncata	0	0	0	0	0	0	1	0	0	0	0
	Hydraena catalonica	0	0	0	0	0	0	1	0	0	0	0
	Hydraena dentipes	0	0	0	0	1	0	0	0	0	0	0
	Hydraena diazi	0	0	0	0	0	0	1	0	0	0	0
	Hydraena emarginata	0	0	0	0	0	0	1	1	0	0	0
	Hydraena exasperata	0	0	0	0	0	0	1	1	1	0	0
	Hydraena excisa	0	1	0	1	1	0	0	0	0	0	0
	Hydraena fosterorum	0	0	0	0	0	0	0	1	0	0	0
	Hydraena gaditana	0	0	0	0	0	0	0	0	1	0	0
	Hydraena gracilidelphis	0	0	0	0	0	0	1	1	1	0	0
	Hydraena gracilis	0	1	1	1	1	1	0	0	0	0	0
	Hydraena hispanica	0	0	0	0	0	0	0	1	0	0	0
	Hydraena iberica	0	0	0	0	0	0	1	1	0	0	0
	Hydraena lapidicola	0	0	0	0	1	0	0	0	0	0	0
	Hydraena lusitana	0	0	0	0	0	0	0	1	0	0	0
	Hydraena madronensis	0	0	0	0	0	0	0	1	0	0	0
	Hydraena manfredjaechi	0	0	0	0	0	0	0	1	1	0	0
	Hydraena monstruosipes	0	0	0	0	0	0	0	1	0	0	0
	Hydraena polita	0	0	0	0	1	1	1	0	0	0	0
	Hydraena producta	0	0	0	0	1	1	0	0	0	0	0
	Hydraena saga	0	0	0	0	1	0	0	0	0	0	0
	Hydraena tatii	0	0	0	0	0	0	0	0	1	0	0
	Hydraena truncata	0	0	0	0	1	1	1	1	0	0	0
	Hydraena zezerensis	0	0	0	0	0	0	0	1	0	0	0
	Hydraena atrata	1	0	0	0	0	1	1	1	1	1	0
	Hydraena hernandoi	0	0	0	0	0	0	0	1	1	1	0
	Hydraena isabelae	0	0	0	0	0	0	0	1	0	0	0
	Hydraena testacea	1	0	1	1	1	1	1	1	1	1	1
	Limnebius aguilerai	0	0	0	0	0	0	0	0	0	0	1

FAMILY	SPECIES	HABITAT	NEU	SSW	NGD	SGE	FCR	PEV	HEI	SEI	NMO	SMO
HYDRAENIDAE	*Limnebius alibeii*	0	0	0	0	0	0	0	0	0	1	0
	Limnebius aluta	2	1	1	1	1	0	0	0	0	0	0
	Limnebius atomus	2	1	0	1	1	1	0	0	0	0	0
	Limnebius bacchus	0	0	0	0	0	0	0	0	1	1	0
	Limnebius cordobanus	0	0	0	0	0	0	1	1	1	0	0
	Limnebius crinifer	2	1	1	1	1	0	0	0	0	0	0
	Limnebius evanescens	1	0	0	0	0	0	1	1	1	1	1
	Limnebius extraneus	1	0	0	0	0	0	0	1	1	1	1
	Limnebius fretalis	0	0	0	0	0	0	0	1	1	1	0
	Limnebius furcatus	1	0	0	0	1	1	1	1	1	1	0
	Limnebius gerhardti	0	0	0	0	0	0	1	1	1	0	0
	Limnebius hilaris	0	0	0	0	0	0	0	0	1	0	0
	Limnebius hispanicus	0	0	0	0	0	0	0	1	1	0	0
	Limnebius ibericus	0	0	0	0	0	0	0	1	0	0	0
	Limnebius ignarus	0	0	0	0	0	0	0	0	1	0	0
	Limnebius kamali	0	0	0	0	0	0	0	0	0	1	0
	Limnebius kocheri	0	0	0	0	0	0	0	0	0	1	0
	Limnebius lusitanus	0	0	0	0	0	0	0	1	0	0	0
	Limnebius maurus	1	0	0	0	0	0	1	1	1	1	0
	Limnebius mesatlanticus	0	0	0	0	0	0	0	0	0	1	1
	Limnebius millani	0	0	0	0	0	0	0	1	1	0	0
	Limnebius monfortei	0	0	0	0	0	0	0	0	1	0	0
	Limnebius montanus	0	0	0	0	0	0	0	1	0	0	0
	Limnebius myrmidon	1	0	0	0	0	1	0	1	0	0	0
	Limnebius nanus	0	0	0	0	0	0	0	1	0	0	0
	Limnebius nitidus	1	1	1	1	1	1	1	1	0	0	0
	Limnebius oblongus	0	0	0	0	0	0	1	0	1	1	0
	Limnebius ordunyai	0	0	0	0	0	0	1	0	0	0	0
	Limnebius papposus	2	0	1	1	1	1	0	1	1	0	0
	Limnebius parvulus	2	1	1	1	0	0	0	0	0	0	0
	Limnebius perparvulus	0	0	0	0	0	0	0	0	0	1	0
	Limnebius pilicauda	0	0	0	0	0	0	0	0	0	1	0
	Limnebius truncatellus	1	1	1	1	1	1	1	1	1	1	0
	Limnebius zaerensis	0	0	0	0	0	0	0	0	0	1	0
	Aulacochthebius exaratus	1	0	0	0	1	0	1	1	1	1	1
	Aulacochthebius libertarius	0	0	0	0	0	0	0	0	0	0	1
	Aulacochthebius narentinus	1	0	0	1	1	0	0	0	0	0	0
	Ochthebius aeneus	1	0	0	0	0	1	1	1	1	1	1
	Ochthebius alpinus	2	1	1	0	0	0	0	0	0	0	0
	Ochthebius auriculatus	2	0	1	1	1	0	0	0	0	0	0
	Ochthebius bellieri	0	0	0	0	0	0	0	1	1	0	0
	Ochthebius bicolon	1	1	1	1	1	1	0	1	0	0	0
	Ochthebius bonnairei	0	0	0	0	0	0	0	1	1	1	0
	Ochthebius corsicus	0	0	0	0	0	1	0	0	0	0	0
	Ochthebius crenulatus	0	0	0	0	0	1	0	0	0	0	0

FAMILY	SPECIES	HABITAT	NEU	SSW	NGD	SGE	FCR	PEV	HEI	SEI	NMO	SMO
HYDRAENIDAE	*Ochthebius czwalinae*	0	1	0	0	0	0	0	0	0	0	0
	Ochthebius dilatatus	1	0	1	1	0	1	1	1	1	1	0
	Ochthebius ferroi	0	0	0	0	0	0	1	0	0	0	0
	Ochthebius figueroi	0	0	0	0	0	0	0	1	0	1	0
	Ochthebius flavipes	2	0	0	1	1	0	0	0	0	0	0
	Ochthebius heydeni	0	0	0	0	0	0	1	1	0	0	0
	Ochthebius hungaricus	1	1	0	0	0	0	0	0	0	0	0
	Ochthebius impressipennis	2	0	0	0	0	0	1	0	0	0	0
	Ochthebius irenae	2	0	0	0	0	0	1	1	1	0	0
	Ochthebius jaimei	0	0	0	0	0	0	1	1	1	0	0
	Ochthebius kaninensis	0	1	0	0	0	0	0	0	0	0	0
	Ochthebius immaculatus	2	0	0	0	0	0	1	0	0	0	0
	Ochthebius maculatus	1	0	0	0	0	0	0	0	0	1	1
	Ochthebius minimus	2	1	1	1	1	1	1	1	0	0	0
	Ochthebius aguilerai	0	0	0	0	0	0	0	1	0	0	0
	Ochthebius colveranus	0	0	0	1	0	0	0	0	0	0	0
	Ochthebius exsculptus	0	0	0	1	1	1	1	1	1	0	0
	Ochthebius gibbosus	0	0	0	1	1	1	0	0	0	0	0
	Ochthebius granulatus	0	0	0	0	1	1	0	0	0	0	0
	Ochthebius legionensis	0	0	0	0	0	0	0	1	0	0	0
	Ochthebius melanescens	0	0	0	0	1	0	0	0	0	0	0
	Ochthebius albacetinus	0	0	0	0	0	0	0	0	1	0	0
	Ochthebius andalusicus	0	0	0	0	0	0	0	0	1	0	0
	Ochthebius anxifer	0	0	0	0	0	0	0	1	1	1	1
	Ochthebius atriceps	0	0	0	0	0	0	0	0	0	1	0
	Ochthebius auropallens	1	0	0	0	0	0	1	1	1	1	1
	Ochthebius bifoveolatus	0	0	0	0	0	0	0	1	1	1	1
	Ochthebius caesaragustae	0	0	0	0	0	0	1	1	0	0	0
	Ochthebius corrugatus	0	0	0	0	0	0	0	0	1	1	1
	Ochthebius cuprescens	0	0	0	0	0	0	0	0	1	1	0
	Ochthebius delgadoi	0	0	0	0	0	0	1	1	1	0	0
	Ochthebius dentifer	1	0	0	0	0	0	1	1	1	0	0
	Ochthebius diazi	0	0	0	0	0	0	0	0	1	0	0
	Ochthebius difficilis	0	0	0	0	0	0	1	1	1	1	1
	Ochthebius fossulatus	2	0	0	0	0	0	0	0	0	0	1
	Ochthebius foveolatus	0	0	0	0	1	1	0	0	0	0	0
	Ochthebius gayosoi	0	0	0	0	0	0	0	1	1	0	0
	Ochthebius glaber	0	0	0	0	0	0	0	1	1	0	0
	Ochthebius grandipennis	1	0	0	0	0	0	1	1	1	0	0
	Ochthebius griotes	0	0	0	0	0	0	0	0	0	1	1
	Ochthebius judemaesi	0	0	0	0	0	0	0	1	1	1	0
	Ochthebius lanarotis	0	0	0	0	0	0	0	0	0	1	0
	Ochthebius lenensis	2	1	0	0	0	0	0	0	0	0	0
	Ochthebius marginalis	0	0	0	0	0	0	0	1	1	0	0
	Ochthebius marinus	2	1	1	1	1	0	1	1	1	0	0

FAMILY	**SPECIES**	**HABITAT**	**NEU**	**SSW**	**NGD**	**SGE**	**FCR**	**PEV**	**HEI**	**SEI**	**NMO**	**SMO**
HYDRAENIDAE	*Ochthebius mauretanicus*	0	0	0	0	0	0	0	0	0	1	0
	Ochthebius mediterraneus	0	0	0	0	0	0	1	1	1	1	1
	Ochthebius meridionalis	1	0	0	0	0	0	1	1	1	1	0
	Ochthebius merinidicus	0	0	0	0	0	0	0	0	1	1	1
	Ochthebius metallescens	0	0	0	1	1	1	1	1	1	0	0
	Ochthebius montesi	0	0	0	0	0	0	0	0	1	0	0
	Ochthebius nanus	2	0	0	0	1	0	1	1	1	1	1
	Ochthebius nilssoni	2	1	0	0	0	0	0	0	0	0	0
	Ochthebius nobilis	0	0	0	0	1	0	0	0	0	0	0
	Ochthebius notabilis	2	0	0	0	0	0	1	1	1	1	0
	Ochthebius perpusillus	0	0	0	0	0	0	0	0	0	1	0
	Ochthebius pilosus	2	0	0	0	0	1	1	1	1	1	1
	Ochthebius poweri	0	0	0	0	0	0	0	0	1	1	0
	Ochthebius praetermissus	0	0	0	0	0	0	0	0	0	1	0
	Ochthebius punctatus	2	0	0	0	0	0	1	1	1	1	0
	Ochthebius pusillus	2	0	0	1	1	1	0	0	0	0	0
	Ochthebius quadrifossulatus	0	0	0	0	0	0	0	0	1	1	0
	Ochthebius quadrifoveolatus	1	0	0	0	0	0	1	1	1	1	1
	Ochthebius salinator	2	0	0	0	0	0	0	0	0	0	1
	Ochthebius semisericeus	0	0	0	0	0	0	1	1	1	0	0
	Ochthebius semotus	0	0	0	0	0	0	0	1	1	0	0
	Ochthebius serratus	0	0	0	0	0	0	0	0	1	1	0
	Ochthebius sidanus	0	0	0	0	0	0	0	1	0	0	0
	Ochthebius silfverbergi	0	0	0	0	0	0	0	0	0	0	1
	Ochthebius subpictus	2	0	0	0	0	0	1	1	1	1	1
	Ochthebius tacapasensis baeticus	0	0	0	0	0	0	0	1	1	0	0
	Ochthebius tacapasensis tacapasensis	0	0	0	0	0	0	0	0	0	1	1
	Ochthebius thermalis	0	0	0	0	0	0	0	0	0	0	1
	Ochthebius tivelunus	0	0	0	0	0	0	0	0	0	0	1
	Ochthebius tudmirensis	0	0	0	0	0	0	0	1	1	0	0
	Ochthebius viridescens	2	0	0	0	0	1	1	1	1	1	0
	Ochthebius viridis fallaciosus	2	0	0	0	0	1	1	1	1	1	0
	Ochthebius viridis viridis	2	0	1	1	0	0	0	0	0	0	0
ELMIDAE	*Potamophilus acuminatus*	0	0	0	1	1	1	0	1	1	0	0
	Dupophilus brevis	0	0	0	0	0	1	1	1	0	0	0
	Elmis aenea	0	1	1	1	1	1	1	1	1	0	0
	Elmis atlantis	0	0	0	0	0	0	0	0	0	1	0
	Elmis latreillei	0	0	0	0	1	0	1	0	0	0	0
	Elmis maugetii	0	0	0	1	1	1	1	1	1	0	0
	Elmis obscura	0	0	0	0	1	1	0	0	0	0	0
	Elmis perezi	0	0	0	0	0	0	1	1	0	0	0
	Elmis rietscheli	0	0	0	0	1	0	0	0	0	0	0
	Elmis rioloides	0	0	0	0	1	1	1	1	1	0	0
	Esolus angustatus	0	0	1	0	1	1	1	1	0	0	0
	Esolus bicuspidatus	0	0	0	0	0	0	0	0	0	1	0

FAMILY	SPECIES	HABITAT	NEU	SSW	NGD	SGE	FCR	PEV	HEI	SEI	NMO	SMO
ELMIDAE	*Esolus filum*	0	0	0	0	0	0	0	0	0	1	0
	Esolus parallelepipedus	0	0	0	0	1	1	1	1	1	1	0
	Esolus pygmaeus	0	0	0	0	1	1	1	1	1	1	1
	Esolus theryi	0	0	0	0	0	0	0	0	0	1	0
	Limnius intermedius	0	0	0	1	0	1	1	1	1	1	1
	Limnius muelleri	0	0	0	0	1	1	0	0	0	0	0
	Limnius opacus	0	0	0	1	1	1	1	1	1	1	0
	Limnius perrisi carinatus	0	0	0	0	0	0	1	1	0	0	0
	Limnius perrisi perrisi	0	0	0	0	1	1	1	1	0	0	0
	Limnius volckmari	0	1	1	1	1	1	1	1	1	0	0
	Normandia nitens	0	1	1	0	1	1	1	1	1	1	0
	Normandia sodalis	0	0	0	0	0	1	1	1	1	0	0
	Normandia substriata	0	0	0	0	0	0	0	0	0	1	0
	Normandia villosocostata	0	0	0	0	0	0	0	0	0	1	0
	Oulimnius aegyptiacus	0	0	0	0	0	0	0	0	0	0	1
	Oulimnius bertrandi	0	0	0	0	0	0	1	1	0	0	0
	Oulimnius cyneticus	0	0	0	0	0	0	0	1	0	0	0
	Oulimnius fuscipes	0	0	0	0	0	0	0	0	1	1	0
	Oulimnius jaechi	0	0	0	0	0	0	0	0	0	0	1
	Oulimnius major	1	0	0	0	0	1	1	1	1	0	0
	Oulimnius perezi	0	0	0	0	0	0	0	1	1	0	0
	Oulimnius rivularis	1	0	0	1	0	1	1	1	1	1	0
	Oulimnius troglodytes	0	0	1	1	0	1	1	1	1	1	1
	Oulimnius tuberculatus	0	1	1	1	1	1	1	0	0	0	0
	Oulimnius villosus	0	0	0	0	0	0	0	0	0	1	0
	Riolus cupreus	0	1	1	1	1	1	1	1	1	0	0
	Riolus illiesi	0	0	0	0	0	1	1	1	1	0	0
	Riolus subviolaceus	0	0	0	0	1	1	1	1	1	0	0
	Stenelmis canaliculata	0	1	1	1	1	1	1	1	1	0	0
	Stenelmis consobrina	0	0	0	1	1	1	0	0	1	1	0
	Stenelmis peyerimhoffi	0	0	0	0	0	0	0	0	0	1	0
	Macronychus quadrituberculatus	0	1	0	1	1	1	0	0	1	1	0
DRYOPIDAE	*Dryops algiricus*	2	0	0	0	0	1	1	1	1	1	0
	Dryops anglicanus	2	1	1	1	1	0	0	0	0	0	0
	Dryops auriculatus	2	1	1	1	1	1	0	0	0	0	0
	Dryops championi	0	0	0	0	0	0	0	1	1	0	0
	Dryops doderoi	0	0	0	0	0	0	1	0	1	1	0
	Dryops ernesti	1	1	1	1	1	1	1	1	0	0	0
	Dryops gracilis	0	0	0	0	0	0	1	1	1	1	1
	Dryops griseus	1	1	1	1	1	1	0	0	0	0	0
	Dryops luridus	0	1	1	1	1	1	1	1	1	0	0
	Dryops lutulentus	0	0	0	0	1	1	1	1	1	1	0
	Dryops mesatlanticus	0	0	0	0	0	0	0	0	0	1	0
	Dryops nitidulus	1	1	1	1	1	1	1	1	0	0	0
	Dryops peyerimhoffi	0	0	0	0	0	0	0	0	0	1	0

FAMILY	**SPECIES**	**HABITAT**	**NEU**	**SSW**	**NGD**	**SGE**	**FCR**	**PEV**	**HEI**	**SEI**	**NMO**	**SMO**
DRYOPIDAE	*Dryops rufipes*	0	0	0	0	1	1	0	0	0	0	0
	Dryops similaris	2	1	1	1	1	1	0	1	0	0	0
	Dryops striatellus	1	0	0	1	0	0	0	1	1	1	0
	Dryops striatopunctatus	1	0	0	0	1	1	0	0	0	0	0
	Dryops subincanus	0	0	0	0	0	1	0	0	0	0	0
	Dryops sulcipennis	0	0	0	0	0	0	1	1	1	1	1
	Dryops viennensis	1	0	0	1	1	1	1	0	0	0	0
	Pomatinus substriatus	0	0	1	1	1	1	1	1	1	1	1

Appendix S2

The establishment of the ten regions which finally configured the study area was mainly supported in three different kind of resources: i) literature; ii) own expertise; and iii) an iterative process finalized with cluster and PCoA analyses (see below) based on political-administrative entities and faunistic records (own data, other unpublished sources and published records from catalogues).

We established two regions within Morocco delimited by the High Atlas, the Sahara desert and the Moulouya river basin based on literature (Brown et al. 2002) and own expertise. We used established divisions from the literature for the Iberian Peninsula (Ribera 2000) and France regions (Queney 2004). Following these authors, we merged the Pyrenean regions of Iberia and France, which also included the Ebro Valley. Regions in Germany were taken from Hess et al. 1999 and drawn following Meynen & Schmithüsen (1953-1962) and Riecken et al. (1994).

Sweden was divided into two main regions by means of a cluster analysis (figure S1) according to the species checklists of their provinces (Hansen 1987; Nilsson & Holmen 1995), which used a UPGMA algorithm based on Sorensen dissimilarity matrices. On the one hand, an area in the north included the provinces of Härjedalen, Medelpad, Jämtland, Norrbotten, Ångermanland, Västerbotten, Åsele Lappmark, Pite Lappmark, Torne Lappmark and Lule Lappmark. On the other hand, another area in the south included the provinces of Gästrikland, Södermanland, Östergötland, Uppland, Småland, Västergötland, Skåne, Öland, Gotland, Bhouslän, Blekinge, Halland, Dalsland, Närke, Västmanland, Värmland, Dalarna and Hälsingland. The island of Gotska Sandön was dismissed following the results of the cluster analysis.

To delimit the regions in central and northern Europe, where clear geographic barriers do not exist, we performed a PCoA analysis based on pairwise fauna similarities between all the regions taken into account (figure S2). The PCoA distance matrix consisted of the average percentage of shared species in 1000 random subsamples which sample size was the richness of the poorest area among

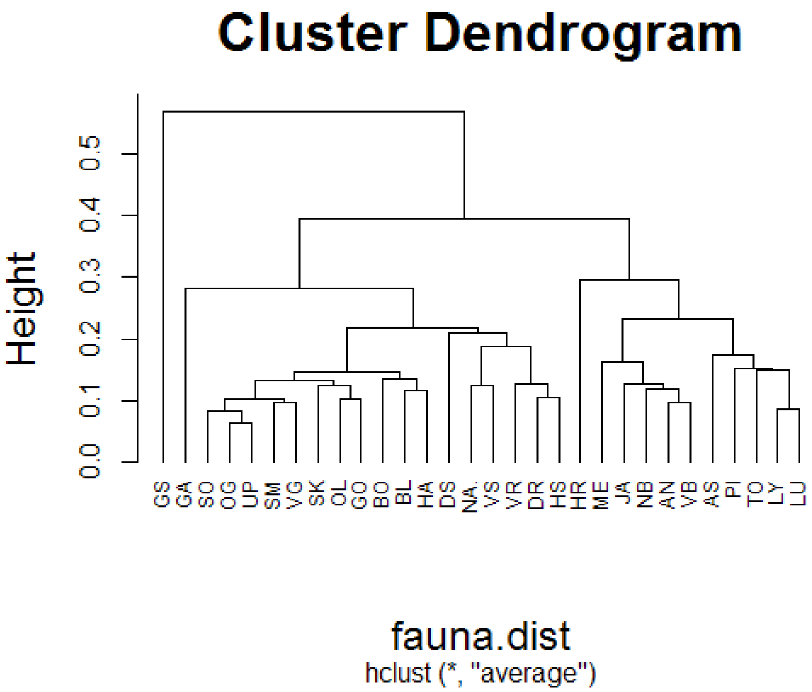

Figure S1 Cluster analysis results. Codes of the provincies extracted from Nilsson & Holmen (1995).

all the zones considered. The analysis included data from a total of 42 areas, which were established mainly based of the countries/regions specified in the Palaearctic catalogues of water beetles (Löbl & Smetana 2003; 2004; 2006), except for those cases we had more detailed information: Iberia (Millán et al. 2014; Sánchez-Fernández et al. 2015), France (Queney, 2004), Germany (Hess et al. 1999), Czech Republic (Boukal et al. 2007) and Sweden (Hansen, 1987; Nilsson & Holmen 1995). Thus, except for those cases in which geographical barriers were crucial to establish the biogeographic regions (from the French Massif Central region to the south, see figure 1), and based on the PCoA analysis, the regions were configured as follows: i) Southern Germany region included Southwestern, Western and Eastern German territories from Hess et al. (1999) but also French 5 region from Queney (2004) and Luxembourg (Löbl & Smetana 2003; 2004; 2006); ii) Northern Germany-Denmark region included Northwestern, Northeastern and Coastal German territories from Hess et al. (1999) and also Denmark (Hansen 1987; Nilsson & Holmen 1995; Löbl & Smetana 2003; 2004; 2006); Southern Sweden region included a number of Swedish provinces based on the cluster analysis explained above; Northern Europe region included several Swedish provinces based on the same cluster analysis, but also Finland, Norway and the North

Territories of Russia established in the Palaearctic catalogues (Löbl & Smetana 2003; 2004; 2006), being delimited by the Ural mountains to the East. In case there were still certain ambiguities, we tend to make southern regions smaller and northern regions bigger, as this bias worked against our predictions.

All statistical analyses were carried out using the statistical computing software R (R Development Core Team, 2012) and the library ade4 (Dray and Dufour, 2007).

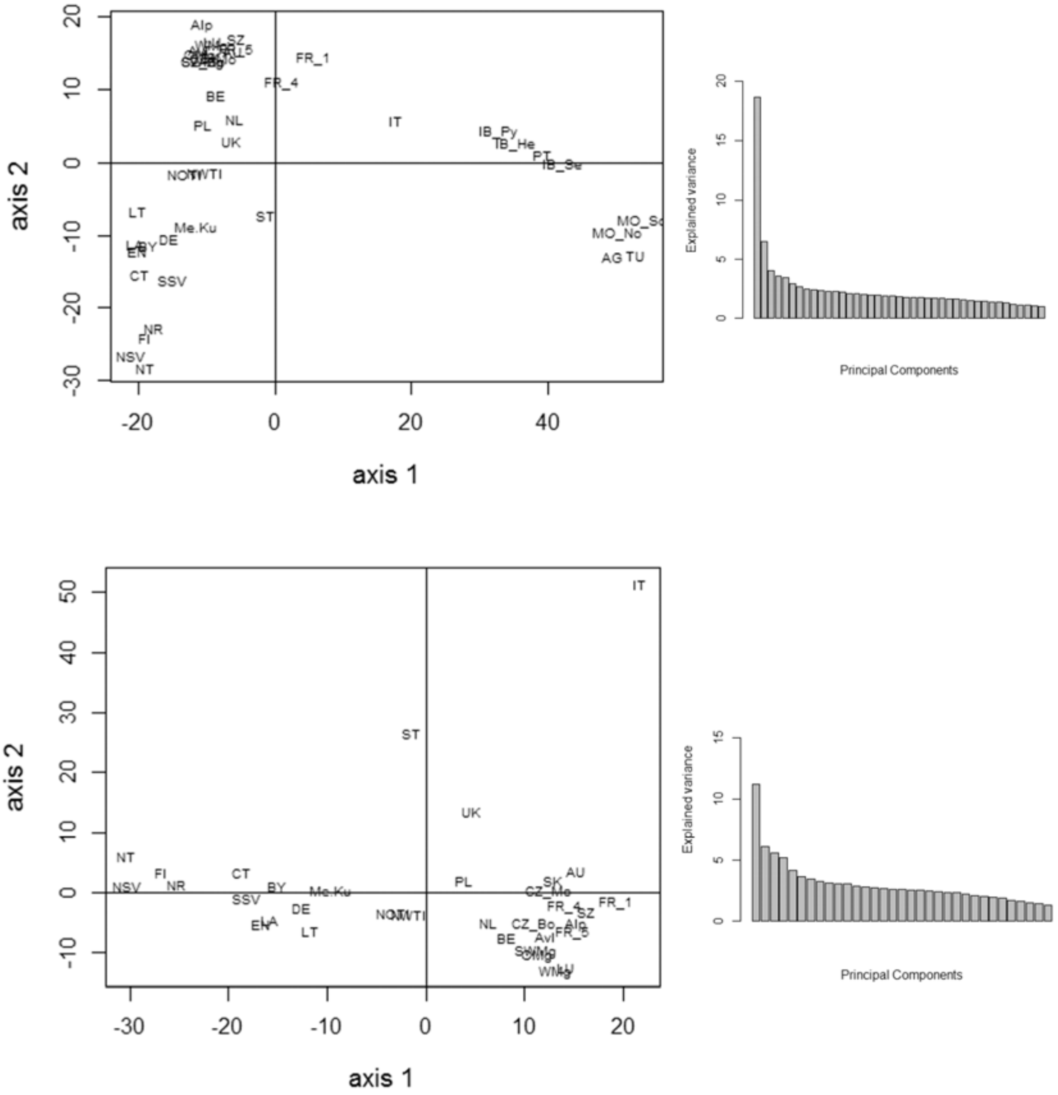

Figure S2 PCoA analysis results. Codes of the areas extracted from Hess et al. (1999), Löbl & Smetana (2003; 2004; 2006) and Queney (2004), except for NSV (North Sweden), SSV (South Sweden), CZ_Bo (Czech region of Bohemia), CZ_Mo (Czech region of Moravia), IB_Py (Pyrenean region of Iberia), IB_He (Hercynian region of Iberia), IB_SE (Southeastern Iberia), MO_No (North Morocco) and MO_So (South Morocco).

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Appendix S3

Local checklist were compiled from: i) own data (Moroccan and Iberian sites); ii) other unplished data (Moroccan, French and German sites, see acknowledgements); and iii) published data (French and Swedish sites). We provided the different sources below, listed by regions:

- Southern Morocco: EA, IR and NB.
- Northern Morocco: EA, IR and NB.
- Southeastern Iberia: EA and IR.
- Hercynian Iberia: EA and IR.
- Pyrenean: EA and IR.
- French Central Massif: PQ and published data (see references).
- Southern Germany: WS.
- Northern Germany-Denmark: WS.
- Southern Sweden: published data (see references).
- Northern Europe: published data (see references).

Acronyms used for databases from which the information was obtained:

NB	Nard Bennas personal database.
EA	Ecología Acuática database (University of Murcia, Spain).
IR	Ignacio Ribera personal database.
PQ	Pierre Queney personal database.
WS	Wolfram Sodermann personal database.

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General Conclusions

"El árbol que planté, benemérita acción porque ya quedan pocos en mi pobre ciudad, era un sauce llorón. Llorón pero sin mocos. Pero resulta que tenían otro plan las urbanizaciones. Pobre sauce llorón, ya secó el alquitrán tus verdes lagrimones".

(El tío Marcial, Javier Krahe)

'La Ramona' continental Salt-pans (Calasparra, Murcia)

Author: Ecología Acuática

Chapter 1:

1. Lentic habitats harboured a high number of standing water specialists but also a notable proportion of facultative species, which demonstrates their crucial role in the metapopulation dynamics of many species. However, only one threatened Iberian endemics (*Ochthebius irenae*) was detected among the whole set of lentic specialists recorded for the Albacete province. These findings highlight the importance that lentic ecosystems have for the maintenance of aquatic biodiversity both at regional and global scale.

2. *Natural pools* was the habitat type showing the highest species richness. However, the highest number of endemics and threatened species was detected in *Endorheic lagoons*. Therefore, both habitat types display the highest conservation value.

3. All the habitat types, with the exception of karstic lagoons, presented indicator species of naturalness, which could constitute a useful tool for biomonitoring, management and conservation of these systems.

Chapter 2:

4. The lentic habitats from the Iberian southeast harboured 35% of all water beetle species recorded for the Ibero-Balearic region, and up to 52% of the lentic specialists. One more time, *Natural pools* was the habitat type showing the highest species richness, whereas *Continental salt-pans*, despite its low richness, showed the highest number of Iberian endemics.

5. Conductivity was the environmental variable which best grouped the sites according to the faunal patterns observed for the whole dataset. In contrast, for the freshwater submatrix the best explanatory variable was the level of disturbance, whereas a combination of disturbance, altitude and conductivity showed the greatest explanatory power in the case of the saline submatrix.

6. The whole set of sites showed a significant nested pattern mainly associated with the level of disturbance. When fresh and saline sites were analysed independently, nested patterns were also detected, although it was more patent in the former case. The level of disturbance was the environmental variable which best

explained this pattern for fresh water sites, whereas conductivity did the same for saline sites.

7. This study highlights the importance of the biodiversity associated to lentic habitats in the Iberian southeast, as well as the impact that human activity exerts on these ecosystems.

Chapter 3:

8. The species richness per family of water beetles was significantly related to both the biological and ecological trait diversity. However, there were families which showed a high diversity of biological traits despite displaying a moderate taxonomic diversity (e.g. Hydrophilidae), and families which showed lower biological trait diversity than other much more diverse from the taxonomic point of view (e.g. Hydraenidae).

9. For biological traits, genera were mostly separated as a function of diet and feeding, respiration and reproduction types, with clear differences at suborder level. For ecological traits, genera were separated according to stream longitudinal distribution, local habitat and current velocity preferences, with no clear differences at suborder level.

10. Water beetles displaying a specific combination of biological traits, concretely those related to respiration, dispersal and diet, tended to occur in particular habitats. In this sense, Elmidae showed the highest congruence between biological and ecological traits, whereas Hydraenidae displayed the lowest as it inhabits a wide set of habitats despite its low biological traits variability.

11. Our results point to the predominance of habitat filtering processes in headwater streams, leading to trait conservatism or trait convergence. Whilst, biotic factors, e.g. interspecific competition, would be more relevant in lentic fresh water bodies, resulting in trait divergence.

12. Further research on biological traits of taxa, especially those concerning physiological aspects, is needed to improve our knowledge about the life strategies of water beetles.

Chapter 4:

13. *Stictonectes abellani* is described as a new species for science.

14. Despite Dytiscidae is a well known family in the Iberian Peninsula and *Stictonectes abellani*, has a relatively wide distribution range in the Iberian Peninsula this new species would have remained undiscovered due to its cryptic aspect in relation to other species of the genus. However, its size and the distinct form of the anterior margin of the clypeus of both sexes allow its differentiation from the other 7 *Stictonectes* species occurring in the Iberian Peninsula. In the most difficult case, the shape of the male genitalia parameres allows to distinguishing *S. abellani* from *S. optatus*.

15. *Stictonectes abellani* is typical from mountainous areas with siliceous geology and continental Mediterraean climate with certain oceanic influence.

16. The potential distribution models for the Iberian endemics *Stictonectes* did barely show overlapping, pointing to differences in the ecological niche of these species.

17. The new species should be catalogued as threatened due to: (i) its high genetic uniqueness within the genus; (ii) its relatively small geographic range at global scale as it only inhabits in the Hercynian Iberia region; and (iii) its high habitat specificity, showing a clear preference for one of the most threatened habitats in the Iberian Peninsula, such as the mid-low altitude streams.

Chapter 5:

18. Gamma diversity, both for lotic and lentic specialists, exhibited marked but contrasting latitudinal patterns in the Western Palaearctic, decreasing towards the north and the south part of the gradient, respectively. Both trends crossed in the Ebro Valley-Pyrenees area, whereas the highest differences were detected north beyond the 0 ºC LGM isotherm. Such findings demonstrate the accumulation of species with low dispersal ability in the more climatically stable southern regions and its scarcity in the recently deglaciated northern regions.

19. Beta diversity diminished in all cases towards the north. However, the factors underlying such patterns were different depending on the habitat. Most of the lotic beta diversity was associated with turnover in the southern half of the gradient, whereas nestedness gained importance towards the northern half. In contrast, the majority of lentic beta diversity was related to nestedness in the southern extreme whilst turnover predominated in the remaining areas.

20. The relationship between alpha diversity and latitude showed similar but less steep trends to those detected for gamma diversity in both kind of habitat. Such finding points to the high influence that regional pools exert on local richness. The fact we did not detect signs of saturation for any kind of habitat and lentic sites contributed in a uniform way across latitude but not in a higher degree than lotic ones reveals our incomplete knowledge of the factors that determine local species richness and the mechanisms underlying their assemblage.

21. Our results also highlight the importance of refugia in eastern Europe and Asia as a source for the recolonization process of central and northern European areas, especially for lentic species.

Appendix

Papers in JCR-indexed journals included in this thesis

“No jugamos para ganar, sino para que nos recuerden”.
(Sócrates de Souza)

‘Pinilla’ stream in Viveros/El Ballestero (Albacete)

Author: Ecología Acuática

CHAPTER 1

Picazo F, Moreno JL, Millán A (2010) The contribution of standing waters to aquatic biodiversity. *Aquatic Ecology*, **44**, 205-216.

Aquat Ecol (2010) 44:205–216
DOI 10.1007/s10452-009-9279-y

The contribution of standing waters to aquatic biodiversity: the case of water beetles in southeastern Iberia

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Received: 6 November 2008 / Accepted: 27 July 2009 / Published online: 11 August 2009

Abstract The southeast of the Iberian Peninsula is a recognized area of high aquatic biodiversity, water beetles being one of the most well-known groups contributing to such biodiversity. The standing waters of this area show a high habitat diversity, occurring fresh, saline, temporary, permanent, karstic, endorheic, and artificial small water bodies. Despite this, there has been no attempt to analyze their contribution to local biodiversity. In this work, we identify the species inhabiting standing waters, analyze their contribution to the checklist from the study area, and recognize the species exclusive to this kind of habitat. We also highlight the most threatened species, identify the habitats which constitute biodiversity hotspots for this group, explore patterns of water beetle assemblage composition, and identify indicator species associated with each habitat type. We collected 125 species, 55 of them being typical to lentic habitats, in the set of 26 sampled standing water bodies, which means the 57% of the 218 species recorded in the most recent checklist for the study area. A total of 10 species are Iberian endemics and four can be considered threatened, *Ochthebius irenae* falling in both categories. Natural ponds showed the highest species richness (91 species), while saline water bodies (endorheic lagoons and continental salt-pans) contributed the most threatened species: *Nebrioporus baeticus*, *Ochthebius delgadoi*, *Ochthebius tudmirensis* and *Ochthebius irenae*. The most representative species for continental salt-pans was *Ochthebius notabilis*, for endorheic lagoons *Ochthebius marinus* and *Hygrotus pallidulus*, while *Hydroglyphus geminus* played this part in rice fields. Our results suggest that rice fields, endorheic lagoons, and continental salt-pans have specific water beetles assemblages, which could be used in bioassessment and conservation studies. In general, standing waters are seriously threatened in this area, particularly as a result of intensive agricultural activities. Thus, taking into account these ecosystems hold a high number of species, their continued degradation is likely to result in a significant loss of biodiversity, including key populations of a number of threatened and endemic species.

Keywords Standing waters · Aquatic biodiversity · Water beetles · Southeastern Iberia · Indicator species · Conservation

Introduction

The Mediterranean Basin is considered to be one of the world's biodiversity hotspots (Myers et al. 2000).

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CHAPTER 2

Picazo F, Bilton DT, Moreno JL, Sánchez-Fernández D, Millán A (2012) Water beetle biodiversity in Mediterranean standing waters: assemblage composition, environmental drivers and nestedness patterns. *Insect Conservation and Diversity*, **5**, 146-158.

Insect Conservation and Diversity

Insect Conservation and Diversity (2012) **5,** 146–158 doi: 10.1111/j.1752-4598.2011.00144.x

Water beetle biodiversity in Mediterranean standing waters: assemblage composition, environmental drivers and nestedness patterns

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Abstract. 1. Nowadays, it is widely accepted that increasing human activity is highly related to the current biodiversity loss, this fact being especially worrying in aquatic ecosystems, mainly in semi-arid areas. To date, studies on the biodiversity of small standing waters are focused on Central and Northern Europe, Mediterranean regions being poorly documented.

2. Here, data for aquatic Coleoptera in SE Iberia have been used to: (i) explore the relative contribution of standing waters to regional aquatic biodiversity, (ii) identify the environmental drivers structuring beetle assemblages, (iii) determine the degree to which standing water assemblages are nested subsets, and (iv) make recommendations for the conservation and management of the habitats studied.

3. Water beetles are a hyperdiverse group of aquatic insects which represent good surrogates of aquatic biodiversity. A total of 95 sites across eight habitat types were sampled, 174 species being recorded (11% were Iberian endemics).

4. Habitat types generally had distinct aquatic beetle faunas; a combination of conductivity, anthropogenic impact and altitude best explaining differences in assemblages across sites. Beetle faunas were significantly nested, this being the case across all sites, and for both fresh and saline systems independently. Disturbance was identified as a key driver of nestedness across sites overall, and particularly in freshwaters, whereas conductivity was more important in saline waters.

5. Our study identifies the biodiversity importance of lentic inland waters in the Iberian southeast, and points to the influence that human activities already exert on the invertebrate faunas of western Mediterranean wetlands.

Key words. Aquatic Coleoptera, community ecology, conservation, nestedness, standing waters.

Introduction

The Mediterranean Basin is one of the most important biodiversity hotspots world-wide (Mittermeier *et al*., 1998; Myers *et al*., 2000). It has supported a high human population since historical times, which, coupled with a rapid increase in anthropogenic environmental change in recent decades, is leading to a high rate of habitat loss in the region (Wilson, 1988; May *et al*., 1995; Fontaine *et al*., 2007), which jeopardises a considerable part of its biodiversity. This is especially the case for inland aquatic ecosystems in Southeastern Iberia. This area is dominated by a semi-arid climate where water bodies, and standing ones in particular are naturally relatively rare at the landscape scale (Gómez *et al*., 2005).

Inland aquatic ecosystems in this region are very diverse due to the wide variation in conductivity, current velocity and temporality found (Millán *et al*., 2006). Such environmental

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CHAPTER 3

Picazo F, Millán A, Dolédec S (2012) Are patterns in the taxonomic, biological and ecological traits of water beetles congruent in Mediterranean ecosystems? *Freshwater Biology*, **57**, 2192-2210.

Freshwater Biology

Freshwater Biology (2012) **57**, 2192–2210 doi:10.1111/j.1365-2427.2012.02859.x

Are patterns in the taxonomic, biological and ecological traits of water beetles congruent in Mediterranean ecosystems?

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SUMMARY

1. Coleoptera species show considerable diversity in life histories and ecological strategies, which makes possible their wide distribution in freshwater habitats, including highly stressed ones such as saline or temporary waterbodies. Explaining how particular combinations of traits allow species to occupy distinctive habitats is a central question in ecology.
2. A total of 212 sites, sampled over a wide range of inland aquatic habitats in the south-eastern Iberian Peninsula, yielded 272 species belonging to 68 genera and 11 families. The affinities of genera for 11 biological and 11 ecological traits, gathered from literature and the authors' own expertise, were used to assess the degree of congruence between taxonomic, biological and ecological traits.
3. Taxonomic richness was significantly related to the number of both biological and ecological trait categories, with the richest families also showing the highest functional and ecological diversity. A fuzzy correspondence analysis performed on the abundance-weighed array of biological traits separated genera according to categories of diet, feeding habits, respiration, reproduction and locomotion. A similar analysis of ecological traits revealed that preferences related to longitudinal distribution (headwater to mouth), local habitat and current velocity best discriminated genera. At the family level, there was a distinctive functional grouping of genera based on biological traits. Only Elmidae showed noticeable homogeneity across genera for both biological and ecological traits.
4. Co-inertia analysis demonstrated a significant match between biological and ecological traits (Rv-correlation = 0.35, $P < 0.001$). Elmidae genera displayed the highest concordance, whereas Hydraenidae demonstrated the lowest.
5. These results indicate that the predominance of habitat filtering processes in headwater streams yields biological trait conservatism (as shown by Elmidae genera), as well as trait convergence for some specific traits (for instance, respiration) among certain Dytiscidae genera and other typical rheophilic taxa, whereas other biotic factors, such as competition among species, appear more prominent in less stressed habitats. Further knowledge of traits, especially regarding physiological capabilities, is needed to better understand water beetle life history strategies.

Keywords: biological traits, ecological traits, habitat templet, Mediterranean region, water beetles

Introduction

Understanding how species assemble locally from a given species pool requires consideration of how their traits are filtered to match local environmental conditions (Poff, 1997). The 'habitat templet' concept suggests that the habitat provides a templet upon which evolution forges characteristic species life history traits

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CHAPTER 4

Millán A, **Picazo F**, Fery H, Moreno JL, Sánchez-Fernández D (2013) *Stictonectes abellani* sp. n. (Coleoptera: Dytiscidae: Hydroporinae) from the Iberian Peninsula, with notes on the phylogeny, ecology and distribution of the Iberian species of the genus. *Zootaxa*, **3745**, 533-550.

Zootaxa 3745 (5): 533–550
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3745.5.3
http://zoobank.org/urn:lsid:zoobank.org:pub:E6FBA088-D1B5-4F57-9DBC-C53BBE0DB48D

Stictonectes abellani sp. n. (Coleoptera: Dytiscidae: Hydroporinae) from the Iberian Peninsula, with notes on the phylogeny, ecology and distribution of the Iberian species of the genus

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Abstract

Stictonectes abellani sp. n. is described from the Iberian Peninsula. On average, the new species is larger and the colouration of the upper surface darker than in most other species of the genus. Seemingly the species has been confounded with others in the past, particularly *S. optatus* (Seidlitz, 1887). Males can be separated from externally similar species by studying the shape of the parameres. Additionally, the anterior margin of the clypeus is provided with a distinct rim in both sexes, which is absent or only weakly present in other species. The habitus and the male genitalia of the new species are illustrated, and compared with those of *S. optatus*. External morphological differences from other members of the genus are discussed. According to studies of the molecular phylogeny, based on fragments of four mitochondrial genes, *S. abellani* sp. n. is clearly separated from previously described species of *Stictonectes* Brinck, 1943, apparently being relatively basal within the genus. The new species is rather widely distributed in the south-western part of the Iberian Peninsula, inhabiting pools in small temporary siliceous streams. We provide distributional maps for all eight Iberian *Stictonectes* and estimate the potential distributional areas of the new species and the other two endemic Iberian species *S. occidentalis* Fresneda & Fery, 1990 and *S. rebeccae* Bilton, 2011, based on environmental niche modelling.

Key words: Dytiscidae, Hydroporinae, *Stictonectes*, new species, Iberian Peninsula, molecular phylogeny, distribution models

Introduction

The genus *Stictonectes* Brinck, 1943 consists of 12 species (including the one described here), all of which are restricted to the western Mediterranean and Macaronesian regions (Bilton 2011; Nilsson & Hájek 2013). The Iberian Peninsula harbours eight of these species, three of which are endemic. *Stictonectes epipleuricus* (Seidlitz, 1887)—mainly distributed in the Iberian Peninsula—is also recorded from the south of France and therefore cannot be considered as a true Iberian endemic. Species of the genus are rather similar externally and even the shape of the male genitalia is of little help if it is not very accurately studied—this all making a reliable identification difficult. In order to identify individual specimens it is mainly necessary to study the dorsal colour pattern, the dorsal and ventral punctation and the shape of the male parameres. In general, *Stictonectes* species have similar habitat preferences, it being common to find more than one species of this genus living together in the same locality; something that can additionally complicate their identification.

In this work we describe a new species which, surprisingly, shows a wide distribution across the south-western part of the Iberian Peninsula. It has probably remained undetected due to its external similarity to *S. optatus* (Seidlitz, 1887), which often co-occurs with the new species. In addition, we include a molecular phylogeny showing the relationships between the new species and all other members of the genus. Finally, based on known

Accepted by M. Toledo: 18 Nov. 2013; published: 9 Dec. 2013

Agradecimientos

"When I go to cross that river, she is comfort by my side. When I try to undernstand, she just opens up her hands. There's a big, a big hard sun, beating on the big people in a big hard world".

(Hard Sun, Eddie Vedder)

'Júcar' river in 'hoces de Alarcón/El Picazo' (Cuenca)

Author: Félix Picazo

La tesis no es sólo un documento en el que se plasma el resultado de un trabajo de investigación original, sino que acaba convirtiéndose en uno de los actos más relevantes de la obra de la vida, pudiendo ser más o menos divertido y tener mayor o menor duración. En mi caso ha sido muy placentero y largo. No sabría decir si lo primero es la causa y lo segundo el efecto, o al contrario. Obviamente, en un período con las características mencionadas anteriormente, ha sido mucha la gente que ha intervenido. Algunos han sido la obra, otros han sido coprotagonistas, otros han tenido un papel más secundario, también ha habido cameos estelares, figurantes, etc., pero todos, absolutamente todos, han sido fundamentales para obtener el resultado que ahora mismo tenéis ante vuestros ojos. Lo que sí que no ha habido es un doble para las escenas de riesgo, pues esa es una de las principales características de esta gran obra que es la vida. La otra es que apenas existe guión, y uno se pasa la mayoría del tiempo improvisando. Hay quien asegura que el acto concreto que comprende la tesis si que tiene un guión cerrado, pero cualquiera que haya participado en alguno de ellos sabe de sobra que eso no es así y que al final las circunstancias se imponen y mandan. Valga como ejemplo el aspecto de las mesas de los funcionarios de postgrado, abarrotadas con los formularios de cambio de título rellenados por prácticamente todos y cada uno de los doctorandos. En fin, como afirma el dicho, por cierto claramente relacionado con la ecología: “en los sistemas complejos no existen problemas y soluciones, sino cambio y adaptación”.

Vaya por delante que probablemente me deje a alguien en el tintero. Es imposible reflejar en unas líneas toda la gente que ha participado en mayor o menor medida en esta etapa y mucho menos transmitir lo imprescindible de su actuación. Así pues, pido disculpas de antemano. Por favor, no me lo tengáis en cuenta.

Quiero comenzar agradeciendo a mis padres el que se hayan dejado la salud, literalmente, para que a día de hoy el que escribe estas líneas esté en disposición de optar al grado de Doctor. Es imposible plasmar en unas líneas, ni siquiera en varios folios, lo afortunado que me siento de haber tenido unos padres como vosotros. Sobre todo, muchas gracias por los valores que me habéis transmitido. Gracias también a mi hermana por su apoyo incondicional. Espero que, aunque muy probablemente me tocará seguir su evolución en la distancia, Leo crezca sano y feliz.

Ahora sí, es el turno de mostrar mi más sincero agradecimiento a los directores de la obra.

Andrés Millán fue quien me abrió las puertas del Departamento de Ecología Acuática. Parece que fue ayer cuando, al concluir una de sus clases de Ecología en 3º de

Ciencias Ambientales, me animé a preguntarle si era posible que me echara una mano para conseguir un proyector que utilizaría el fin de semana siguiente en Segura de la Sierra para dar una charla sobre huellas y rastros de carnívoros. Pocos días después ya estaba subiendo al laboratorio para echar una mano en los trabajos que por aquel entonces se estaban llevando a cabo. Después vendría la fase de alumno interno y finalmente la beca para hacer la tesis. Fue una apuesta arriesgada. Tuve que renunciar a algún proyecto con financiación en firme que había en aquel momento sobre la mesa en otra parte, pero la calidad humana de la gente que componía el grupo de Ecología Acuática y una llamada por teléfono de Andrés el día que salí de un examen de estadística con no muy buenas sensaciones, me animó a jugármela. Ahora puedo decir que la apuesta salió bien. Muy bien, añadiría. Muchas gracias Andrés. Por introducirme en el mundo de la ecología acuática, por despertarme el interés por la taxonomía de los escarabajos y por iniciarme en el resto de tareas científicas, pero también por haberme escuchado y apoyado durante todo este tiempo. No ha habido tema que no hayamos tratado: economía, política, deporte, música, cine, incorches, etc. Han sido muchas horas de lupa y de campo, y también muchos kilómetros compartiendo coche por toda la geografía ibérica (igual al final acabas echando de menos a este copiloto tocapelotas). Y, aunque algunas veces hayan ocurrido ciertas perturbaciones en el ecosistema en el que se ha desenvuelto la tesis, creo que hemos sabido dotarle de la resiliencia necesaria para que los procesos se mantuvieran perfectamente funcionales. También quiero agradecerle a Pepa Velasco su labor durante todos estos años, y es que, aunque su nombre no figure en ningún documento oficial, también la considero supervisora de esta tesis. Muchas gracias por haberte dejado la piel en sacar adelante a la familia ecoacuática, incluso durante algún momento bastante duro que hoy afortunadamente ha sido superado.

De la mano de José Luis Moreno empecé a conocer los ríos, arroyos, fuentes, lagunas, charcas, salinas, etc. de Castilla-La Mancha. Qué grandes recuerdos de todas esas jornadas de campo y cuánto se echan de menos. Gracias por enseñarme las 4 cosas que se sobre macrófitos, pero también por todas las conversaciones sobre aves, mamíferos, reptiles, anfibios, peces, ácaros, limnología, en fin, lo que surgiera. Un todo terreno “made in Tobarra”, vaya. Muchas gracias por haberme aceptado como doctorando y por el tiempo que le has dedicado a esta tesis. Lamento profundamente que no hayamos podido pasar más tiempo trabajando codo con codo debido a la distancia geográfica. Por supuesto, gracias al resto del equipo del Centro Regional de Estudios del Agua (CREA) y en especial a Mari Cruz Cano y Laura Monteagudo por su inestimable colaboración en algunas tareas concretas. Venga Laura, ¡qué esa tesis va a salir genial!

Y luego está David Sánchez, el brujo bueno del noroeste, el "papa" de Ecología Acuática. Muchas gracias por tu buen hacer, por tus palabras, pero sobre todo por tu trabajo, ya que has conseguido evitar en más de una ocasión cuando estaba asomado al precipicio que acabara despeñándome por él. Gracias también por poner la guinda a las portadas de los capítulos con ese toque tan tuyo, ¡me encantan!. Por más que busco y rebusco, no se me ocurre ningún motivo por el que te pueda dar cera (y mira que me gusta sacarle puntica a todo). Y si hay alguno, ahora mismo se me ha olvidado. Ya sabes cómo están las cabezas y los despistes que tiene uno. Mira, hablando de eso...bueno, nada, da igual, dejémoslo. Fuera de broma, eres un ejemplo a imitar, tanto en lo profesional como en lo personal. Creo que nunca seré del todo consciente sobre la buena suerte que tenido al conocerte. Aquí me gustaría también agregar a Pedro Abellán, el otro hermano mayor de la familia ecoacuática. Como David, siempre dispuesto a echar una mano en lo que hiciera falta, pero en este caso el mérito es doble al no tener responsabilidad como supervisor (aunque al igual que ocurre con Pepa, moralmente también lo considero como tal). Y vaya si está preparado el muchacho. Da igual el tema que tengas que tratar con él: teoría ecológica, genética, SIG, maquetación, softwares de todo tipo, estadística, etc. Pedro siempre está dispuesto a ayudar y siempre aporta cosas interesantes. Muchas gracias a ambos. Sinceramente, os considero los hermanos mayores que nunca tuve, y es por ello que siento a Cehegín como el Villalgordo murciano. Así es como se hace patria.

La familia ecoacuática se complementa con un puñado de retoños que han crecido tanto, que algunos ya se han independizado. Creo que a nadie le sorprenderá que empiece este apartado hablando de Tano Gutiérrez. No hace falta que me extienda. Todos los que me conocéis sabéis de sobra quién es este mangurrián y el papel clave que ha tenido en mi evolución durante estos últimos años, incluso aunque nunca hayáis coincidido con él (que ya es difícil). Tano es todo. Ni siquiera el archivo de radio televisión española tendría capacidad suficiente para albergar las grabaciones de todos los ratos que hemos pasado juntos. Pero tampoco hace falta, nosotros somos más de seguir rodando capítulos nuevos cada día que de ponernos a visionar grabaciones anteriores. Como dijo aquel sabio, "no jugamos para ganar, sino para ser recordados". Muchas gracias por todas las cosas que me has enseñado, por todas las experiencias compartidas y por toda la gente que me has presentado y que ahora también son parte fundamental de mi vida. Has conseguido que ahora Cartagena sea mi Albacete murciano.

Y qué decir del resto de la camada. Empezaré por Paula Arribas. No se si tienes idea de cuánto he aprendido y espero seguir aprendiendo de ti. No estaba allí, pero yo diría que cuando Paula nació, el médico les dijo a sus padres "han tenido ustedes una científica”. Muchas gracias por tu ejemplo, por tu ayuda siempre que la he necesitado y por tu amistad. Aprovecho para mandar un fuerte abrazo también a Carmelo y a toda la familia Arribas Blázquez-Andújar Fernández ¡Qué buenos ratos hemos echado en la granja! Tres hurras por Albacete y por Hellín. Continuaré los agradecimientos por Óscar Belmar. Estoy seguro de que algún día cuando en una conversación se mencione el Infante, a continuación alguien apuntará “sí, el barrio de Murcia que vió crecer a Óscar Belmar”. Gracias por todos estos años que hemos compartido, literalmente, codo con codo (en este caso a mi izquierda). A mi derecha, y con ¿? kilos de peso, Daniel Bruno, el vendaval de la Alameda. Nunca nadie fue capaz de hacerle morder la lona. Muchas gracias a ti y a Ana por vuestra amistad. Buena gente, joder. José Antonio Carbonell es mi compañero de chanzas y performances de todo tipo. Qué pena que no hayamos pasado más tiempo juntos porque para él bajar a Murcia desde Molina de Segura y tener que buscar aparcamiento es poco más o menos como si le cortaran una mano, ¡all right! Simone Guareschi es el fichaje estrella, la estrella internacional que aportó talento y equilibrio al centro del campo ecoacuático y del piso de Ronda de Garay. Muchas gracias a ti y a Rocío por vuestra amistad. Hay una visita a Parma pendiente (estoy deseando conocer los Apeninos y degustar esa delicia que es el queso parmesano en su tierra de origen). El equipo titular lo completa Susana Pallarés, que ya dejó de ser promesa y se convirtió en realidad, quien, además de cumplir con creces con su cometido como científica, ha dejado su sello de calidad en algunos eventos de la vida social de la familia ecoacuática. Muchas gracias a ti y a Abraham por vuestra amistad y autenticidad. No puedo cerrar este apartado sin acordarme del resto de gente del grupo: María Dolores Belando, Piedad Sánchez, Javi Lloret, Lázaro Marín, Laura Guerrero, María Botella Delphine Rocklin (de France), Irene Rojo, Katie Hogg (from UK) y cómo no, el figura de Suk-ueng Kritawitt (from Thailand). Tampoco me quiero dejar en el tintero al resto de compañeros del Departamento (María del Mar Sánchez, Viqui García, Marisa Arce, Javi Martínez, Rubén del Amo, Paqui Carreño, Jesús Miñano, Víctor Zapata, Viqui Jiménez, Isa Hernández, Pablo Farinós, Mario León, Marta García y José Antonio García-Charton). Muchas gracias por todos estos años repletos de buenos momentos, chicos.

También quisiera dar las gracias a 2 grandes ecólogos de la Universidad de Elche, como son Toni Sánchez Zapata y Juanma Pérez, por las interesantes discusiones que siempre han surgido cada vez que hemos coincidido, haya sido en la ciudad o en el campo.

Otras colaboraciones fundamentales para el desarrollo de esta tesis han venido de la mano de los investigadores que me integraron en sus grupos de investigación y supervisaron mis estancias investigadoras. I want to thank Dr. David T. Bilton, who hosted me during my first stay abroad, all the good times we spent together, not only in relation to scientific matters but also concerning music and gastronomy. It was absolutely the beginning of a beautiful friendship. Many thanks to the rest of the Plymouth lab team as well: Stacey, Andy, Simon, Tony, Paul, Balbina, Emma, Maria, Waz, Valentina, etc. Je tiens à exprimer mes sincères remerciements pour Dr. Sylvain Dolédec pour sa grande aide pendant mon stage à Lyon. Merci beaucoup pour ton collaboration fondamentale dans le troisiéme chapitre de ma thèse. Je remercie aussi toute l'équipe du Laboratoire d'Ecologie des Hydrosystèmes Naturels et Anthropisés, spécialement à Chloé, Nicolas, Sylvie, Bernard, Max, Samuel, David, Julian, Laetitia, Chafik, Natacha, Jules, etc pour me faire sentir comme chez moi. Mi última estancia fue en el Instituto de Biología Evolutiva de Barcelona, un sitio que ya conocía de alguna visita previa y al que ahora me hace mucha ilusión seguir visitando cada vez que puedo. Muchas gracias a Ignacio Ribera por querer acogerme en un centro tan puntero y por su inestimable colaboración, fundamental en el último capítulo de la tesis pero también en muchos otros momentos a lo largo de la misma. Agradecimiento que quiero hacer extensivo a todos los miembros de su grupo, grupos aledaños y algún que otro consorte: Amparo, Valeria y Michele, Rocío, Josep, Chus y Anabela, Ali, David, Gissela, Andrei, las Cristinas, Enric, Joan, Salvi, etc. Muchas gracias por los buenos momentos. Por supuesto, me gustaría tener un recuerdo muy especial para Margarita. Qué mala suerte, joder. Todos te echamos mucho de menos.

También quiero agradecer a los revisores externos de la tesis, David Angeler (Uppsala University) y María Sánchez Montoya (Leibniz Institute of Freshwater Ecology and Inland Fisheries) su colaboración en este apartado, así como a los investigadores que han formado parte del tribunal de la misma, tanto titulares como suplentes (Dani Boix, Christian Hof, Ana Filipa Filipe, Julio Camargo y, especialmente, a Rosa Gómez y Francisco Robledano, que además fueron de gran ayuda durante toda la burocracia que acompaña al proceso de depósito de la tesis).

Otro párrafo, más corto de lo que me gustaría, pero ya me estoy extendiendo demasiado, lo merecen mis compañeros en la Asociación de Jóvenes Investigadores de la Universidad de Murcia (AJIUM): David Verdiell, Óscar Belmar, Lucía Colodro, María Ángeles Bonmatí, María Ruiz, Gala Cano, Ana Pozo, Ana Pagán, Susana Pallarés, Paula Arribas, Tano Gutiérrez, José Antonio Carbonell, Daniel Bruno, María Sánchez Tornel, Vicente Martínez, Carlos Martínez, José Manuel Pereñíguez, Elvira Sánchez, Imna Navarro y Carlos Gómez. Gracias por vuestro esfuerzo altruista ahora reconvertido en amistad. También me gustaría agradecer a todos los ponentes que han participado en el ciclo I+D+c de charlas de investigadores en bares, y en especial a Pedro e Israel por darnos cobijo en sus establecimientos (Ítaca y El Sur, respectivamente)

Una de mis últimas andanzas me llevó a hacer radio. Muchas gracias a Elena García por darnos la oportunidad de poner en marcha el proyecto 'Ecomandanga' junto a mis compadres Tano Gutiérrez y Daniel Bruno. Sin duda, una de las historias más bonitas en las que me he embarcado. Gracias también a todos los que accedisteis a ser entrevistados (la lista es muy larga). De entre todos ellos quisiera destacar a Ana Bonilla y Luis Resines (PELOPANTÓN para los amigos), porque son unos artistas, por la bonita sinergia surgida tras la entrevista y por esa pedazo de portada para la 'tesis no oficial'. Gracias también a mi primo Luis por dejarme poner mi granito de arena en el proyecto 'Radio la rambla'.

No quisiera terminar este apartado sin agradecer al resto de familiares (tíos y primos), amigos (los malotes y los mangurrianes) y compañeros de piso (Eli, Rodri, Ander, María, Tano, Simone, Baldo, Laura y Luis) vuestro cariño y compañía a lo largo de todos los buenos momentos, pero especialmente en los malos, que alguno ha habido, compartidos durante todo este tiempo. Muchísimas gracias de corazón. Os quiero.

Funding

The work developed by F. Picazo in this thesis, including surveys, as well as his stays in other research centers, have been funded by the following institutions:

- Séneca Foundation, Regional Agency of Science and Technology from the Autonomous Government of Murcia: predoctoral grant-contract.
- Ministry of Environmental and Rural and Marine Affairs, research project 'Atlas and red book of Iberian water beatles'.
- Ministry of Education and Science: research project no. CGL2006-04159/BOS.
- Ministry of Environment: research project no. 023/2007.
- Ministry of Science and Innovation: research project no. CGL2010-15378.
- Spanish Agency of International Cooperation (AECI): research project 'Aquatic ecosystems of high conservation interest in the Western Mediterranean region: the case of the Rif (North of Morocco) and the Segura river basin (Southeast of the Iberian Peninsula)'.
- Water Euromediterranean Institute: research project 'Hydrological classification of the rivers from the Segura basin and macroinvertebrate communities associated'.
- Regional Government of Castilla-La Mancha: research projects no. PO1109-0190-8090; PPII10-0271-1349; PREG01-0016; and PREG06-027.
- University of Castilla-La Mancha: research project no. TC20080557.
- Séneca Foundation, Regional Agency of Science and Technology from Autonomous Government of Murcia, framed in the PCTRM 2007-2010, funded by INFO and FEDER up to 80%: research stay at the Evolutive Biology Institute (CSIC-UPF).

Financiación

El trabajo desarrollado por F. Picazo en esta tesis, incluyendo muestreos, así como sus estancias en otros centros de investigación, ha sido financiado por las siguientes instituciones:

- Fundación Séneca, Agencia Regional de Ciencia y Tecnología de la Región de Murcia: beca-contrato predoctoral.
- Ministerio de Medio Ambiente, Medio Rural y Marino: proyecto de investigación “Atlas y libro rojo de los coleópteros acuáticos ibéricos”.
- Ministerio de Educación y Ciencia: proyecto de investigación nº CGL2006-04159/BOS.
- Ministerio de Ciencia e Innovación: proyecto nº CGL2010-15378.
- Agencia Española de Cooperación Internacional (AECI): proyecto de investigación, proyecto de investigación “Ecosistemas acuáticos con especial interés de conservación en el Mediterráneo occidental: caso del Rif (Norte de Marruecos) y la Cuenca del Segura (Sureste de la península ibérica)”.
- Instituto Euromediterráneo del Agua: proyecto de investigación “Clasificación hidrológica de los ríos de la cuenca del Segura y comunidades de macroinvertebrados asociadas”.
- Junta de Comunidades de Castilla-La Mancha: proyectos de investigación nº PO1109-0190-8090; PPII10-0271-1349; PREG01-0016; y PREG06-027.
- Universidad de Castilla-La Mancha: proyecto nº TC20080557.
- Fundación Séneca, en el marco del PCTRM 2007-2010, con financiación del INFO y del FEDER de hasta un 80%: estancia externa en el Instituto de Biología Evolutiva (CSIC-UPF).