Estructura de comunidades de Odonata en sistemas mediterráneos

Tesis Doctoral

Esther Soler Monzó

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ESTRUCTURA DE COMUNIDADES DE ODONATA EN SISTEMAS MEDITERRÁNEOS

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Marcos Méndez Iglesias, Profesor Titular de Universidad del Departamento de Biología y Geología de la Universidad Rey Juan Carlos, y Joaquín Baixeras Almela, Profesor Titular de Universidad del Instituto Cavanilles de Biodiversidad y Biología Evolutiva de la Universidad de Valencia

CERTIFICAN:

que el trabajo de investigación desarrollado en la memoria de tesis doctoral:

"Estructura de comunidades de Odonata en sistemas mediterráneos", es apto para ser presentado por Esther Soler Monzó ante el Tribunal que en su día se consigne, para aspirar al Grado de Doctor por la Universidad de Valencia.

VºBº Director Tesis	VºBº Director Tesis
Dr. Marcos Méndez Iglesias	Dr. Joaquín Baixeras Almela

a Espe.

Let the rain come down and wash away my tears
Let it fill my soul and drown my tears
Let it shatter the walls for a new sun
A new day has come

A new day has come. CÉLINE DION

ποταμοῖς τοῖς αὐτοῖς ἐμβαίνομεν τε καὶ οὐκ ἐμβαίνομεν, εἶμεν τε καὶ οὐκ εἶμεν τε.

En los mismos ríos entramos y no entramos, [pues] somos y no somos [los mismos].

HERÁCLITO, en Diels-Kranz, *Die Fragmente Vorsokratiker,* 22 B12.

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RESUMEN

En ecología, una comunidad es un conjunto de especies que coexiste en un mismo momento y lugar (Mittelbach 2012) pero la forma en que se han conceptualizado las comunidades ecológicas ha cambiado con el tiempo. A principios del siglo XX, la comunidad se consideró una entidad discreta principalmente regulada por factores ambientales lo que condujo al debate entre las visiones clementsiana y gleasoniana de las comunidades. Más tarde, el debate se centró en los mecanismos que permitían la coexistencia de especies en función de la manera en la que las diferentes especies explotaban los recursos disponibles. Fue la época en la que Hutchinson (1957) enunció su teoría del nicho. En esa línea, Diamond (1975) describió la formación de una comunidad como un “ensamblaje de especies” que sigue una serie de reglas, determinadas principalmente por las relaciones interespecificas (competencia por recursos), la respuesta diferencial que tienen las especies a la hora de explotar dichos recursos y las respectivas tasas de dispersión. La comunidad se consideró una entidad cerrada hasta que McArthur & Wilson (1967) enunciaron su Teoría de la Biogeografía de Islas en la que, además de posibles interacciones entre especies y el efecto ambiental, se esbozó la posibilidad de que en la formación de una comunidad también intervenían sucesos de extinción y colonización. En este nuevo contexto en el que una comunidad no está aislada ni cerrada, Ricklefs (1987) remarcó la importancia de reconocer explícitamente una escala regional y una escala local, en las cuales actúan diferentes procesos en el ensamblaje de una comunidad local.

Actualmente, se reconoce una comunidad local como el resultado de la interacción de procesos locales y regionales. Los procesos locales están relacionados con factores abióticos y bióticos mientras que los procesos regionales están relacionados con capacidad de dispersión de las especies y sus procesos demográficos. Consecuentemente, el concepto de metacomunidad (comunidades que interactúan mediante la dispersión de al menos parte de las especies que las forman) se ha convertido en el nuevo escenario para abordar el estudio de las comunidades y en la bibliografía los procesos locales son llamados procesos deterministas mientras que los regionales se asimilan a los procesos espaciales.

En el estudio de la estructura de metacomunidades existen básicamente dos enfoques. El primero de ellos se centra en la descripción de patrones mientras que el segundo enfoque intenta desentrañar los procesos que subyacen a dichos patrones. Además, las comunidades cambian en su composición y/o estructura. Discernir si estos patrones o estos cambios en la composición y estructura se producen al azar o están motivados por mecanismos específicos es uno de los retos actuales de la ecología. Los procesos subyacentes se han clasificado en dos grandes grupos: procesos deterministas y procesos estocásticos. Por procesos deterministas se entienden los relacionados con la teoría de nicho y actúan a nivel local. Los procesos estocásticos se relacionan con los mecanismos que tienen ámbito regional y pueden ser intrínsecos al organismo (capacidad de dispersión, tamaño, posición trófica) o extrínsecos (configuración del paisaje, fenómenos de extinción o colonización).

Dentro del estudio de metacomunidades, los ecosistemas dulceacuícolas han recibido una notable atención. Por una parte, el hidroperíodo representa un amplio gradiente abiótico que a su vez, condiciona el componente biótico de los sitios. Por otra parte, ofrecen un marco idóneo para establecer qué papel tienen los procesos regionales en el ensamblaje de las comunidades de organismos con diferentes capacidades de dispersión. Además, dilucidar los mecanismos que subyacen a su estructura ha dejado de tener un mero interés teórico y ha pasado a ser un hecho de vital importancia para una correcta gestión y conservación de los mismos pues estos sistemas están entre los más amenazados por la acción antrópica. Esto es especialmente cierto en los ecosistemas dulceacuícolas mediterráneos que no sólo cuentan con gran variedad de especies endémicas sino que algunos de estos hábitats se consideran de protección prioritaria.

Las libélulas (Odonata) son un grupo importante en las comunidades de aguas continentales, pues precisan de estos ecosistemas para completar su ciclo vital. Es un grupo adecuado para el estudio del ensamblaje de comunidades puesto que se conocen muchos aspectos de su distribución, biología y requerimientos del hábitat, además de que no todas las especies presentan la misma capacidad de dispersión. A raíz del interés por recuperar los hábitats acuáticos, ha sido utilizado para evaluar las consecuencias de las perturbaciones antrópicas. Las comunidades de libélulas también se han estudiado en un contexto de metacomunidades, aunque los trabajos en los que prevalece este marco conceptual son escasos. Además, larvas y adultos han recibido atención desigual y ello dificulta un acuerdo acerca de los modelos y dinámicas que prevalecen.

En los ecosistemas mediterráneos, a pesar de ser un grupo bien estudiado, las comunidades de Odonata sólo han sido descritas en función de los principales factores abióticos que influyen en la estructura de su ensamblaje. Se tiene cierto conocimiento de su dinamismo pero los únicos trabajos en los que se estudian bajo un punto de vista de metacomunidad son aquellos en los que se han incluido como parte de las comunidades de macroinvertebrados. Consecuentemente, resulta conveniente establecer la metacomunidad como marco conceptual de las comunidades de Odonata, sobre todo si se tiene en cuenta que en el área mediterránea, una de cada cinco especies está amenazada de extinción a nivel regional.

De esta manera, se plantea la presente tesis doctoral con el objetivo de contribuir a este cambio de perspectiva e incrementar el conocimiento de los patrones y dinámicas asociados a las comunidades de Odonata. Este objetivo general se concreta en cuatro objetivos específicos: (1) establecer los factores que determinan la riqueza de especies de libélulas en humedales temporales, (2) establecer la estructura

que se observa en las metacomunidades de libélulas y su estabilidad en el tiempo, (3) evaluar cuál es la diversidad beta temporal de las comunidades de libélulas y (4) analizar cómo se produce el ensamblaje de las comunidades de libélulas en hábitats de nueva creación. Para acometer cada objetivo el trabajo de campo se llevó a cabo en dos áreas de estudio muy diferentes, la isla de Menorca (dentro del archipiélago de las Islas Baleares) y el humedal de Banyoles (Girona, Catalunya). En Menorca, el trabajo de campo incluyó, por una parte, el seguimiento de comunidades de adultos en charcas temporales y, por otra parte, el seguimiento de las comunidades de larvas en diferentes tipos de hábitats. En el humedal de Banyoles sólo se estudiaron comunidades de adultos ligadas a hábitats permanentes y semipermanentes. La metodología utilizada para el seguimiento de larvas incluyó la captura, conservación e identificación de los ejemplares atendiendo a su tamaño. En el seguimiento de adultos se utilizaron dos metodologías diferentes en Menorca (muestreo adaptativo) y en Banyoles (SLIC). En ninguna de ellas se incluyó la captura de los individuos a excepción de los casos de identificación dudosa.

Para el trabajo de campo con comunidades de adultos, las prospecciones han consistido en avistamientos de adultos (machos y hembras) en los puntos de agua o en sus inmediaciones. Estas prospecciones se hacen semanal o quincenalmente en las horas centrales de días preferentemente soleados y no demasiado ventosos en el período comprendido entre marzo y noviembre aproximadamente. Para el muestreo llevado a cabo en charcas temporales, el observador caminó a lo largo de transectos o utilizó puntos de conteo y a cada especie nueva que registró se le añadieron 20 minutos más de prospección. Este trabajo se realizó en 2008. Para prospectar las charcas de nueva creación, se ha seguido el método SLIC (*Seguiment de Libèl•lues de Catalunya*), desarrollado por el grupo naturalista *Oxygastra*. En este caso, los observadores hacen conteos semanales de insectos adultos a lo largo de un transecto lineal y cuando existe la imposibilidad de acceder a algunos de los hábitats lacustres se agregan puntos de conteo que consisten en sesiones de 5 minutos desde un punto fijo. Los conteos de adultos en el humedal de Banyoles se hicieron a lo largo de siete años.

En el muestreo de larvas, cada sitio fue visitado dos veces para asegurarse de capturar las larvas en sus estados más avanzados de desarrollo tanto de las especies primaverales como de las veraniegas por lo que el período de muestreo empezó a finales de invierno y finalizó a principios de verano. Se siguió una metodología similar a la descrita por autores en la que las larvas son capturadas con una red de 1 mm de luz al menos durante 3 minutos intentando abarcar todos los mesohábitats existentes. El muestreo de larvas constituyó una réplica del trabajo realizado por García-Avilés et al. (1995) 22 años antes.

La caracterización ambiental de los parajes estudiados se hizo incluyendo las variables más comúnmente medidas en este tipo de estudios, es decir, parámetros fisicoquímicos del agua, vegetación, conectividad o características del entorno de los sitios. Los métodos de análisis utilizados en la presente tesis englobaron técnicas de estadística descriptiva, de contraste de hipótesis y de estadística multivariante. También se utilizaron programas específicos para cuantificar la diversidad beta, establecer los patrones de las metacomunidades y analizar la rareza y dinámica de las comunidades. Además, se utilizó el DBI (*Dragonfly Biotic Index*) para contrastar si la medida de crear nuevas lagunas había mejorado la diversidad odonatológica del humedal de Banyoles.

Los resultados más importantes que se desprenden de la presente tesis doctoral se pueden agrupar según cada objetivo. En el caso de las comunidades de adultos de charcas temporales (Objetivo 1) se comprobó que factores regionales tales como área y conectividad tuvieron un papel relevante en la riqueza de especies de las comunidades. Estos ensamblajes, constituídos por especies generalistas y raras, contribuyen de manera importante a la diversidad regional a pesar de que sólo un bajo

porcentaje (alrededor del 20%) cuenta con mecanismos concretos para resistir la desecación. Las comunidades de larvas mostraron un patrón de su metacomunidad cuasi-anidado en 1988 y un patrón al azar en 2010 (Objetivo 2). Estos patrones podrían estar provocados por diferencias en la capacidad de dispersión y en el grado de especialización del hábitat. Las comunidades de larvas registraron una alta variabilidad en su composición tanto en 1988 como en 2010 (Objetivo 3) y, aunque no se pudo establecer una relación directa, se constató que los diferentes hábitats incluidos en el estudio representaron una importante heterogeneidad ambiental. De hecho, junto con la distancia al mar y la temperatura, el tipo de hábitat fue la variable que más influencia tuvo en la diferenciación de los ensamblajes tanto en 1988 como en 2010 (Objetivo 3). Las comunidades de larvas de Odonata son altamente dinámicas y tras 22 años, se registró una variabilidad en su composición cercana al 75%. Este dinamismo no se pudo relacionar con el grado de cambio ambiental y estuvo negativamente correlacionado con las especies registradas en cada estación en 1988. A pesar de ello, el número de especies registrado en cada localidad se mantuvo más o menos constante tras este período de tiempo (Objetivo 3). En hábitats de nueva creación las comunidades de Odonata de adultos no siguieron una dinámica sucesional sino más bien estocástica (Objetivo 4). Este tipo de dinámica también se observó en ensamblajes de hábitats más maduros. En ambos tipos de ensamblajes se registró una variabilidad espacial cercana al 50%. Este porcentaje fue muy parecido al de su variabilidad interanual, a pesar de que la riqueza de especies se mantuvo más o menos constante (Objetivo 4). Según los valores de DBI, las lagunas de nueva creación parecen haber mejorado la diversidad odonatológica de la zona.

Las principales conclusiones de la presente tesis doctoral ponen de manifiesto que las comunidades de Odonata pueden estar influenciadas tanto por factores locales como regionales, sobre todo, en el caso de hábitats altamente fluctuantes. En las comunidades de larvas, el patrón de metacomunidad que se observa puede estar relacionado con el compromiso existente entre la capacidad de dispersión y el grado de especialización del hábitat y no es estable en el tiempo. Existe una gran variabilidad en la composición de las comunidades de Odonata (en estado adulto y larvario) tanto a escalas locales como regionales, sobre todo si se tienen en cuenta diferentes tipos de hábitats. Las comunidades de Odonata son altamente dinámicas tanto en estado adulto como larvario pero conservan estable el número de especies que las conforman. Los mecanismos subyacentes a estas dinámicas parecen tener un fuerte componente estocástico.

CAPÍTULO 1. INTRODUCCIÓN GENERAL

Desarrollo conceptual en ecología de comunidades: de la comunidad a la metacomunidad.

En ecología, una comunidad es un conjunto de especies que coexiste en un mismo momento y lugar (Mittelbach 2012). La descripción de una comunidad consiste en detallar la composición y abundancia de las especies que la forman (Begon et al. 2006). La forma en que se han conceptualizado las comunidades ecológicas ha cambiado con el tiempo. En 1877, Karl Möbius utilizó el término “biocenosis” para hablar de ciertas entidades formadas por conjuntos de especies que interactuaban (Nyhart 1998). Esta consideración de una comunidad como una entidad discreta fue compartida posteriormente por ecólogos vegetales y condujo al debate entre las visiones clementsiana y gleasoniana de las comunidades. Según Clements (1916) una comunidad es el resultado de un grupo de organismos que responden de igual manera al ambiente que les rodea a modo de súper-organismo. Gleason (1927), por su parte, consideraba que a pesar de estar formada por un conjunto de especies, la comunidad era el resultado de la respuesta independiente que cada especie tenía al ambiente.

Más tarde, el debate se centró en los mecanismos que permitían la coexistencia de especies, que es lo que se ha llamado la teoría de nicho (Hutchinson 1957). En esta teoría, el número de especies que conforma una comunidad está limitada por la cantidad de recursos y por la similaridad que presentan las especies a la hora de utilizar dichos recursos (MacArthur & Levins 1967). En esa línea, Diamond (1975a) describió la formación de una comunidad como un “ensamblaje de especies” que sigue una serie de reglas, determinadas principalmente por las relaciones interespecificas (competencia por recursos), la respuesta diferencial que tienen las especies a la hora de explotar dichos recursos y las respectivas tasas de dispersión.

La comunidad se consideró una entidad cerrada hasta que McArthur & Wilson (1967) enunciaron su Teoría de la Biogeografía de Islas en la que, además de posibles interacciones entre especies a propósito de los recursos y el efecto que el ambiente pudiese tener, se esbozó la posibilidad de que en la formación de una comunidad también intervenían sucesos de extinción y colonización. En este nuevo contexto en el que una comunidad no está aislada ni cerrada, Ricklefs (1987) remarcó la importancia de reconocer explícitamente una escala regional y una escala local, en las cuales actúan diferentes procesos en el ensamblaje de una comunidad local. A escala regional, existe un acervo regional de especies (*regional species pool*), compuesto por el conjunto de especies potenciales que pueden formar parte de las comunidades locales (Pärtel et al. 1996). Los procesos regionales son los que van a determinar que sean unas especies del acervo regional y no otras las que lleguen a una localidad concreta y su naturaleza es diversa. Por una parte, pueden estar relacionados con características del propio organismo (factores intrínsecos) como por ejemplo su capacidad de dispersión (HilleRisLambers et al. 2012) o con la configuración espacial que determine el grado de aislamiento y conectividad entre comunidades (factores extrínsecos) (Hanski 2001). Los procesos locales, que incluyen tanto factores abióticos como bióticos (Chesson 2000), están relacionados con la influencia que tiene el entorno sobre los organismos y condicionan la supervivencia de las especies en una determinada localidad (Weiher & Keddy 2001), una vez han conseguido llegar a ella, por lo que se les conoce como filtros ambientales (Kraft et al. 2015).

En la visión aceptada actualmente, una comunidad local es el resultado de la interacción de procesos locales y regionales y lo más importante de este nuevo enfoque es que en la formación de las comunidades están implicados procesos que actúan a diferentes escalas espaciales y temporales (Ricklefs 2008). Consecuentemente, las comunidades han dejado de estudiarse como entes aislados. El concepto de metacomunidad (Leibold et al. 2004), esto es, comunidades que interactúan mediante la dispersión de al menos parte de las especies que las forman, se ha convertido en el nuevo escenario para abordar el estudio de las comunidades (Fig. 1.1).

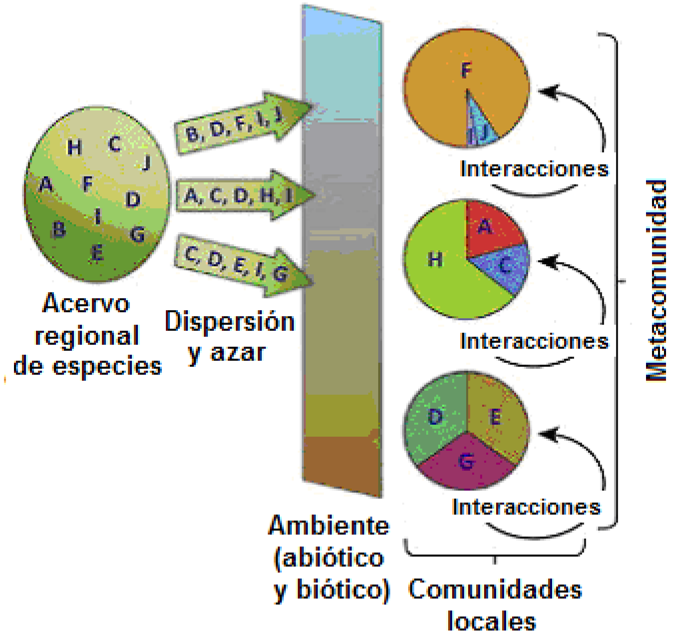


Fig.1.1. Representación esquemática de cómo a partir de un acervo regional de species se configuran las diferentes comunidades locales que componen la metacomunidad. Dicha configuración depende la acción conjunta de procesos regionales (dispersión y azar) y de los filtros ambientales (modificado de Mittelbach & Schemske 2015).

El estudio de las metacomunidades: patrones y procesos

En el estudio de la estructura de metacomunidades existen básicamente dos enfoques. El primero de ellos está centrado en la descripción de patrones. Leibold & Mikkelson (2002) describieron seis patrones básicos de estructura de las metacomunidades, basados en el aspecto de una matriz presencia-ausencia de especies por sitios (Fig.1.2).

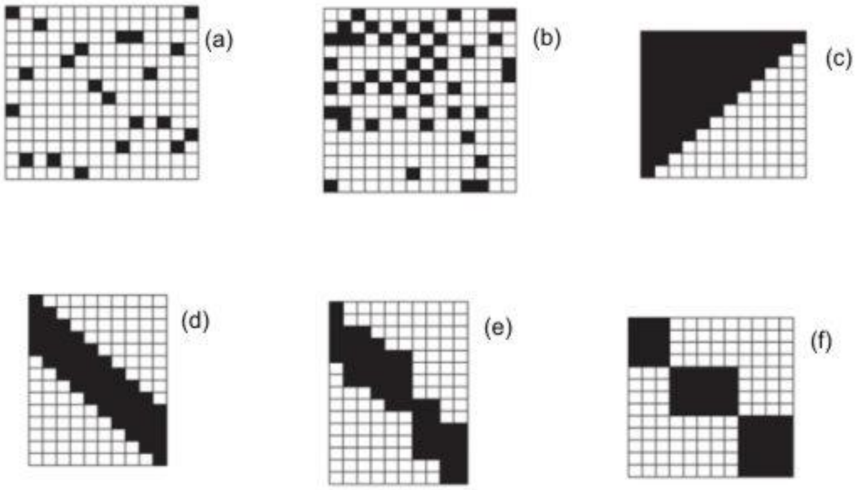


Fig. 1.2. Aspecto de las matrices de presencia (cuadrados rellenados en negro)-ausencia (cuadrados en blanco) para los seis modelos de metacomunidad descritos por Leibold & Mikkelson (2002). Patrón de tablero de ajedrez (a), patrón obtenido por azar (b), patrón de anidamiento (c), patrón de gradiente de igual separación (d), patrón de gradiente gleasoniano (e) y patrón de gradiente clementsiano (f).(Modificado de Henriques-Silva et al. 2013).

Estos patrones se identificaron en buena medida en etapas previas de la ecología de comunidades y se han atribuido a la actuación de distintos procesos ecológicos. El patrón en tablero de ajedrez (Diamond 1975) otorgaba especial relevancia a los factores bióticos. El patrón anidado (Patterson & Atmar 1986) se relacionaba con factores abióticos y con fenómenos de colonización y extinción. Para comunidades en las que la distribución de especies forma un continuo a lo largo de un gradiente espacial aunque también con una clara influencia abiótica se utilizaron los patrones de gradiente clementsiano (Clements 1916), de gradiente gleasoniano (Gleason 1926) y de gradiente con igual separación (Tilman 1983). Finalmente, el patrón al azar (Simberloff 1983) se asigna cuando no se observa ningún patrón evidente (Fig. 1.2). Leibold & Mikkelson (2002) sugieren un protocolo de análisis para distinguir unos patrones de otros. Dicho protocolo analiza tres elementos descriptores de las metacomunidades: la coherencia, el recambio de especies (*turnover*) y la agrupación de los límites. La coherencia hace referencia al modo con el que las especies responden a los factores ambientales (abióticos y bióticos) a través de diferentes comunidades. El recambio de especies mide la frecuencia con la que una especie reemplaza a otra en el conjunto de los sitios. El estudio de la agrupación de los límites permite separar bloques de especies en función de si la respuesta de la comunidad a la variabilidad ambiental se da de manera conjunta (gradiente clementsiano) o por el contrario, es el resultado del conjunto de respuestas de cada una de las especies que la conforman (gradiente gleasoniano). Presley et al. (2010) han refinado esta clasificación añadiendo estructuras intermedias que se han llamado cuasi-estructuras. Aunque se han atribuido diferentes patrones a procesos específicos, es necesario ser cauteloso. Inferir procesos a partir de patrones generales es un tema que plantea controversia pues se ha demostrado que un mismo patrón puede estar originado por diferentes procesos (Heino & Soininen 2005; Henriques-Silva et al. 2013; Ulrich & Gotelli 2013).

El segundo enfoque para abordar el estudio de las metacomunidades es desentrañar los procesos que subyacen a dichos patrones (Cottenie 2005). Estos procesos se dividen en procesos de nicho y procesos espaciales. Los procesos de nicho engloban los procesos locales (fundamentalmente filtros abióticos y bióticos) mientras que los procesos espaciales le otorgan más importancia a los procesos regionales (dispersión) en el ensamblaje de las comunidades. Holyoak et al. (2005) describieron cuatro modelos de metacomunidades en función del rol que tenían los diferentes procesos: filtrado de especies, efecto de masa, modelo neutral y dinámica de parches. Estos modelos se diferencian por la importancia que conceden a tres factores (Logue et al. 2011): la diferenciación de nichos entre especies, la dispersión y la heterogeneidad del hábitat (Fig. 1.3). El modelo neutral considera que la diferenciación de nichos entre especies es irrelevante y que el hábitat es homogéneo y el único factor importante es la dispersión (Fig. 1.3).Los otros tres modelos consideran que existe diferenciación de nicho entre especies y consideran la influencia relativa de la dispersión y la heterogeneidad del hábitat. El modelo de dinámica de parches considera que no hay heterogeneidad ambiental entre parches de hábitats y que la dispersión es limitante para algunas especies (Fig. 1.3). Si hay heterogeneidad ambiental entre parches de hábitats, el modelo de filtrado de especies considera que la dispersión entre parches de hábitats es eficiente para la mayoría de especies consideradas (Fig. 1.3). Por el contrario, el modelo de efecto de masa considera que el grado de dispersión es lo suficientemente alto en algunas especies como para enmascarar o anular estas diferencias de nicho (Winegardner et al. 2012) (Fig. 1.3).

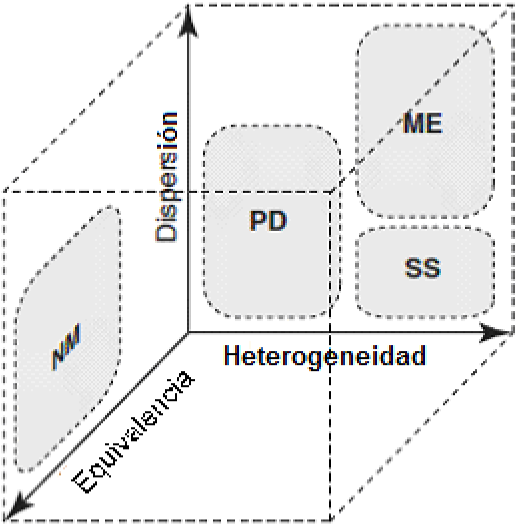


Fig. 1.3. Localización de los cuatro modelos dinámicos de metacomunidades en el espacio definido por la heterogeneidad del hábitat, las diferencias de nicho entre especies (equivalencia) y la dispersión. NM: modelo neutral, PD: dinámica de parches, ME: efecto de masa y SS: filtrado de especies (modificado de Logue et al. 2011).

Estos cuatro modelos no son incompatibles y a veces es difícil separar las predicciones de unos y otros (Chase & Bengtsson 2010). La relación entre estos modelos es compleja (Chase & Bengtsson 2010). Unos se aplican más naturalmente a escalas grandes (neutral) y otros a escalas pequeñas; se pueden ordenar en un continuo de intensidad de movimiento de las especies y de heterogeneidad espacial (efectos de masa y dinámica de parches), de la importancia de la dinámica local vs. la regional (filtrado de especies, dinámica de parches y efecto de masas). Los modelos de dinámica de parches y de efecto de masa pueden ser considerados casos especiales del establecimiento de especies en los que la dispersión tiene un papel limitante o alto, respectivamente (Winegardner et al. 2012). Por ello, tratar de diferenciar entre estos modelos simplemente evaluando la riqueza y abundancia de especies empírica no es evidente (Chase & Bengtsson 2010).

Cambios de composición en el espacio y en el tiempo: diversidad beta

Las comunidades cambian en su composición y/o estructura. Discernir si estos cambios se producen al azar o están motivados por mecanismos específicos es uno de los retos actuales de la ecología.

La diversidad beta se define como el cambio en la composición de especies a lo largo del espacio y del tiempo (Whittaker 1960, 1972) y el interés en su estudio ha aumentado en los últimos años (Vellend 2001; Koleff et al. 2003; Legendre et al. 2005; Tuomisto 2010; Anderson et al. 2011). Las comunidades dinámicas (con altas tasas de cambio) muestran valores altos de diversidad beta. Con la diversidad beta se relacionan principalmente dos conceptos: el decaimiento de la similitud con la distancia (*distance decay*) y el recambio de especies (*species turnover*) (Whittaker 1956, 1960). El decaimiento de la similitud con la distancia indica que la similitud entre comunidades locales disminuye conforme aumenta la distancia que las separa (Whittaker 1956, Nekola & White 1999). Este patrón de decaimiento se ha relacionado tanto con procesos deterministas (de nicho) o procesos estocásticos o deriva ecológica (Chase & Myers 2011). Los procesos deterministas están relacionados con los procesos de nicho que incluyen los factores abióticos, los factores bióticos y el compromiso (*trade-off*) que muestren las especies a la hora de aprovechar los recursos en detrimento de otras características (Kneitel & Chase 2004). Los procesos estocásticos hacen referencia a la dispersión de las especies y a lo que se conoce como deriva ecológica (Chase 2010), es decir, aquellos procesos relacionados con variaciones aleatorias en parámetros demográficos (tasas de nacimiento, muerte y episodios de extinción y colonización) de las poblaciones que componen la comunidad. Por su parte, el recambio de especies debe entenderse como el cambio en la composición de especies que se da a lo largo de gradientes ambientales o espaciales predefinidos, lo que implica que existe algún tipo de estructura en el paisaje que modela el cambio observado (Vellend 2001).

A pesar de plantear una dialéctica muy similar entre la prevalencia de procesos de nicho y estocásticos (Leibold & Geddes 2005) todavía se está lejos de poder integrar la diversidad beta con los patrones y los procesos de las metacomunidades descritos anteriormente (Logue et al. 2011; Mittelbach 2012). De hecho, con la metodología descrita por Leibold & Mikkelson (2002) al analizar el elemento del recambio de especies sólo se está midiendo dicho recambio a lo largo de gradientes y este parámetro no necesariamente coincide con otras medidas de diversidad beta (Vellend 2001) (Fig. 1.4).

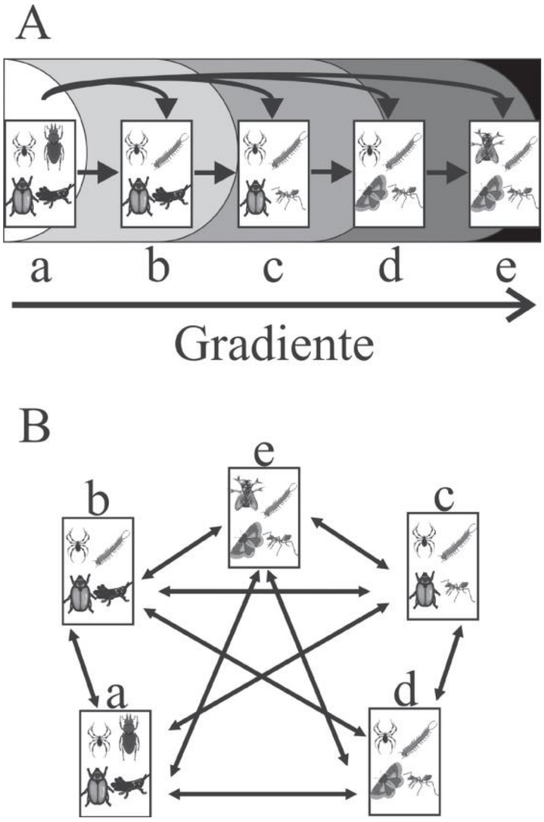


Fig. 1.4. Dos maneras de entender la diversidad beta. (A) El cambio en la composición de especies que forman una comunidad obedece a un gradiente espacial, temporal o ambiental. (B) La diversidad beta se entiende como el grado de cambio o diferenciación en la composición de comunidades que no están inmersas en ningún tipo de gradiente (tomado de Calderón-Patrón et al. 2012).

Los ecosistemas dulceacuícolas en el estudio de las metacomunidades: el caso de los sistemas mediterráneos.

Dentro del estudio de metacomunidades, los ecosistemas dulceacuícolas han recibido una notable atención (Jeffries 1994; Wilbur 1997; Spencer et al. 2002; Cottenie et al. 2001; Urban 2004; Mcabendroth et al. 2005; Van de Meutter et al. 2006; Wissinger et al. 2009; Logue et al. 2011; Heino 2013). Las principales razones para ello son:

- Los sistemas dulceacuícolas en conjunto ofrecen un paisaje heterogéneo. Esta heterogeneidad viene dada por un gradiente abiótico muy influenciado por el hidroperíodo pero también por un gradiente paralelo de tipos de depredadores en función del hidroperíodo, lo que condiciona el componente biótico de los sitios (Welborn et al.1996).
- Están “embebidos” en una matriz terrestre que puede resultar inhóspita para la mayoría de sus habitantes. En este sentido, tanto los hábitats más discretos como lagos y charcas, como sistemas dendríticos y, a priori, más conectados como los ríos, ofrecen un marco idóneo para establecer qué papel tienen los procesos regionales en el ensamblaje de las comunidades de organismos con una débil, intermedia o alta capacidad de dispersión (Heino 2011).
- Estos sistemas están entre los más amenazados por la acción antrópica (Sala et al. 2000; Jenkins 2003). Dilucidar los mecanismos que subyacen a su estructura resulta de vital importancia para una correcta gestión y conservación del medio natural. En este sentido, la construcción de nuevos hábitats o la restauración de hábitats degradados han demostrado ser medidas eficaces (Zedler 2000, Zedler & Kercher 2005) y además han proporcionado la oportunidad de estudiar los principales mecanismos que rigen el ensamblaje de las comunidades (Allen et al. 2011; Heino 2013).

En los sistemas dulceacuículas existen muchas formas de vida, pasando por organismos unicelulares hasta vertebrados, lo que ha permitido en los últimos años, establecer algunas generalidades. Por ejemplo, Soininen et al. (2007a) comprobaron que la diversidad beta espacial en sistemas dulceacuículas no es muy diferente de la observada en sistemas terrestres pero si es mayor que en ambientes marinos. En algunos trabajos, estos valores altos de diversidad beta se relacionaron con patrones anidados (Heino 2011) o con el área, el grado de aislamiento y la heterogeneidad del hábitat como principales procesos subyacentes (McAbendroth et al. 2005; Heino

2011). Sin embargo, también se han encontrado patrones provocados por relaciones interespecíficas (de tablero de ajedrez) (Heino 2005) o por respuestas abióticas a lo largo de gradientes (Henriques-Silva et al. 2013). Además, en hábitats con alto grado de perturbación se pueden observar estructuras al azar (McCreadie & Bedwell 2013).

Independientemente del tipo de patrón considerado, lo que parece evidente es que la dinámica del filtrado de especies prevalece en los sistemas dulceacuícolas, especialmente en ríos y lagos (Heino & Mykrä 2008). Según estos resultados las especies sólo se encuentran en sitios ambientalmente favorables. No obstante, dependiendo del tipo de ecosistema y de la escala espacial considerada (grado de aislamiento) también se puede observar una dinámica de efecto de masa. En este contexto, las limitaciones de dispersión del organismo estudiado determinarán qué procesos -relacionados con el nicho o con la dispersión- son más importantes (Cottenie & De Meester 2004; Heino et al. 2015). Aunque algunos autores han destacado que algunos de estos ecosistemas son altamente cambiantes, tener una perspectiva general de la diversidad beta temporal o de cómo cambia con el paso del tiempo la estructura de las metacomunidades es una asignatura pendiente (Cottenie et al. 2001; Heino et al. 2015).

Los ecosistemas dulceacuícolas mediterráneos son particularmente interesantes para el estudio de las metacomunidades puesto que son diversos en cuanto a sus características ambientales (Picazo et al. 2012). La presencia de hidroperiodos estocásticos de duración limitada influye en otras muchas variables abióticas (Williams 1997; Collinson et al. 1995; Della Bella et al. 2005) y en la biota que puede establecerse en estos sistemas (De Meester et al. 2005). Además, albergan un alto número de especies endémicas y algunos hábitats que son únicos (Ribera et al. 2003; Abellán et al. 2005; Gascón et al. 2008). De hecho, algunos de ellos figuran como hábitats prioritarios en la conservación (Zacharias et al. 2007). Cuando se estudia la diversidad beta entre hábitats de diferente hidroperíodo, se constata que la heterogeneidad ambiental y la conectividad entre hábitats son imprescindibles para preservar la diversidad de los macroinvertebrados en general (Florencio et al. 2014) y de algunos grupos en particular (Picazo et al. 2012). En dichos sistemas, se han destacado patrones anidados para las metacomunidades de escarabajos (Picazo et al., 2012) y para la sucesión de macroinvertebrados (Ruhí et al. 2013). No obstante, este patrón puede perder relevancia bien porque hay especies que de manera individual se apartan del patrón (llamadas idiosincráticas) (Florencio et al. 2014) o bien porque el hábitat es muy variable temporalmente en cuanto a la permanencia del agua y por lo tanto, también en riqueza de especies (Urban 2004).

Odonata como grupo modelo para el estudio de las metacomunidades

Las libélulas (Odonata) son un grupo importante en las comunidades acuáticas, pues precisan de estos ecosistemas para completar su ciclo vital (Corbet & Brooks 2008). Es un grupo adecuado para el estudio del ensamblaje de comunidades puesto que se conocen muchos aspectos de su distribución (Askew 2004; Dijkstra & Lewington 2006), taxonomía (Carchini 1983; Dijkstra & Kalkman 2012) y biología (Cordero Rivera et al. 2005; Corbet & Brooks 2008) y su conservación despierta gran interés (Keil et al. 2008; Samways et al. 2011). Se conocen las principales variables ambientales que influyen en la composición de sus comunidades: la vegetación, el área o parámetros físcoquímicos del agua son los más frecuentemente destacados (Oertli et al. 2002; Schlider et al. 2003; Osborn 2005). Además, se considera que los dos subórdenes de Odonata tienen diferencias en cuanto a su capacidad de dispersión, más limitada en el suborden Zygoptera que en el suborden Anisoptera (McCauley 2006).

Es un grupo versátil en cuanto a su hábitat (Corbet & Brooks 2008) y a raíz del interés de recuperar los hábitats acuáticos, ha sido utilizado para evaluar las consecuencias de las perturbaciones antrópicas (Foote et al. 2005; Simaika &

Samways 2009a; Silva et al. 2010; Ferreras-Romero 2013). Además, presentan adaptaciones que les permiten sobrevivir en hábitats temporales (Hamasaki et al. 2009), donde su condición de organismo depredador se acentúa en ausencia de peces (McPeek & Brown 2000; Knight et al. 2005).

Las comunidades de libélulas también se han estudiado en un contexto de metacomunidades, aunque larvas y adultos han recibido atención desigual y ello dificulta un acuerdo acerca de los modelos y dinámicas que prevalecen. El hidroperiodo y el tipo de depredadores parecen jugar un papel clave como determinante de la estructura, riqueza de especies y dinámica de las comunidades de libélulas (Suhling et al. 2004; McCauley et al. 2008). La estructura de las comunidades cambia en función de si se trata de hábitats temporales, hábitats permanentes con presencia de peces y hábitats permanentes con macroinvertebrados como depredador superior (Stoks & McPeek 2003). Las comunidades asociadas a hábitats temporales se consideran poco diversas y constituídas por especies generalistas (McCauley 2007), En hábitats efímeros la dispersión es importante en la estructura de las comunidades (Johansson et al. 2006). En los hábitats permanentes es la depredación y no la dispersión el factor que se considera más crucial (Johansson et al. 2006). En casos de heterogeneidad en grado de permanencia de los hábitats, la principal dinámica que se observa es la de fuente-sumidero, en la que los hábitats temporales actúan como sumidero de las especies que no son capaces de hacer frente a la desecación y los hábitats más permanentes pueden actuar de fuente o sumidero en función de la capacidad de las especies para coexistir con diferentes tipos de depredadores (Crumrine et al. 2008).

La estructura de las comunidades de adultos se ha considerado tradicionalmente como anidada. Esta estructura frecuentemente emerge cuando se la relaciona con el área, el grado de perturbación o el número de especies de macrófitos acuáticos (Kadoya et al. 2004; Craig et al. 2008; Sahlén & Ekkestube 2001). Sin embargo, cuando los análisis incorporan técnicas estadísticas más complicadas (Leibold & MIkkelson 2002) se han identificado patrones relacionados con gradientes ambientales (clementsiano, gleasoniano y cuasi-estructuras) tanto para larvas como para adultos (McCauley et al. 2008; Bried et al. 2015).

No obstante, no se han explorado posibles patrones que pueden emerger cuando las metacomunidades están formadas por diferentes hábitats acuáticos ni tampoco cuál es la estabilidad de las comunidades de libélulas a través del tiempo puesto que en los únicos estudios donde se contempla la variabilidad temporal son aquellos que describen o bien trayectorias sucesionales (Moore 1991; Chovanec & Raab 1997) o bien cómo afecta el cambio climático a la fenología de las especies (Hassall et al. 2007; Dingemanse & Kalkman 2008; Bush et al. 2013). Además, se tienen muchas evidencias de que las comunidades de Odonata son dinámicas pero la cuantificación de su diversidad beta está muy poco documentada (Juen & De Marco 2011).

En la cuenca Mediterránea, las comunidades de libélulas han sido descritas en distintos tipos de hábitats (García- Avilés et al. 1995; Carchini et al. 2005, 2007; Sato & Riddiford 2007; Márquez-Rodriguez 2014). Sólo Domingo (2002) utilizó los cambios en la odonatofauna para describir cambios estructurales del hábitat a través del tiempo. De este modo, los únicos trabajos en los que se puede encontrar alguna referencia parcial a la dinámica que existe entre comunidades de libélulas son aquellos en los que se ha estudiado para el conjunto de macroinvertebrados (Boix et al. 2004; Leitão et al. 2007; Florencio et al. 2009, 2011) lo que implica la relevancia de profundizar en el establecimiento de los patrones de las metacomunidades de Odonata, las dinámicas que los causan y su estabilidad en el tiempo.

Objetivos de la tesis doctoral

El objetivo general de esta tesis doctoral es el estudio de la estructura de las comunidades de libélulas en humedales mediterráneos y de los procesos que influyen en dicha estructura. Este objetivo general se concreta en cuatro objetivos específicos:

1. Establecer los factores que determinan la riqueza de especies de libélulas en humedales temporales, que suponen un hábitat azaroso por su inestabilidad en zonas mediterráneas. En concreto, se analizarán las charcas temporales de Menorca y se hará énfasis en la importancia relativa de variables fisicoquímicas del hábitat, variables de calidad del hábitat en los alrededores de las charcas y variables espaciales relacionadas con el área y la conectividad de las charcas.

2. Establecer la estructura que se observa en las metacomunidades de libélulas y su estabilidad en el tiempo. En concreto, se analizarán el recambio de especies, la coherencia y la agrupación de límites de las comunidades que García-Avilés et al. (1995) describió para 68 localidades de Menorca en 1988 y que han sido examinadas de nuevo en el presente trabajo.

3. Evaluar cuál es la diversidad beta temporal de las comunidades de libélulas. Para ello, se compararán las comunidades previamente descritas para la isla de Menorca por García-Avilés et al. (1995) con las estudiadas en el presente trabajo. Se cuantificará el recambio espacial y temporal de especies y se valorará si depende de cambios en el hábitat y del grado de especialización de las especies.

4. Analizar cómo se produce el ensamblaje de las comunidades de libélulas en hábitats de nueva creación. Para ello se estudiará como modelo la colonización por libélulas, a lo largo de siete años, de las lagunas creadas con el objetivo de recuperar la fauna del lago de Banyoles (Girona).

Organización de la tesis doctoral

Para acometer el estudio de la estructura de las comunidades de Odonata en sistemas mediterráneos, la presente tesis doctoral se ha dividido en diferentes apartados. En el apartado siguiente se repasa la metodología general utilizada en la tesis. A continuación, los cuatro capítulos centrales se corresponden con cada objetivo descrito en el apartado anterior. En el primero de ellos, la totalidad de los datos empíricos son propios. En el segundo y tercer capítulo se cuenta con datos empíricos propios y con los facilitados por Javier García-Avilés. En el último capítulo, los datos empíricos han sido facilitados por Michael T. Lockwood.

Los cuatro capítulos centrales se encuentran estructurados en formato de artículo científico. De esta manera pueden leerse independientemente y en el orden deseado, aunque el orden que siguen en la tesis está pensado para facilitar el hilo argumental del estudio de las metacomunidades. Los capítulos están escritos en inglés por ser éste el idioma estándar de comunicación científica. En el campo de la ecología de comunidades se dispone de poca literatura en castellano lo que hubiese complicado enormemente realizar el desarrollo argumental de cada capítulo. No obstante, la tesis doctoral cuenta con un séptimo apartado de discusión general en el que se integran todos los resultados y se discuten sus implicaciones en la estructura de comunidades de Odonata en sistemas mediterráneos para terminar con las conclusiones generales de la tesis doctoral.

CAPÍTULO 2. METODOLOGÍA GENERAL

Área de estudio

El área de estudio de esta tesis doctoral incluye dos zonas de la cuenca Mediterránea: Menorca (Islas Baleares) y Banyoles (Catalunya). En Menorca se han estudiado todos los tipos de sistemas dulceacuícolas existentes mientras que en Banyoles el área de estudio abarcó el humedal que incluye el lago de Banyoles y cuatro de las cinco lagunas recientemente creadas para recuperar la biodiversidad de la zona.

Menorca

En Menorca se llevaron a cabo los estudios encaminados a cumplir los objetivos 1, 2 y 3. Menorca es una isla del archipiélago de las Islas Baleares, España (39° 47' 57'' a 40° 05' 40'' N, 3° 47' 27'' a 4° 19' 40'' E) y tiene 702 km^2. A grandes rasgos, la geología de Menorca incluye una parte norte con sustratos impermeables, arcillosos en su mayoría, y una parte sur donde la presencia de roca caliza posibilita una mayor cantidad de barrancos por donde discurren torrentes y se forman acuíferos (Rosell & Llompart 2002). El clima de Menorca es típicamente mediterráneo, con temperaturas medias anuales de 16,7°C. Las precipitaciones anuales medias son de 600 mm, concentradas principalmente en otoño y primavera y con un período de sequía estival. No obstante, existe una importante variación estacional e interanual en el régimen de lluvias. El viento predominante tiene componente Norte (Tramontana), seguido por el viento de componente Sudoeste (Llebeig) (Dídac & Dubon 1997). El escaso relieve de la isla (358 m de altitud máxima) no supone un obstáculo para los fuertes vientos de Tramontana cargados con grandes cantidades de sal. Esto dificulta el desarrollo de una vegetación de superficie y explica que la vegetación sea más densa y abundante en la parte sur de la isla.

La vegetación principal incluye diferentes tipos de bosque mediterráneo - acebuchares (*Olea europaea*), pinares de pino carrasco (*Pinus halepensis*) y encinares (*Quercus ilex*)- así como brezales de *Erica arborea* y *E. multiflora*, pastizales y comunidades halófilas de acantilados costeros. El paisaje consiste en un mosaico agroforestal donde el conjunto de vegetación mediterránea supone el 45% de cobertura de la tierra mientras que los campos de pastoreo y cultivos agrícolas un 50%. El 5% restante del territorio son zonas urbanas (*www.obsam.cat*).

En Menorca los hábitats de aguas continentales están representados tanto por aguas corrientes -torrentes y arroyos temporales-, como por sistemas lénticos, entre los que se encuentran algunos pantanos, el humedal permanente de S'Albufera y muchas charcas temporales diseminadas por toda la isla (Fig. 2.1a). Aunque algún torrente puede conservar agua en las estaciones más cálidas, la mayoría de ellos no pueden ser considerados permanentes (Fig. 2.1b) (*www.obsam.cat).*

(a)

(b)

Fig. 2.1. (a) Es Mall Lloc, charca temporal incluída en el trabajo de campo del objetivo 1. (b) Tres localidades incluidas en el muetreo de larvas de Menorca (objetivos 2 y 3); de izquierda a derecha, Albufera de Es Grau, Morella y torrente de Algendar.

Banyoles

El humedal de Banyoles fue la zona de estudio para llevar a cabo el objetivo 4. Se trata de un humedal mediterráneo único rodeado por un conjunto de lagunas y manantiales que albergan valiosos hábitats para la Unión Europea (*www.consorcidelestany.org*). El Lago de Banyoles (Girona, NE España; 42° 07' 37,15'' N, 2° 45' 24,01'' E; 174 m s.n.m.; profundidad máxima: 62 m; longitud: 2110 m, anchura máxima: 750 m) se encuentra en una gran llanura cárstica y es permanente. Es el segundo lago más grande de la Península Ibérica. El clima de la zona es típicamente mediterráneo. La temperatura media interanual es de 15°C y la pluviosidad es bastante abundante con una media anual de 815 mm. Los vientos dominantes son del noroeste, durante todo el año, y del sureste, más notorios en la primavera y el verano y asociados a la marinada (*www.banyoles.cat*).

Es una zona de recreo tradicional para deportes acuáticos y lugar de esparcimiento, lo que sin duda habrá tenido repercusiones negativas para la biota. La orilla oriental del lago ha experimentado un considerable desarrollo urbano, mientras que la costa occidental ha conservado sus bosques junto al lago y las llanuras de inundación, a pesar de que gran parte de la tierra ha sido dedicada a uso agrícola (*www.consorcidelestany.org*). A orillas del lago de Banyoles se encuentra una diversidad de comunidades vegetales acuáticas, incluyendo Characeae, *Potamogeton*, *Phragmites*, *Typha*, *Scirpus*, *Carex*, *Juncus* y *Euphorbia*. En su parte sur, el lago está bordeado por una línea estrecha de álamos y alisos que da a la ciudad de Banyoles (Fig. 2.2). El resto del lago está rodeado por una franja variable de arbolado aluvial bien desarrollado (5-150 m de anchura), que rápidamente se convierte en una mezcla de tierras agrícolas, bosque mediterráneo y zonas verdes (*www.consorcidelestany.org*) Como parte de un proyecto LIFE (LIFE03NAT/E/000067), se excavaron cinco nuevas lagunas semipermanentes poco profundas en 2005 al NE del lago para restaurar parte de los hábitats inundables y pantanosos que rodeaban el lago. Cuatro de estas lagunas se incluyeron en el objetivo 4 (Fig. 2.2).

Fig. 2.2. Lago Bayoles, al fondo, con algunas de las lagunas de nueva creación en primer plano.

Trabajo de campo

El trabajo de campo consistió en el muestreo de libélulas en estado larvario o adulto y en la toma de variables ambientales asociadas a los hábitats estudiados.

El muestreo de libélulas adultas (tanto machos como hembras) en las charcas temporales de Menorca (objetivo 1) se hizo semanal o quincenalmente en las horas centrales de días preferentemente soleados y no demasiado ventosos desde marzo a noviembre aproximadamente. Para el muestreo llevado a cabo en charcas temporales, el observador caminó a lo largo de transectos (Steytler & Samways 1994) o puntos de muestreo (Sutherland 2006). El muestreo fue adaptativo, en el sentido de que la duración del muestreo por charca y día fue variable en función del tiempo transcurrido desde la detección de la última especie nueva (Sato & Riddiford 2007).

El muestreo de libélulas adultas en el humedal de Banyoles (objetivo 4), siguió el método SLIC (Seguiment de Libèl·lues de Catalunya), desarrollado por el grupo naturalista *Oxygastra*. En este caso, los observadores hacen conteos semanales de adultos (tanto machos como hembras) a lo largo de un transecto lineal que se divide en secciones, que se suman para generar un índice anual de abundancia. Además, dada la imposibilidad de acceder a algunos de los hábitats lacustres, se agregaron puntos de conteo que consistieron en sesiones de 5 minutos desde un punto fijo (por ejemplo, la plataforma de observación en la orilla del lago).

En el muestreo de larvas (objetivos 2 y 3), cada sitio fue visitado dos veces para asegurarse de capturar las larvas en sus estados más avanzados de desarrollo tanto de las especies primaverales como de las veraniegas (Corbet & Brooks 2008). Por lo tanto, el período de muestreo empezó a finales de invierno y finalizó a principios de verano. Se ha seguido una metodología similar a la descrita en Torralba-Burrial & Ocharan (2007) en la que las larvas son capturadas con una red de 1 mm de luz (Fig. 2.3) al menos durante 3 minutos en cada mesohabitat (Della Bella et al. 2005) de cada sitio.

La caracterización ambiental de los sitios estudiados se realizó principalmente para los objetivos 1 y 2. En el objetivo 1 se incluyeron las características físicoquímicas del agua (Carchini et al. 2007), los tipos de vegetación (Schlinder et al. 2003) y variables espaciales de los sitios tales como el área (Gaines 2006), la conectividad (Yamanaka et al. 2009) y el uso del suelo en franjas de 500 m alrededor de cada sitio (Raebel et al. 2012a). En el objetivo 2, la caracterización ambiental consistió en características fisicoquímicas del agua, el tipo de sustrato, la distancia al mar y la presencia/ausencia de macrófitos (García-Avilés et al. 1995). Para la medición de las características físcoquímicas del agua se utilizó una sonda multiparámetrica Hanna HI-9829 (Fig. 2.3).

Fig. 2.3. Detalle del trabajo de campo en el muestreo de larvas en el que se aprecia el tipo de red utilizada y la sonda multiparamétrica.

Análisis de los datos

En la presente tesis doctoral se han utilizado tanto estadística descriptiva como contraste de hipótesis (Quinn & Keough 2002) y sobre todo estadística multivariante (Kruskal 1964; Braak 1986; Kenkel & Orlóci 1986; Wold et al. 1987; Abdi 2007; Anderson 2005). Dentro de la estadística multivariante se incluyeron métodos de ordenación indirecta (PCA, CA, NMDS), métodos de ordenación directa (RDA, CCA) y métodos de correlación multivariante (PLS). Además se utilizó PERMANOVA y SIMPER para el análisis de las diferencias en composición entre comunidades.

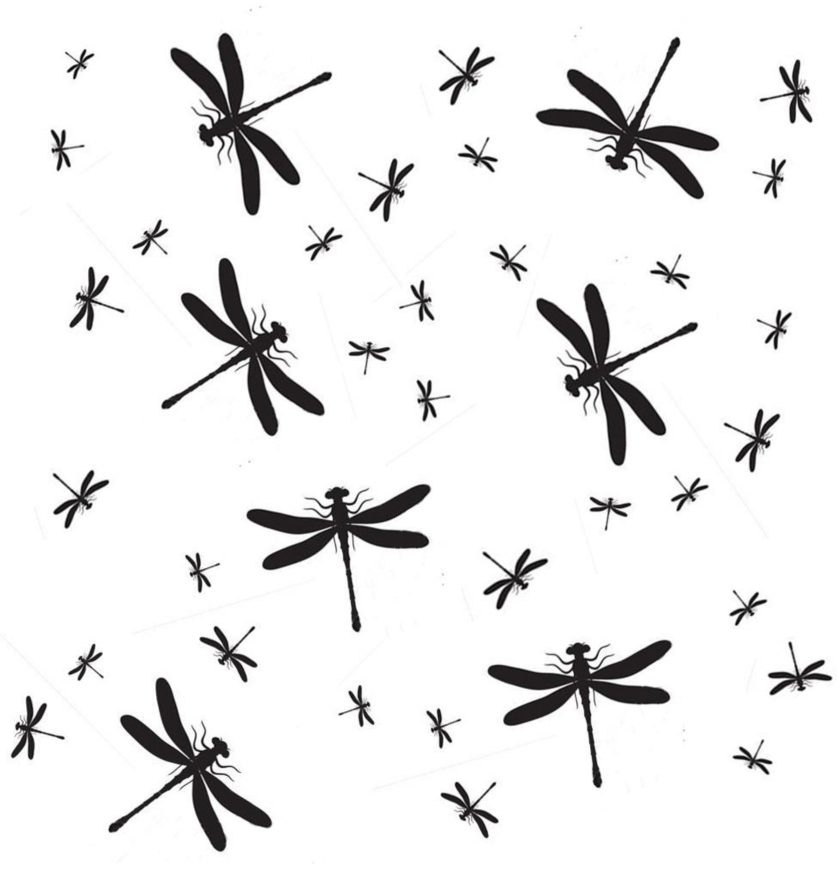
Otro conjunto de técnicas de análisis estuvo relacionado con el análisis de patrones de diversidad. Se estudió la diversidad beta (Cardoso et al. 2015), la calidad de los inventarios de especies cuando fueron registradas por diferentes investigadores (Jiménez-Valverde & Hortal 2003) y la estructura de las metacomunidades (Dallas 2014).

Finalmente, se usaron técnicas miscelánea para análisis puntuales. Para el objetivo 4 se utilizaron el cálculo de DBI (Dragonfly Biotic Index) (Simaika & Samways

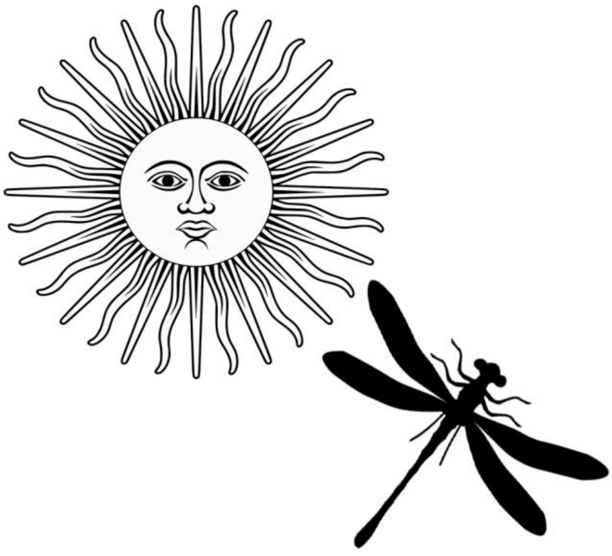
2009a) y un análisis de la convergencia temporal en la composición de las comunidades (Collins et al. 2000). Para determinar la rareza de las especies que configuraron el acervo regional de especies en Menorca tanto en estado adulto como larvario se aplicó el crieterio de Gaston (1994).

Para estos análisis se utlizó el programa PAST (Hammer et al. 2001), el programa Canoco 4.5 (Leps & Smilauer 2003), el programa Statistica 7.0 (Jiménez-Valverde & Hortal 2003) y el entorno de programación R 3.1.0.

RESULTADOS



CAPÍTULO 3. REGIONAL, RATHER THAN LOCAL, FACTORS INFLUENCE THE ADULT ODONATA ASSEMBLAGES IN MEDITERRANEAN TEMPORARY PONDS



INTRODUCTION

Disentangling the factors that determine local species diversity is a longstanding question in ecology (Gleason 1927; Clements 1938; MacArthur & Wilson 1967; Terborgh 1973; Diamond 1975a; Chase 2003; Mittelbach 2012). It is accepted that assembly of local communities is not independent from regional diversity (Terborgh & Faaborg 1980; Cornell 1985; Ricklefs 1987; Rajaniemi et al. 2006; Cornell & Harrison 2014). In this context, the metacommunity concept, i.e. a set of communities linked by dispersal (Leibold et al. 2004) allows to integrate regional and local processes in the assembly of local communities from a regional species pool (Pärtel et al. 1996). Therefore, the composition of a local community is the outcome of: (a) factors that determine what species from the regional pool can occupy a specific site by dispersal and chance (HilleRisLambers et al. 2012), (b) abiotic factors that filter those species intolerant to local conditions (Weiher & Keddy 2001) such as climate variability, productivity or the amount and periodicity of disturbance and (c) biotic factors (predation or competition) which regulate local coexistence (Chesson 2000).

Lentic freshwater ecosystems are one of the habitats where metacommunity patterns and processes have been more frequently studied (Chase 2003; Ruhí et al. 2009; Allen et al. 2011; Alahuhta & Heino 2013). For several organisms it seems that both local and regional factors may have combined effects on freshwater assemblages regardless of the scale considered (Heino 2001; Soininen 2014; Brendonck et al. 2015). However, local abiotic factors have been considered dominant over spatial factors (Soininen 2014). The exception are passive dispersers (Chase 2007; Vanchoenwinkel et al. 2007), for which biotic interactions together with dispersal influence community assembly (Shuring 2001; Cottenie & De Meester 2004).

Within freshwater ecosystems, ponds are considered to be diverse ecosystems (Collinson et al. 1995; Biggs et al. 2005) which contain a large proportion of the regional diversity (Williams et al. 2004; Davies et al. 2008). Ponds are ideal model systems to test metacommunity theory due to their discrete nature (Cottenie & De Meester 2003; Welsh & Hodgson 2011; Hassall et al. 2012; Lescano et al. 2015). At temporary ponds, an important abiotic factor is the natural and unpredictable fluctuation of water table (Williams 1997). Water table fluctuation may kill or stress organisms if it becomes too extreme (Williams 1997; Chase 2007) but has also been pointed out as essential to maintain diversity (Urban 2004; Lake 2013). Inhabitants of temporary ponds must be able to survive the drought period (by means resistance structures) or moving to permanent waters (by means of a terrestrial adult form). As a result, temporary ponds hold rich communities (Oertli et al. 2005; Williams 2006), in most cases clearly differentiated from permanent waters, and including a combination of species with broad distributions as well as rare, endangered or endemic species (Céreghino et al. 2008). Not surprisingly, temporary ponds, especially in the Mediterranean basin, have been considered as prioritary habitat by the Habitats Directive (Zacharias et al. 2007).

Dragonflies (Odonata) are part of many aquatic systems including temporary ponds (Williams 1997; Oertli et al. 2005; Corbet & Brooks 2008) where, in absence of fish, play an important role as top predators (Welborn et al. 1996; Foote & Rice-Hornung 2005; Honkanen et al. 2011). Due to their well-known taxonomy and different life stages (aquatic larvae and vagile flying adults) dragonflies have emerged as model organisms in freshwater community ecology (Crowley & Johnson 1982; Shuling 2004; McCauley 2007). Studies on dragonfly assemblies have stressed interspecific biotic interactions (Maezono & Miyashita 2004; Knight et al. 2005; Stamper et al. 2008) and the monitoring of natural and human-induced environmental changes (Clark & Samways 1996; Dingemanse & Kalkman 2008; Reece & McIntyre 2009). Usually, these studies have included only the larval stage (McCauley 2007; McCauley et al. 2008; Wissinger et al. 2009). Consequently, dragonfly adult assemblages of temporary waters are poorly known. This situation is particularly true for the Mediterranean basin, where much attention has been given to the influence of abiotic factors such as hydroperiod, alkalinity or vegetation on species richness and community assembly (Della Bella et al. 2005; Carchini et al. 2007; Florencio et al. 2009). Whether these factors play the same role on adult assemblages or remains understudied, especially for areas where permanent freshwater bodies are scarce.

The present work studied the main factors influencing adult dragonfly assemblages in a set of temporary ponds located in a Mediterranean island, Menorca (Spain). The specific aims of this study were: (1) to describe the dragonfly species richness and rarity of temporary ponds, (2) to characterize the environmental variation in Menorca temporary ponds, (3) to assess whether local environmental variables or regional variables were influencing dragonfly species richness, and (4) to assess the role of temporary ponds for the species diversity of dragonflies at a landscape scale.

MATERIALS & METHODS

Sampling sites

In total, 12 temporary ponds and the permanent wetland were studied in Menorca (Fig.3.1). Temporary ponds in Menorca follow a hydroperiod similar to other Mediterranean temporary ponds, with the seasonal succession of three or four phases, based on changes in flooding and drying periods (Boix et al. 2004; Florencio et al. 2009). Temporary ponds were selected to include all the geomorphologically-based categories described for Menorca by Fraga et al. (2007) and the hydroperiod categories established by Estaún et al. (2010) (Table 3.1). The permanent wetland, S’Albufera des Grau, was chosen as a reference wetland. It is a Paleozoic lagoon in the inland part of a coastal dune system and gets water from three streams.

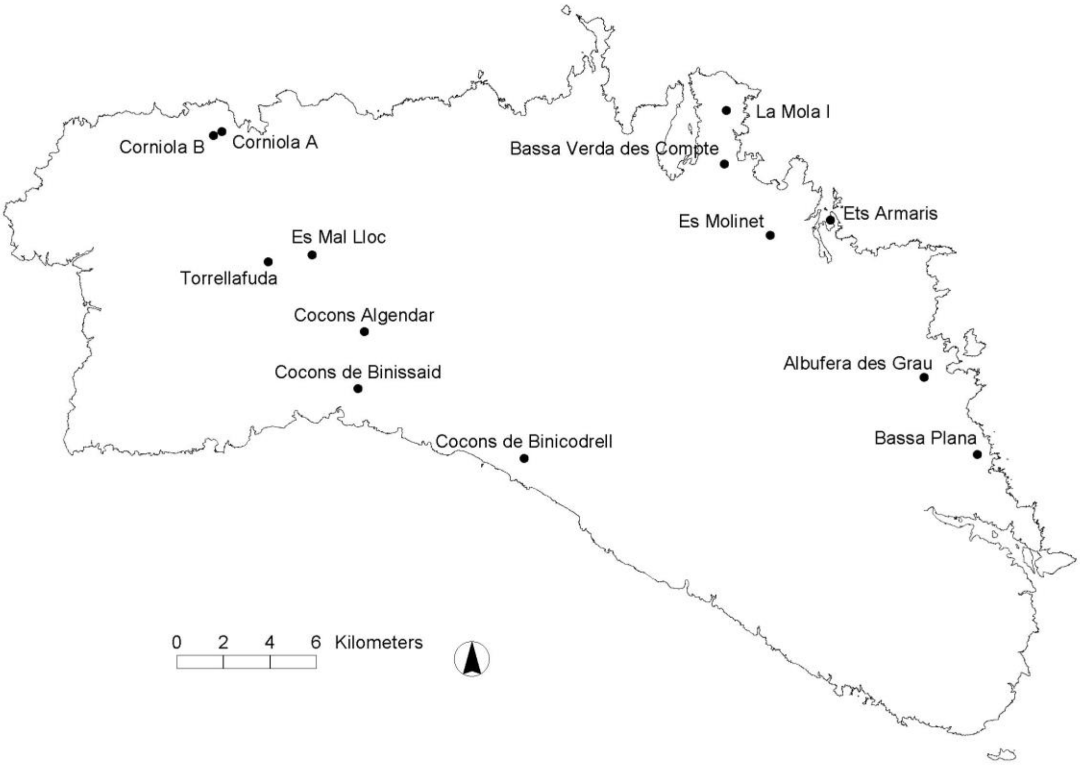


Fig. 3. 1. Location of the temporary ponds and the permanent wetland studied in Menorca.

Table 3.1. Location, category and hydroperiod of temporary ponds and the permanet wetland included in this study. The abrevations used in the figures are given in brackets.

Pond	Coordinates	Pond category	Hydroperiod type
Cocons d'Algendar (Alg)	39˚58'06''N 3˚58'18''E	Rock pond	Ephemeral and discontinous
Cocons de Binissaid (Bss)	39˚56'47''N 3˚58'06''E	Rock pond	Ephemeral and discontinous
Cocons de Binicodrell (Bc)	39˚55'07''N 4˚03'06''E	Rock pond	Ephemeral and discontinous
La Mola I	40˚03'09''N 4˚09'19''E	Sinkhole	Ephemeral and discontinous
Bassa Verda d'es Compte (Comp)	40˚01'55''N 4˚09'15''E	Sinkhole	Ephemeral and discontinous
Bassa Plana (Plana)	39˚55'04''N 4˚16'45''E	Small depression on paleozoic soil	Intermediate
Ets Armaris (Arm)	39˚59'36''N 4˚12'31''E	Small depression on paleozoic soil	Long
Torrellafuda (Torre)	39˚59'46''N 3˚55'26''E	> 5 ha sinkhole on deep sandy soil	Intermediate
Corniola A (Cor A)	40˚02'49''N 3˚54'04''E	> 5 ha sinkhole on deep sandy soil	Long
Corniola B (Cor B)	40˚02'43''N 3˚53'49''E	> 5 ha sinkhole on deep sandy soil	Long
Es Mal LLoc (MalLL)	39˚59'55''N 3˚56'46''E	Rock depression on sandy siliceous soil	Long
Es Molinet (Moli)	40˚00'14''N 4˚10'35''E	Rock depression on sandy siliceous soil	Intermediate
S'Albufera d'es Grau (Grau)	39˚56'48''N 4˚14'58''E	Paleozoic back-dune lagoon	Permanent

Dragonfly sampling

Dragonfly sampling targeted adult individuals and was carried out between 8 April and 3 November 2008. All sites were visited in clear and windless days fortnightly, or weekly for those ponds having a shorter hydroperiod. The same observer, ES, carried out all surveys. In spring, the number of visits ranged from two to ten, in summer from one to five and in autumn from two to four, to a total of eight to 18 of visits per pond. At each site, sampling was conducted between 10:00 and 16:00 when adult Odonata are most active according to local weather conditions (Carchini et al. 2003; Sato & Riddiford 2007) except during hot summer days, where visits extended until 18:00. Sampling consisted of counts of individuals of each species seen in a 2.5 m band on either side of a transect along the bank of the pond (Steytler & Samways 1995) or from point transects (Sutherland 2006). Number of point transects per pond ranged 1-3, depending on pond size. When necessary, individuals were caught with a handnet and released after identification. Sampling effort per visit was adjusted to the discovery rate of new species as follows. In principle, 30 min were spent searching and 20 min were added to the survey after the discovery of each new species. The survey finished after 20 min without recording any new species. Survey time spent per pond and visit ranged from 30 min when no species were recorded to 166 min. Total time spent per pond during the study ranged from four to 12 hours. This sampling effort was similar to that used by other authors (Sato & Riddiford 2007; Bried et al. 2012). Adult species were identified using Dijkstra & Lewington (2006), Lockwood & Oliver (2007) and Baixeras et al. (2006).

During each visit, the following information was recorded: (1) number of species observed, (2) number of individuals of each species if their abundance allowed good sight from a point transect, or a semi-quantitative abundance estimate when individuals were on wing across the transect. Semi-quantitative abundance estimate consisted of four categories, similar to the ones used in Schmidt (1985): rare (1 individual), scarce (3 individuals); common (7 individuals); and abundant (11 individuals), (3) newly hatched imagoes (hereafter immatures) and reproduction behavior (copulae, tandems, egg deposition) was recorded to identify resident fauna (Chovanec & Waringer 2001).

Furthermore, larvae samples were taken twice per pond (summer and autumn) during 2008 and 2009 to improve the data set. Larvae were caught by sweeping the main mesohabitats (Della Bella et al. 2005) with a 1 mm mesh pond net during at least 3 min according to the methodology fowolled in Collinson et al. (1995) and Torralba Burrial & Ocharan (2007). Dragonflies were sorted *in situ* and conserved in 70º ethanol until their identification in the laboratory. Larvae were identified using Carchini (1983), Askew (2004), Heidemann & Seidenbusch (2002) and Belevich (2009). Only larvae identified to species level have been taken into account in this study. Odonata species nomenclature follows Dijkstra & Kalkman (2012).

Habitat characterization

At each site, seven physicochemical variables of the water were measured: water temperature (ºC), pH, redox potential (ORP), dissolved oxygen (DO, mg/l), conductivity (mS/cm), total dissolved solids (TDS, mg/l) and salinity. These variables were recorded with a multiparametric probe Hanna HI-9829. DO readings were used to calculate a new binary variable, anoxy, indicating the existence of anoxic conditions (DO = 0). Water depth was taken on the deepest point of the pond, except in the permanent wetland, where it was recorded only at the sampling site. Approximate lenght of the dry period was calculated for each pond as the number of days in which the pond was dry (variable coded as drought). Moreover, the following weather variables were recorded: air temperature (˚C), with a weather station Silva ADC-IR, and wind speed (Beaufort scale). All physicochemical and weather variables were measured at each visit.

Percent of plant cover was estimated along a transect with 50 points separated 0.5 m apart whenever pond size allowed it. Percentage of plant cover was divided into 'emergent' (Veg-E) for plants with some aerial parts and 'submerged' (Veg-S) if plants did not have any abovewater part. Plant cover was measured once in spring and once in autumn, giving a total of four plant cover-related variables.

Altitude (m) and pond area (m^2) were taken from two unpublished reports from a LIFE project on temporary ponds in Menorca. Connectivity of each pond (sensu Biggs et al. 1994) was estimated as the number of water points potentially useful for adult dragonflies in a radius of 500 m around the pond. This estimate is similar to previous works (Gascón et al. 2008; Florencio et al. 2011) and is considered realistic according to the dispersal capacity of dragonflies (Angelibert & Giani 2003; Yamanaka et al. 2009). The area of influence (buffer) of each pond, defined as the area around the perimeter pond in a radius of 500 m, was included (m^2). Buffer provides roosting resources for larvae and adults (Rouquette & Thompson 2007a) and increase water quality by reducing surface run-off (Lovell & Sullivan 2007). Moreover, percentage of agricultural land of the buffer (coded as land use) was chosen as surrogates of habitat antropoghenic-disturbance because these practices are considered among the most important threats to Mediterranean temporary ponds (Zacharias et al. 2007; Cardona et al. 2010). For these variables, SIG maps from the Consell Insular de Menorca were used.

Statistical analysis

A multivariate ordination of the dragonflies found at each pond was carried out by means of a correspondence analysis (CA) in Canoco 4.5 (Lepš & Šmilauer 2003). For this analysis, the average abundance of each species was calculated as the total number of individuals of each species per time spent at each pond. In this analysis, La Mola pond was excluded due to its lack of dragonflies. Downweighthing of rare species (Lepš & Šmilauer 2003) was applied and *S. fusca* and *O. cancellatum*, present at a single site each, were included as passive species.

Dragonfly rarity was assessed using the 25% criterium of Gaston (1994), i.e. as the 25% of species showing the smallest incidence and/or abundance. Since each pond was surveyed a different number of times, for this analysis, abundance was calculated as follows. First, the maximum number of individuals of each species recorded was divided between the time spent at each pond for each fortnight (i.e. an species effort coefficient). Second, average of effort coefficients was calculated and log transformed. This abundance estimate was highly positively correlated ($r = 0.89$, $p < 0.001$, $n = 15$) with the average number of individuals of each species recorded at each pond.

Environmental variability among sites was summarized by means of a principal components analysis (PCA) in Canoco 4.5. The seven physicochemical variables, the two weather variables, water depth, drought, the four plant cover variables, altitude, pond area, connectivity, area of influence and land use were included in this analysis. Quantitative variables were $\log_{10} + 1$ transformed for analysis, due to their different measurement scales. To determine which variables significantly influenced each principal component, the broken-stick model was used (Peres-Neto et al. 2003).

To ascertain which environmental variables influenced species richness per pond, a partial least squares (PLS) regression (Carrascal et al. 2009) was performed by using the package pls (Mevik & Wehrens 2007) of the programming environment R 2.15.2. PLS regression is a method analogous to multiple regression, but suitable where, as in this case, independent variables show collinearity and the number of independent variables exceeds the number of cases (Carrascal et al. 2009). For this analysis, all independent variables, as well as species number, were log-transformed and NIPALS's algorithm was followed. The number of components was decided by examining the plot of RMSEP values -obtained by leave one-out cross validation- in relation to the number of components (Wold et al. 2001). The number of components where the minimum RMSEP value was achieved, were considered as significant (Mevik & Wehrens 2007). The interpretation of the PLS regression components was done using the loadings of those original independent variables that were higher than 0.4 in each component (Wold et al. 2001).

RESULTS

Odonata species richness, assemblage composition and rarity

Overall, 15 dragonfly species were found at the temporary ponds studied (Table 3.2). The number of species recorded per pond ranged from zero to 12, the mean value being 7.45 ± 2.81 (mean ± SD) after excluding the only pond with no species. The reference permanent wetland had six species, all of them also found in the temporary ponds. Larvae of seven species were recorded in the temporary ponds, compared with one species in the permanent wetland (Table 3.2). When larvae were present, they accounted from 11 to 75% of the species recorded as adults (Table 3.2). There were two ponds where no species showed breeding evidence (Cocons de Binicodrell and Mola I) and two species (*A. isoceles* and O. *coerulescens*) did not show breeding evidence at any pond (Table 3.2).

The CA produced an ordination with two axes that accounted for 62.8% of the total variance, 31.6% in the first axis and 23.6% in the second one. Three groups of ponds could be distinguished in the resulting biplot (Fig. 3.2). Group 1, in the positive side of the first axis, consisted of two ponds and the permanent wetland with a high abundance of *A. parthenope* and *I. elegans* and included the only locality with *C. scitulum* (Fig. 3.2). Group 2, in the negative side of the first axis, consisted of two ponds with high abundance of *L. barbarus* (Fig. 3.2). Group 3, in the positive side of the second axis, consisted of three ponds with high abundance of *S. fusca*, *A. isoceles* and *S. striolatum* and included the only locality with *O. coerulescens* (Fig. 3.2). The rest of localities grouped around the origin of the biplot axes, indicating a dominance of widespread dragonfly species (Fig. 3.2).

Table 3.2. Temporary ponds surveyed and species recorded at each pond. See Table 1 for full name of ponds. Species abbreviations are indicated in brackets. Presence of adults only is indicated by X. Increasing evidence of breeding is indicated by squares with increasing grey depth, from tandem (light grey), through egg laying (intermediate grey), immature (dark grey) to larval records (black).

Species	Alg	Bss	Bc	Mola	Comp	Plana	Arm	Torre	Cor A	Cor B	MalLl	Moli	Grau	Total ponds (adult)	Total ponds (larva)	% of pond found as larvae
Lestes barbarus (Lbar*)*					█	X	█		█	█		█	X	6	5	83
Chalcolestes. viridis (Cvir)	X								X	X	░	█		5	1	20
Sympecma fusca (Sfus*)*					█					░	X			2	1	50
C. scitulum (Csci)						░								1	0	0
Ischnura elegans (Iele*)*					░	█	▓	█	░	░	░	█	█	8	4	50
Aeshna isoceles (Aiso)			X		X									2	0	0
Aeshna mixta (Amix*)*					X	X						█	X	3	1	33
Anax parthenope (Apar*)*	X				X	X	░	▒			X	X	X	7	0	0
Anax imperator (Aimp*)*	▒	X			X	X		X	X	▒	X		X	8	0	0
Crocothemis erythraea (Cery*)*					▓	▒	X	X	X	X	X			7	0	0
Orthetrum cancellatum (Ocan*)*	X				X				░	░	X			5	0	0
Orthetrum coerulescens (Ocoe*)*			X											1	0	0
Sympetrum fonscolombii (Sfon*)*	█		X		█	█	█	█	▒	░	█	█	X	10	7	70
Sympetrum meridionale (Smer*)*			X		▓	X	▓			X	X	X		8	0	0
Sympetrum striolatum (Sstr*)*	█	▒	X		█	█	▓	▒	░		█	█		9	5	56
total species (adults)	6	2	5	0	12	10	6	6	8	9	10	8	6			
total species (larvae)	2	0	0	0	4	3	2	2	1	1	2	6	1			
% of spp found as larvae	33	0	0	0	33	30	33	33	13	11	20	75	17			

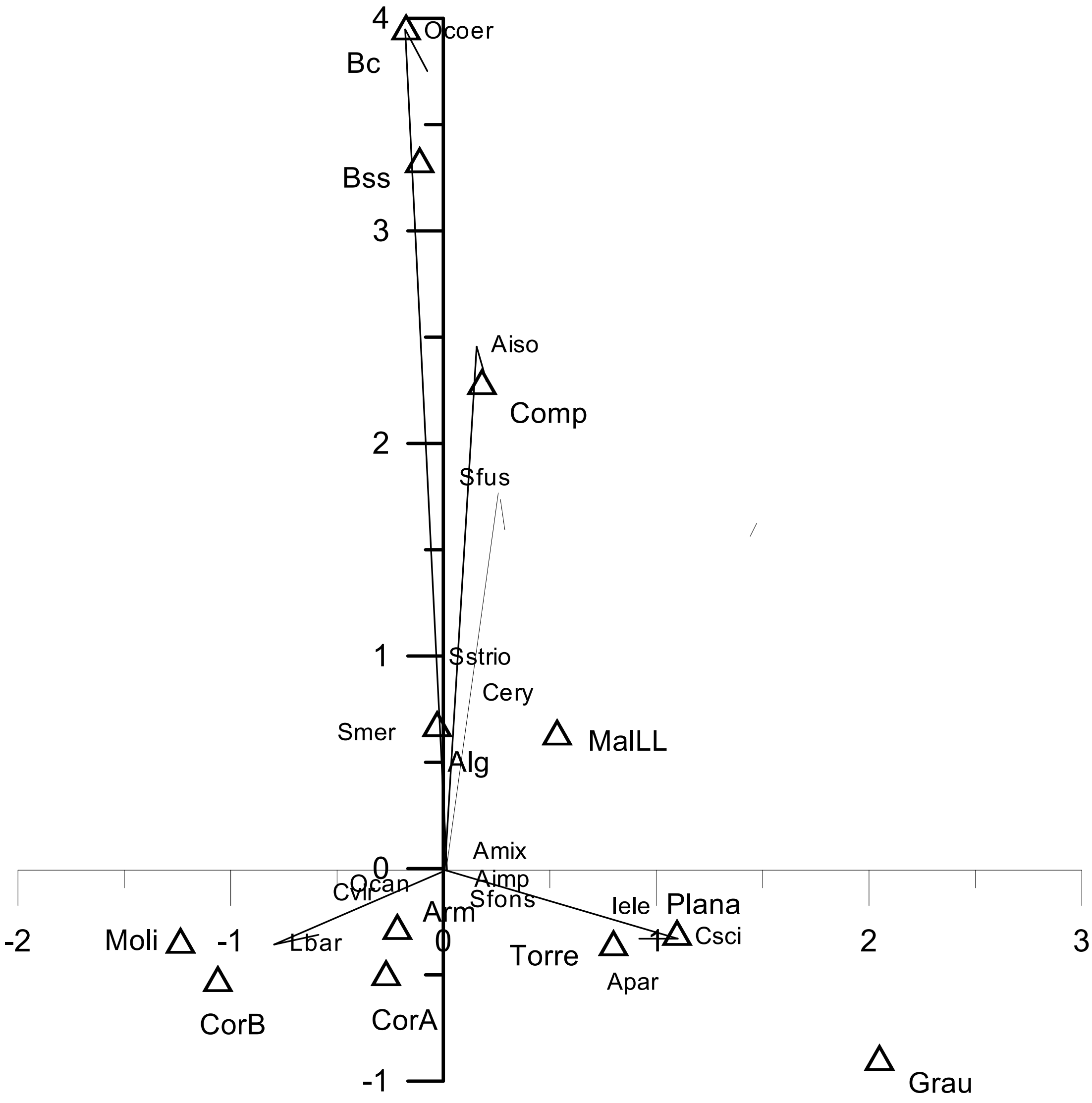


Fig. 3.2. Biplot of the ordination of dragonflies in the studied temporary ponds and the permanent wetland. Triangles indicate ponds (see Table 1 for abbreviations) and arrows indicate the species with the highest score in one direction of each ordination axis. Species were shortened as indicated in Table 3.2.

The proportion of Anisoptera was double than that of Zygoptera and the most widespread and abundant species was *S. fonscolombii* (Fig. 3.3). Six species could be considered as rare (Fig. 3.3). *C. scitulum, S. fusca* and *O. coerulescens* were rare due to their restricted distribution, *A. mixta* and *A. imperator* were rare due to their low abundance, and *A. isoceles* was rare due to both its restricted distribution and low abundance (Fig. 3.3).

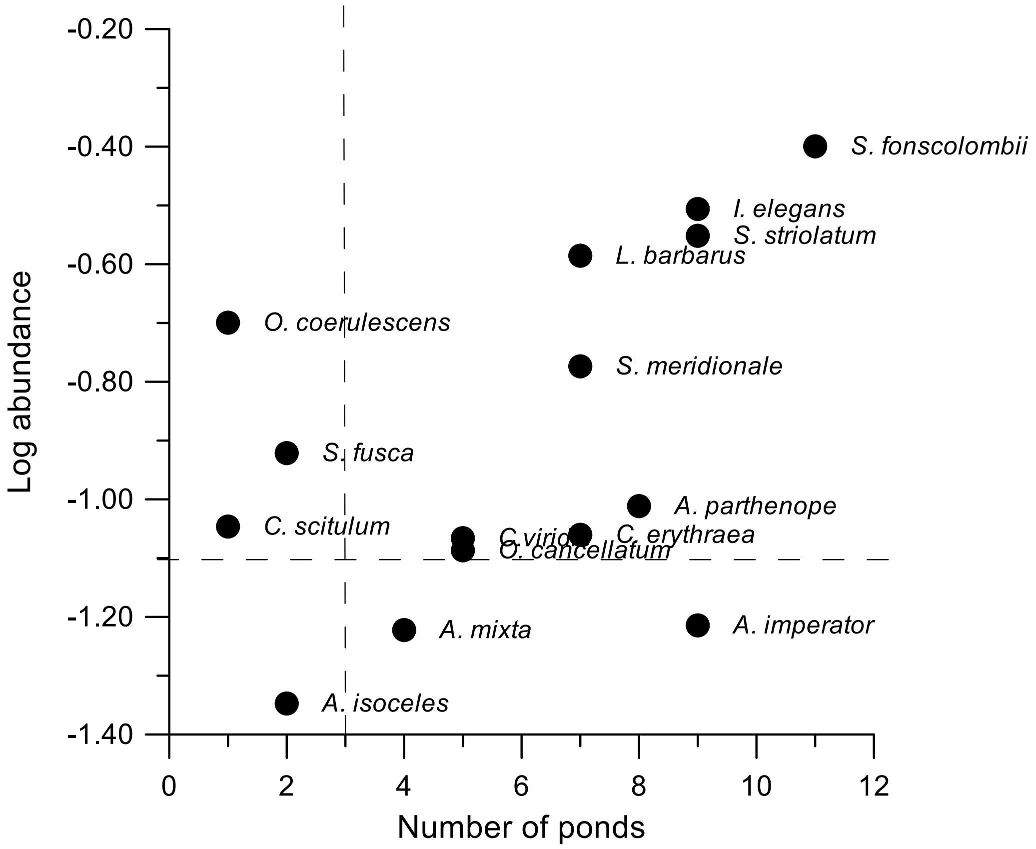


Fig. 3.3. Relationship between log species abundance at each pond and the number of ponds occupied. Dotted lines separate rare species according to the Gaston (1994) criterium of the 25%, based on their distribution (left side), abundance (bottom side) or both (lower left corner).

Environmental characterization of the temporary ponds

Environmental variables showed a very broad range of variation, as indicated by coefficients of variation from 2 (air temperature) to 124 (area pond) (Table 3.3).

Table 3.3. Mean ± SD values, coefficient of variation (CV) and range of the environmental variables measured at the temporary ponds. Measured values for the permanent wetland, Es Grau, are shown in the rightmost column.

Variable	Mean ± SD	CV	Minimum	Maximum	Es Grau
Depth (cm)	29.7 ± 22.3	75.2	5.3	80.9	71.7
Air temperature (envtem)(ºC)	26.4 ± 0.6	2.4	25.1	27.3	26.7
Water temperature (wattem)(ºC)	21.8 ± 3.1	14.1	16.5	28.3	24.2
pH	7.6 ± 0.5	6.7	6.7	8.6	8.9
ORP	42.5 ± 17.8	42.0	3.0	63.4	46.0
DO (mg/l)	6.3 ± 2.8	44.2	1.9	12.0	7.3
Conductivity (cond)(mS/cm)	0.8 ± 0.8	106.7	0.2	3.4	17.8
TDS (mg/l)	388.1 ± 393.9	101.5	117.5	1583.9	8888.3
Salinity (sal)	0.4 ± 0.5	107.4	0.1	1.8	11.7
Altitude (alt) (m a.s.l)	57.8 ± 34.1	59.0	2.0	110.0	2.0
Area (m^2)	1210.4 ± 1510.7	124.8	0.9	4446.0	725000.0
Submerged vegetation spring (Veg1s) (%)	63.9 ± 31.7	49.6	18.0	100.0	100.0
Emergent vegetation spring (Veg1e) (%)	26.1 ± 19.4	74.5	4.0	64.0	0.0
Submerged vegetation autumn (Veg2s) (%)	68.8 ± 27.1	39.3	25.0	100.0	100.0
Emergent vegetation autumn (Veg2e) (%)	26.8 ± 10.0	37.4	12.0	42.0	0.0
Area of influence (buff)(m^2)	823986.1 ± 55269.2	6.7	778695.0	928691.0	3570820.0
Drought (days)	39.3 ± 20.5	52.2	16.7	77.8	0.0
Land use (%)	42.7 ± 33.6	78.6	0.0	87.7	17.0
Connectivity (conn)	2.1 ± 1.9	92.6	0.0	5.0	2.0

The PCA analysis extracted three factors, explaining 44.6, 28.9 and 11.3% of the variance, respectively, to a total of 84.8% of the total variance in the environmental variables. Six environmental variables were significantly related to these three factors according to the broken stick method: connectivity, conductivity, TDS, pond area, altitude, and submerged plant cover in spring. Connectivity increased with increasing values of the first factor (Fig. 3.4a).

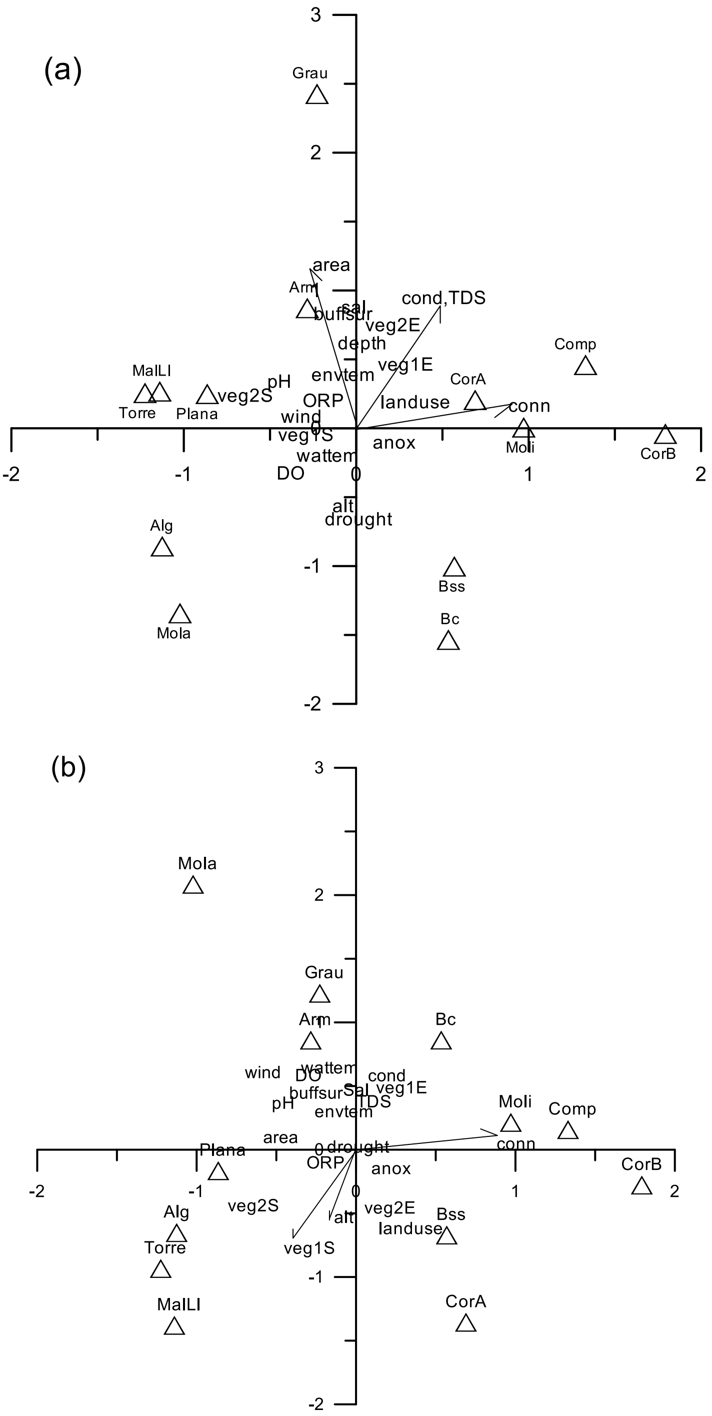


Fig. 3.4. Axes 1 and 2 ***(a)*** and axes 1 and 3 ***(b)*** of the ordination diagram (PCA) of temporary ponds in terms of the environmental variables (see Table 3 for abbreviations). Arrows indicate significant environmental variables according to the brocken stick method. Triangles indicate temporary ponds (see Table 1 for abbreviations).

Conductivity, TDS and pond area increased with increasing values of the second factor (Fig. 3.4a). Submerged plant cover in spring and altitude increased with decreasing values of the third factor (Fig. 3.4b).

Relationship between environmental variables and species richness

The PLS regression identified a single significant component, explaining 52% of variation in the data. This component was positively related to connectivity (loading = 0.847) and pond area (loading = 0.496).

DISCUSSION

Dragonfly assemblages at temporary ponds were mainly habitat generalists

Macroinvertebrates of temporary ponds include habitat generalists (Batzer et al. 2004) but also specialists (Williams 1997). In this study, no species exclusive of temporary ponds were found. Dragonflies related to temporary waters have different strategies to overcome drought such as egg diapause, high activity and high gowth rate (Johansson & Suhling et al. 2004; Carchini et al. 2007; McCauley et al. 2008). In our study, species described as able to tolerate drought (Carchini et al. 2007) only accounted for 30% of the total. Another strategy to overcome drought is a high dispersal ability (Urban 2004) usually related to body size in dragonflies (Raebel et al. 2012b). Anisoptera, larger than Zygoptera, have been described as broadly-dispersing (Steytler & Samways 1995) and are considered to be more common than Zygoptera in temporary ponds (Osborn & Samways 1996). Due to the generalist habit of many of the dragonfly assemblages in our study, we suggest that temporary ponds could be acting as a “second choice habitat” for some species related to other kind of habitats (Carchini et al. 2003), or as a feeding habitat (Corbet & Brooks 2008).

Temporary and permanent waters are assumed to show little overlap in macroinvertebrate assemblages (Welborn et al. 1996; Williams 1997; Zacharias et al.

2007). In our results, however, some temporary ponds formed a group with the permanent wetland. Dominant species in this group (e.g. *Anax* spp., *I. elegans*) have been related to permanent waters (Carchini et al*.* 2007) whereas species related to temporary waters like *Lestes* spp. and *Sympetrum* spp. (Schlinder et al. 2003; Carchini et al*.* 2007) characterized the other two groups. The group formed by Torrellafuda, Bassa Plana and Es Grau should not be necessarily interpreted as temporary ponds having a similarity with a permanent wetland but the opposite. Es Grau is a rather unusual permanent wetland in its dragonfly fauna and is more similar to temporary ponds than to other permanent wetlands in the Balearic Islands (Sato & Riddiford 2007).

Environmental variation and its influence on community structure

Ponds included in this study covered a large environmental heterogeneity. Several features have been used for characterizing ponds (Cottenie et al. 2001; Nicolet et al. 2004; Williams 2006; Raebel et al. 2012a) but in the Mediterranean basin, environmental differences between ponds have been documented mainly for hydroperiod (Carchini et al. 2007; Florencio et al. 2009), macrophyte diversity (Carchini et al. 2007), water chemical properties (Carchini et al. 2007; Gascón et al. 2008), substrate type (Zacharias et al. 2007; Petrus et al. 2010) and variables related to human disturbance (Carchini et al. 2007). In this work physicochemical variables such as conductivity and TDS as well as submerged vegetation were significant in the ponds ordination. However, biological interpretation of the main ordination axes summarizing environmental variability in the ponds studied was not intuitive, because in two cases it combined physicochemical and landscape variables. In general, the most influential variables for the ordination showed an high coefficient of variation (Table 3) except for the case of altitude, whose importance probably is related to the effect of saline spray and sea proximity as has been pointed out previously (J. García-Avilés, pers. comm.).

Canonical Correspondence Analysis (CCA) is a common technique to evaluate the effect of abiotic factors on community assemblages (Schlider et al. 2003; Carchini et al. 2007; Sato & Riddiford 2007). In this study, statistical problems prevented its application due to unstable results and only PLS was used. Area and connectivity were the only variables significantly positively correlated to dragonfly richness in the PLS. This is consistent with a larger influence of regional or dispersal factors in metacommunity assembly (Leibold et al. 2004). A positive species-area relationship has been found for dragonflies (Oertli et al. 2002; Bazzanti et al. 2003; Carchini et al. 2003; Kadoya et al. 2004; Gaines 2006; see, however, Carchini et al. 2005; Hinden et al. 2005) and other aquatic organisms (Broenmarck 1985; Fryer 1985; Hugueny 1989). The importance of area for species richness is probably due to a higher colonization probability of larger areas (Báldi 2008) and lower extinction probability, as highlighted for beetles and amphibians of temporary ponds (Fairchild et al. 2000; Lescano et al. 2015). The importance of connectivity has been pointed out for the assembly of new communities at restored or created freshwater habitats (Moore 1991; Chovanec 1994; Oertli 2008). For dragonflies, the availability of aquatic habitat around temporary ponds may be capital when species do not have strategies to cope with drought and are forced to leave temporary ponds (Carchini et al. 2007) and also to facilitate recolonization (De Block et al. 2005; Raebel et al. 2012b).

These results do not match previous findings in which local factors were more important for species richness (Steytler & Samways 1995; Heino 2002; Della Bella et al. 2005; Carchini et al. 2007; Honkanen et al. 2011; Florencio et al. 2014), mainly hydroperiod (Williams 1997; Nicolet et al. 2004; Boix et al. 2004). However, the effect of area can not only be interpreted as a dispersal factor, but also as a surrogate of local habitat factors (MacArthur & Wilson 1967; Báldi 2008). For example, in temporary ponds hydroperiod is sometimes difficult to separate from pond size (Della Bella et al. 2005; Carchini et al. 2005; Lescano et al. 2015) or from chemical variables (Della Bella et al. 2005). The low importance of local factors in this study could be partially due to our focus on adult dragonflies, for which hydroperiod or physicochemical variables can be less relevant than for larvae (Osborn & Samways 1996; D'Amico 2004; Sato & Riddiford 2007). Nevertheless, the lack of importance of vegetation was unexpected, because this variable is known to be of importance at different moments of dragonflies life cycle including adult habitat selection (Stewart & Samways 1998; Remsburg & Turner 2009; Corbet & Brooks 2008).

Implications for conservation

Two results support the importance of temporary ponds as habitat for dragonflies in our study area: their large share of the species pool and the presence of rare species. The studied temporary ponds hosted 68% of the Menorcan Odonata pool (15 of the 22 species recorded) (Ocharan 1987; Pons 1991; Garcia-Avilés et al. 1995; Dijkstra & Lewington 2006). This percentage was slighty higher than in other studies (>60%: Carchini et al. 2003; Schindler et al. 2003). Larval species richness accounted for 47% of adult species. This mismatch, with higher adult than larval presence, is common in Odonata studies (D'Amico et al. 2004; Gaines 2006; see however, Carchini et al. 2007) the so called dragonfly delusion (Raebel et al. 2010). The main reason causing this is that adults can attempt to breed at unsuitable locations for larval development (Horváth & Zeil 1996; Torralba Burrial & Ocharan 2003). This phenomenon has caused a controversy in the literature that remain unsolved (Bried et al. 2011). Nevertheless, and accepting that is highly probable that not all the recorded species as adults can complete their life cycle in this kind of habitat, our data agree with other larval surveys carried out in Menorca (Boix et al. 2010; Chapter 5) which reinforce the importance of temporary ponds as breeding habitats for dragonflies. In fact, Florencio et al. (2014) showed that temporary habitats can account up to 82% of the regional species pool when they are the prevalent habitat.

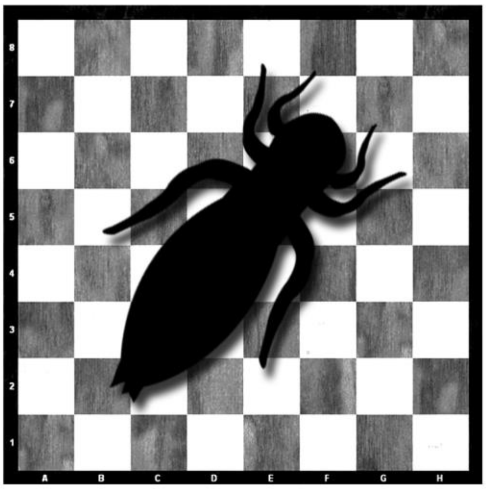
When temporary and permanent waters are compared, species richness is often slighty higher at permanent ones for dragonflies (Carchini et al. 2007) and other macroinvertebrates (Collinson et al. 1995; Nicolet et al. 2004; Della Bella et al. 2005) (see, however, Céreghino et al. 2008; Florencio et al. 2009). In Menorca, the permanent wetland surveyed as a reference had similar or even slightly lower species richness than most temporary ponds, no matter if larvae or adults were considered (Table 3.2). The list of Odonata for the permanent wetland could be actually higher, up to nine species (K. Crick, pers. comm.). Yet, this number is far from those for other permanent wetlands in Balearic Islands (Sato & Riddiford 2007).

Temporary ponds hold rare, endemic and threatened plant and macroinvertebrate species (Collinson et al. 1995; Nicolet et al. 2004; Della Bella et al. 2005; Zacharias et al. 2007). Two of the rare dragonflies detected at the present work have been classified as vulnerable (*C. scitulum*) or rare (*A. isosceles*) in Balearic Islands (Pons, 1991) and included in conservation lists at Spanish (Verdú & Galante 2006) and European level (Kalkman et al. 2010). Although our assessment of rarity was based on a limited amount of ponds, it agrees with a rarity assessment for the whole of Menorca, based on larvae (Chapter 5).

Development of suitable conservation measures may be challenging giving the large number of temporary ponds present in Mediterranean landscapes, e.g. over 76 in Menorca. At first sight, conservation of a few large ponds would retain almost all the species richness of dragonflies linked to these habitats (Diamond, 1975b; Simberloff and Abele 1982; Tjørve 2010). However, for effective policies, large and small habitats must be conserved because small areas can have valuable species not present in large habitats (Oertli et al. 2002; Biggs et al. 2005; Báldi 2008). Furthermore, conservation value of a pond may not be stable (Hassall et al. 2012) and dragonfly communities change over time (Chapter 5, Chapter 6). Thus, our results agree with the pondscape concept (Boothby 1997) in which ponds should not be viewed as isolated habitats (Williams et al. 2008) but connectivity among ponds, in addition to their diversity, must be considered (Florencio et al. 2014).

Dragonfly species linked to temporary ponds were habitat generalists. Nevertheless, temporary ponds were an important habitat for dragonflies because they hosted a large proportion of Menorca dragonfly species, including two species of conservation concern. Species richness in the temporary ponds was similar or higher than a permanent wetland used as a reference. Although temporary ponds were very variable in their local environmental characteristics, the main influence on species richness was pond area and connectivity, suggesting an influence of regional factors, rather than local conditions. Therefore, conservation planning should try to preserve the pondscape as a whole, rather than singular ponds.

CAPÍTULO 4. TEMPORAL STABILITY OF A LARVAL DRAGONFLY METACOMMUNITY STRUCTURE IN A MEDITERRANEAN ENVIRONMENT.



INTRODUCTION

A key aspect of community structure refers to the patterns of species coexistence, and their underlying processes (Weiher & Keddy 2001). The first pattern of species assembly was described by Clements (1916) who viewed association of plants as a kind of superorganism, resulting from similar responses of each species to the environment. By contrast, other plant ecologists such as Gleason (1926) and Tansley (1939) described communities as the outcome of the individual response of species with different ecological needs. Whittaker (1956) introduced the idea of the communities as a continuum along environmental gradients and the importance of the scale. In the study of animal communities, emphasis was given to competition, based on the Gause's competitive exclusion principle and the notion of limiting similarity (Hutchinson 1957; MacArthur & Levins 1967; May 1974). This led to an assembly pattern called "checkerboard" (Diamond 1975). In parallel, attention was being paid to geographical and historical processes in community assembly (MacArthur & Wilson 1967) in addition to interespecific competition. Patterson & Atmar (1986) described the "nested pattern", originated by local colonisation and extinction events on islands, such that species that make up smaller biotas are a perfect subset of the species that are found in all larger ones.

Patterns of species coexistence have been continually reviewed as long as ecologists have admitted that diversity of local communities results from a balance between local (abiotic and biotic interactions) and regional (habitat age, history of extinctions, rates of speciation and inmigration) processes (Ricklefs 1987; Hillebrand & Blenckner 2002) which act at multiple spatial and temporal scales (Ricklefs 2008; Wilson 1992; Hanski & Gilpin 1997). Connected communities (real or potentially) have been called metacommunities (Wilson 1992; Leibold et al. 2004). Hence, metacommunities provided an updated theoretical framework for analysis of how species are distributed across local communities.

Originally, research on spatial structure was mainly descriptive but recently several quantitative tests were developed to contrast empirical data (Connor & Simberloff 1979; Patterson & Atmar 1986; Hoagland & Collins 1997). Leibold & Mikkelson (2002) described six hypothetical metacomunity patterns which can be deduced from a site per species matrix (Table 4.1) and can be related to the main processes mentioned previously (e.g. environmental gradients, biotic interaction and stochastic processes). Leibold & Mikkelson (2002) suggested a methodology for judging if a given data matrix fits any of the idealized patterns by means the analysis of three meta-community structure elements (EMS): coherence, species turnover and boundary clumping. Coherence is observed in the ordered species per site matrix, when the sequence of species presences is not interrumped by the absences of other species. The more interruptions, the less coherent is the matrix (Leibold & Mikkelson 2002). Species turnover reflects the tendency for species to replace each other across sites or gradients (Leibold & Mikkelson 2002). Boundary clumping is the degree to which the boundaries of different species's ranges are clustered together (Leibold & Mikkelson 2002). Furthermore, Presley et al. (2010) increased the number of potential metacommunity structure patterns by including quasi-structures that are intermediate between the basic metacommunity structures.

Before the EMS approach was introduced, studies searching for metacommunity patterns usually tested only one potential pattern (Ulrich & Gotelli 2013). In case of negative results, a random structure was assumed (Henriques-Silva et al. 2013). For more than a decade, nestedness has been considered to be the most common pattern in biological communities (Cook & Quinn 1995; Wright et al. 1998). However, more than one pattern should be simultaneously tested .The prevalence of nestedness is being challenged (Ulrich & Gotelli 2007), mainly in freshwater ecosystems, where it seems to be related to the spatial scale and the type of ecosystem studied (Heino 2011). Indeed, when the EMS are analysed, although nestedness or checkerboard are the pattern for the whole incidence matrix, these patterns can coexist with Gleasonian and Clementsian gradients (Henriques-Silva et al. 2013; Heino et al. 2015).

Table 4.1. Description of the six theoretical patterns described by Leibold & Mikkelson (2002).

Pattern	Description	Main underlying processes
Checkerboard	Species pairs have mutually exclusive distributions	Biotic interaction
Nested subset	Species-poor sites are a subset of the richest ones	Colonisation and extinction events
Clementsian	Communities form discrete units that replace each other	Environmental gradients (similar responses)
Gleasonian	Community composition changes gradually across space	Environmental gradients (idyosincratic responses)
Evenly spaced gradients	Discrete communities are not observed but species ranges are arranged more evenly spaced tan expected by chance	Competition along an environmental gradient
Random	Species are randomly distributed	Stochastic processes

Dragonflies are important organisms in freshwater communities. Previous metacommunity studies of freshwater metacommunities have reported nested patterns (McAbendroth et al. 2005; Heino 2011; Ruhí et al. 2013; Florencio et al. 2014). Nested patterns have also been found for dragonflies when analysed separately from other macroinvertebrates (Craig et al. 2008; Wissinger et al. 2009; Sahlén & Ekestubbe 2001). This is probably caused by the relationship of species richness in dragonflies to different ecological factors such as area, water permanence, disturbance effects or shading (Kadoya et al. 2004; McCauley 2006; Hall et al. 2015; De Marco et al. 2015). However, when dragonfly metacommunities are analysed applying the EMS approach, nested pattern is far from being the prevalent pattern. Instead, Clementsian (McCauley et al. 2008) or up to five structures (including a random one) (Bried et al. 2015) have been found. Despite these advances, much remain to be done. First, previous works included only one type of habitat, a factor that could influence metacommunity structure. For example, lakes and ponds are island-like systems (Logue et al. 2011; De Meester et al. 2005) whereas lotic habitats offer higher potential connectance (Vannote et al. 1980). Second, how constant these patterns are remains mostly unexplored. Temporal stability of metacommunity structure has been highlighted for improving the match between empirical and idealised portraits (Heino et al. 2015, but see Block et al. 2007; Erös et al. 2014; Bonthoux & Balent 2015). Changes in Mediterranean odonatefauna have been reported (Cano & Carpintero 2014) but since our knowledge about the structure of their communities is limited (Florencio et al. 2014), potential consequences of these changes are uncertain. Third, it remains to be studied if Odonata differing in dispersal ability, as occurs with suborders Anisoptera and Zygoptera (Raebel et al. 2012b; De Marco et al. 2015), show differences in their metacommunity structure.

The main goal of the present work was to study the dragonfly metacommunity pattern and evaluate this temporal stability. This general aim was divided in three specific objectives: (1) to find out the pattern for a dragonfly metacommunity including five types of habitats, (2) to assess the stability of this pattern along time. This was studied by comparing the metacommunity structure in two time periods 22 years apart, and (3) to assess whether the metacommunity structure differs among two Odonata suborders with different dispersal abilities.

MATERIAL AND METHODS

Sampling sites and Odonata sampling

We studied a larval dragonfly metacommunity in two different moments, 1988 and 2010, The original sampling in 1988 (García-Avilés et al. 1995) included 68 sites. In 2010, only 54 sites could be resampled because seven were not relocated, four were not accessible and three were dry , thus only those 54 sites were included in the data set (Fig. 4.1). Sampling sites covered different freshwater habitats present in Menorca: (a) running waters (including temporary streams and springs) and (b) lentic systems (marshlands, wetlands and temporary ponds, including man-made ponds for cattle).

Sampling was carried out between March and June 2010. Each site was visited twice, a month apart when hydroperiod allowed it. The sampling point at each site was chosen to encompass the maximum number of suitable microhabitats for Odonata larvae according to aquatic plant cover, depth (Corbet & Brooks 2008) and behavior (Remsburg & Turner 2009).

The same observer, ES, carried out all surveys. Odonate larvae were collected with a pentagonal frame hand net (30 x 20 cm, 145 cm length, 1 mm mesh size) by moving the sediment vigorously with the feet. At each site three swipes were done making an S as long as the area allowed. This protocol, although slightly modified, is common in similar works (Ferreras-Romero & Corbet 1999; Torralba-Burrial & Ocharan 2007). The content of each swipe was filtered with PVP sieve with 1 mm mesh size. Filtered larvae were selected i*n situ* and there were preserved in 70% ethanol for further identification. When larvae size so allowed, individuals were identified to species following Carchini (1983) and Askew (2004), sometimes complemented with Heidemann & Seidenbusch (2002) and Belevich (2009). *Sympetrum meridionale* larvae were not distinguisible from those of *S. striolatum* with the available keys, so these two species were pooled in this work. This should not affect the results since *S. meridionale* was not recorded by García-Avilés et al. (1995). Odonata species nomenclature follows Dijkstra & Kalkman (2012).

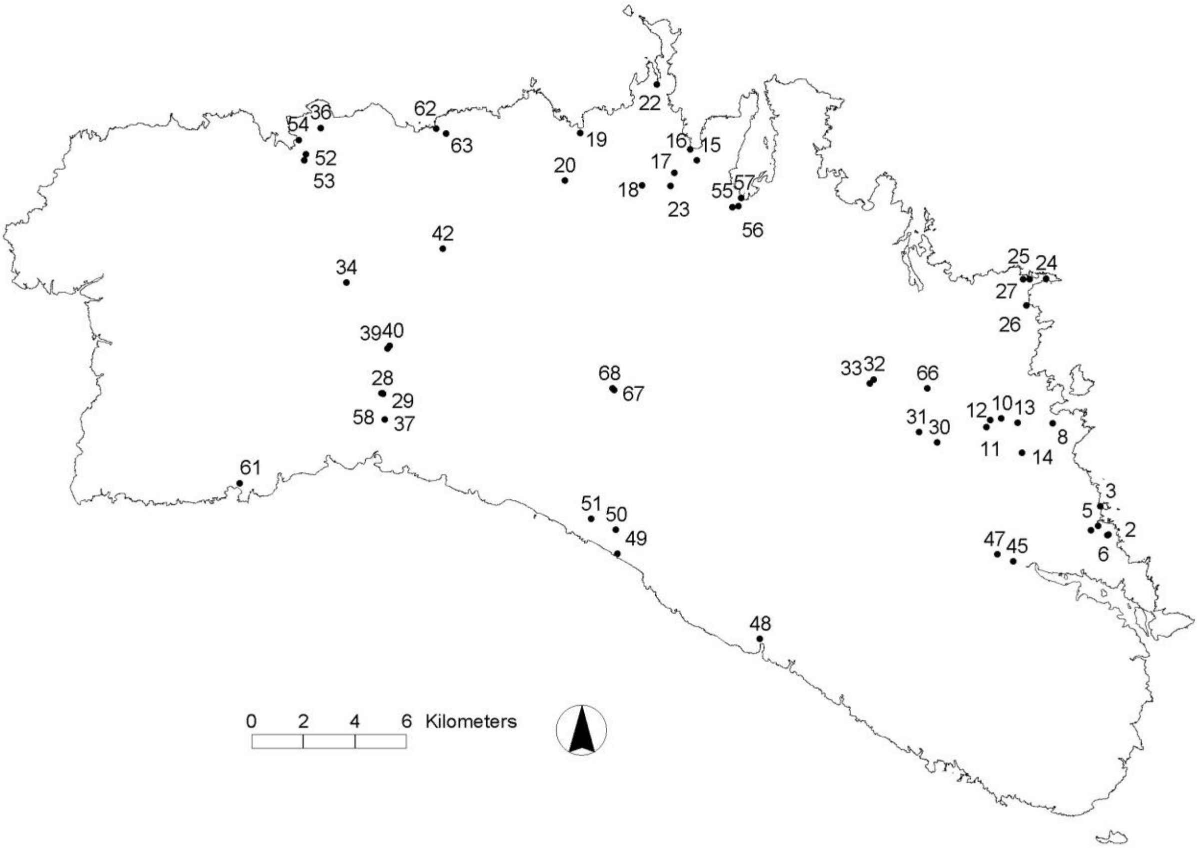


Fig. 4.1. Location of the sampling sites studied in Menorca.

Data Analysis

Elements of metacommunity structure (EMS) were assessed following Leibold & Mikkelson (2002) and Presley et al. (2010) using the R package *metacom* (Dallas 2014 in the R environment (version 3.1.0, R Development Core Team 2014). Firstly, site-by-species presence-absence matrices were ordinated using reciprocal averaging

(Leibold & Mikkelson 2002). This produces an incidence matrix were sites with similar species composition were close to each other along an ordination axis but also species with similar occurrence were close to each other (Gauch 1982). In total, we used three matrices for each year: one matrix for all the species and one matrix for analyzing each suborder (Anisoptera and Zygoptera) separately.

Random matrices were produced by the “r1” method for the fixed-proportional null model (the species richness of each site was maintained) and by “quasiswap” (fixed-fixed) method in which species richness per site and species frequencies are maintained (Oksanen et al. 2013). We used 1000 simulations to provide simulated matrices and to test the significance of the test ($\alpha = 0.05$). In a few cases in which 1000 provided only marginal significance, 5000 simulations were done. This problem may occur when a fixed-fixed model is applied and probabilities of incurring in type error II (failing to reject the null hypothesis when it is false) (Presley et al. 2010). In order to establish the metacommunity patterns that better fit the empirical data we followed the protocol described in Presley et al. 2010 in which the significance of each EMS is analysed hierarchically (Fig. 4.2). First the coherence is assessed. Coherence is obtained by calculating the number of embedded absences (i.e. gaps in a species appearance) in the ordinated matrix. The number of embedded absences is then compared to those obtained from simulated matrices according to a null distribution of this element (Leibold & Mikkelson 2002). A number of embedded absences significantly higher than that expected by chance is indicative of a checkerboard pattern (Fig. 4.2). Non significant coherence indicates a random pattern whereas a number of embedded absences significantly lower than that expected by chance requires checking for turnover (Fig. 4.2).

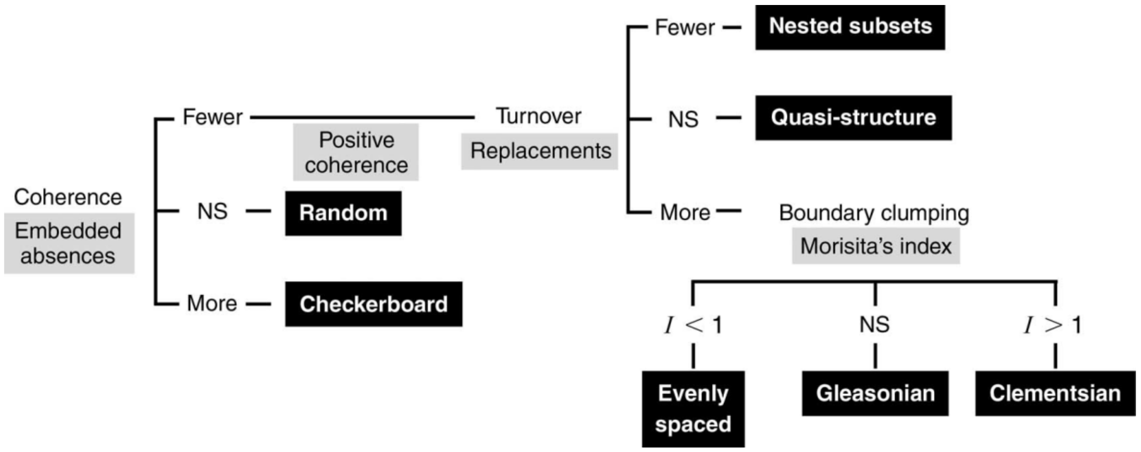


Fig. 4.2. Protocol followed in metacommunity structure analysis, showing the order of the steps in the analysis as well as the interpretation of the results (taken from Mihaljevic et al. 2015). Text in grey boxes indicates the metric used to estimate each element of the metacommunity structure. NS: non significant. Fewer and More refer to the comparison between the observed and expected values for each metric.

Turnover measurement includes the number of times one species replaces another between two sites in an ordinated matrix. If observed replacements are significantly lower than expected by chance, a nested pattern is present (Fig. 4.2). When observed replacements are significantly higher than expected by chance, metacommunity structure is related to environmental gradients (Fig. 4.2). Lastly, boundary clumping index is analysed using Morisita's dispersion index and a chi-square test comparing observed and expected distributions of range boundary locations. In this case, metacommunity patterns will be assigned depending on observed values of the index are signicantly different from 1 (Leibold & Mikkelson 2002). Values significantly greater than 1 mean that range boundaries are more clumped than expected (Clementsian structure) whereas the opposite situation means that they are over-dispersed (Evenly spaced distribution) (Fig. 4.2). This metacommunity element, in addition to turnover, can be useful to distinguish among the quasi-stuctures (Presley et al. 2010) (Fig. 4.3).

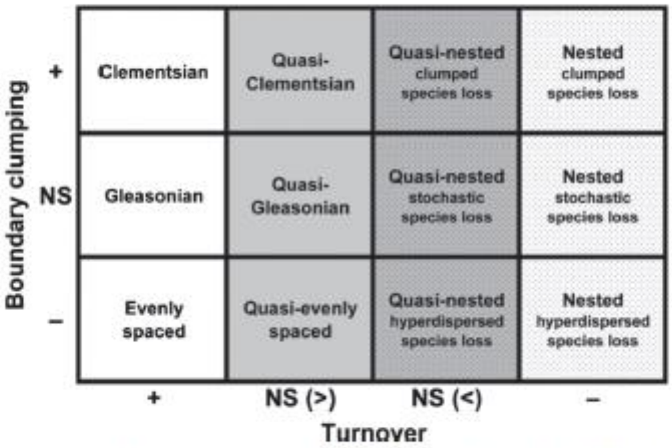


Fig. 4 3. Metacommunity patterns based on range turnover and boundary clumping, in coherent matrices. Quasi structures are observed when turnover is nonsignificant. For the meaning of +, NS and - see Fig. 2. NS (>): more replacements than the average number in random matrices; NS (<): less replacements than the average number in simulated random matrices (taken from Presley et al. 2010).

RESULTS

In 1988 15 species (6 Anisoptera and 9 Zygoptera) were recorded whereas in 2010, 20 species (11 Anisoptera and 9 Zygoptera) were recorded. Independently of the null model utilised, the metacommunity structure in 1988 was a quasi-structure and in 2010 was random (Fig. 4.4a, Fig. 4.5a, Table 4.2). There was no concordance between the quasi-structure identified by r1 and quasiswap models. According to the r1 model, the quasi-structure was quasi-nested (clumped species loss) whereas quasi-Clementsian was the pattern identified according to quasiswap model (Table 4.2, Fig. 4.3).

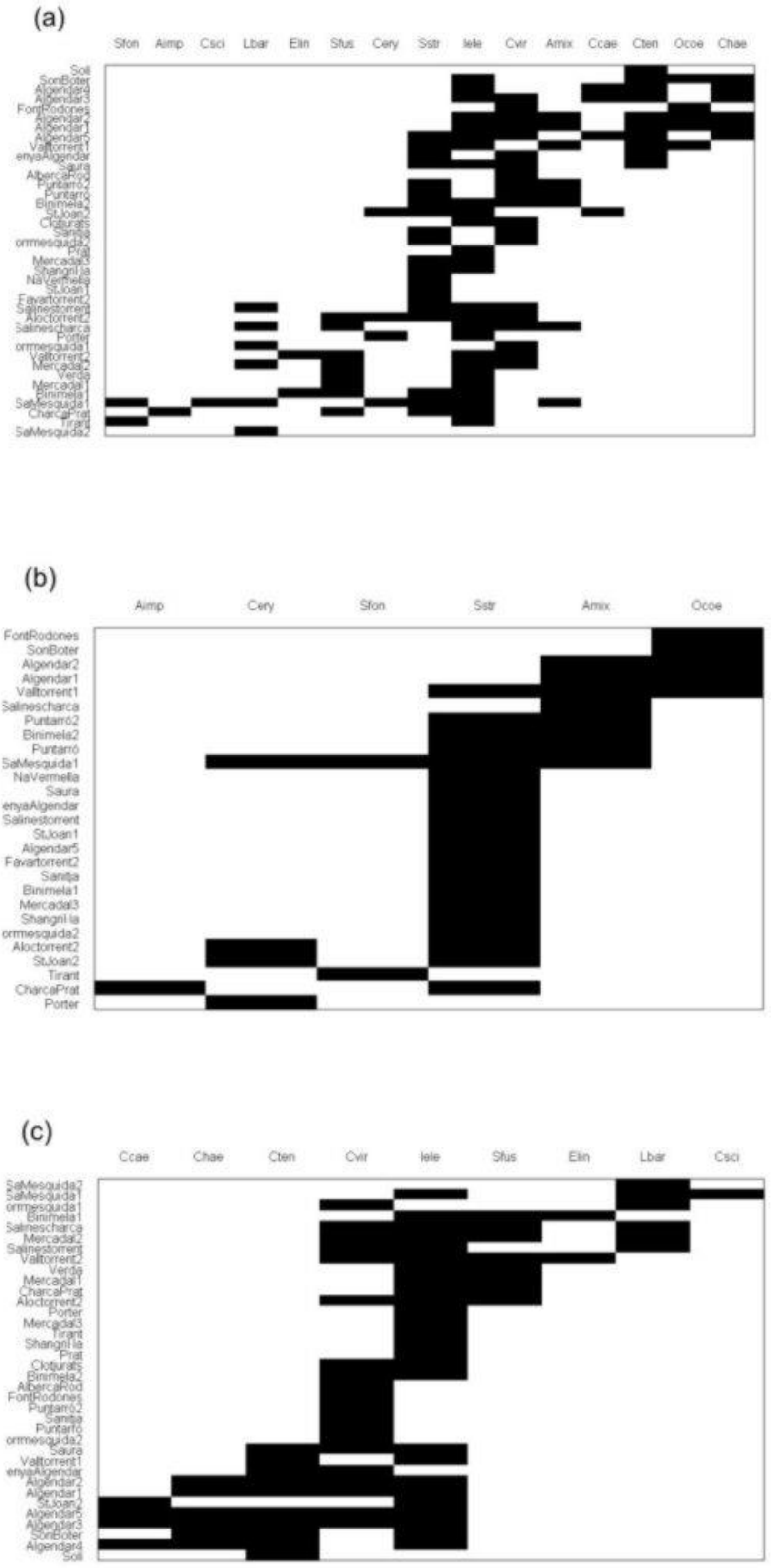


Fig. 4.4. Incidence matrix for 1988. (a) All species, (b) Anisoptera, (c) Zygoptera

Anisoptera (Fig. 4.4b, Fig. 4.5b) and Zygoptera (Fig. 4.4c, Fig. 4.5c) showed different metacommunity structure in both years. While the metacommunity pattern for Anisoptera was random in both years (Table 4.2) Zygoptera showed a quasi-nested (clumped species loss) structure in both years (Table 4.2).

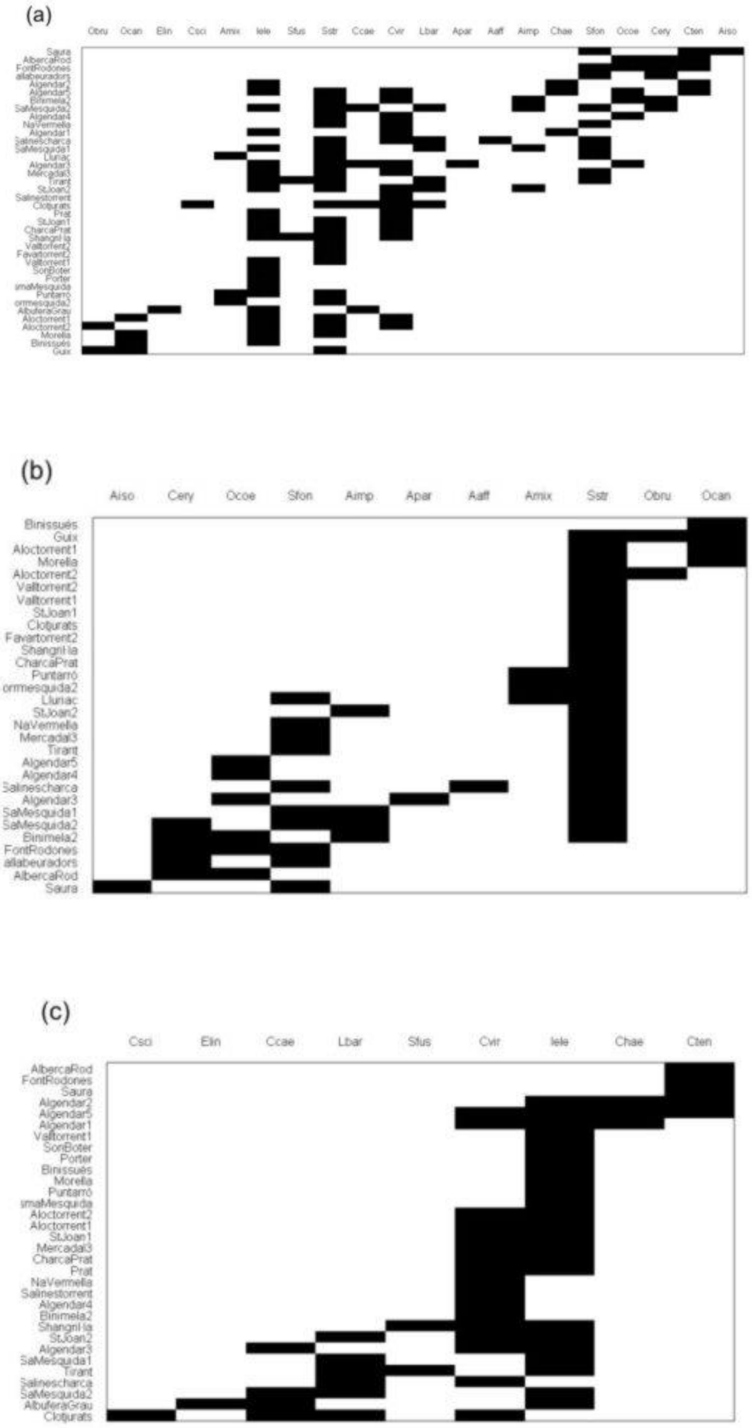


Fig. 4.5. Incidence matrix for 2010. (a) All species, (b) Anisoptera, (c) Zygoptera.

Table 4.2. Results of the EMS analysis for the whole dataset (all) and for the Anisoptera and Zygoptera separately. Abs: number of embedded absences; Repl: number of replacements. For Coherence and Turnover, the mean ± SD Abs and Repl in simulated matrices are indicated for the r1 and quasiswap models after 1000 simulations (* after 5000 simulations). For Boundary clumping is indicated the Morisita's index regardless null models because was coincident. P = p value; in bold, significant values.

		All	**Anisoptera**	**Zygoptera**
1988				
Coherence	Observed:	Abs = 123	Abs = 31	Abs = 33
	R1	199 ± 22.8	19.9 ± 8.0	86.7 ± 13.34
		P = 0.0008	P = 0.164	**P < 0.001**
	quasiswap	195 ± 22.4	18.8 ± 8.8	85.4 ± 14.5
		P = 0.001	P = 0.167	**P = 0.0003**
Turnover	Observed:	Repl = 4435	Repl = 554	Repl = 850
	R1	4462 ± 1212	405 ± 131	1536 ± 436
		P = 0.982	P = 0.255	P = 0.116
	quasiswap	4015 ± 1048	316 ± 95	1284 ± 392
		P = 0.689	**P = 0.012**	P = 0.268
Boundary Clumping	Morisita's Index	1.873	1.947	1.804
		P < 0.001	**P < 0.001**	**P < 0.001**
		Df = 12	Df = 3	Df = 6
Pattern	R1	Quasi-nested Clumped species loss	Random	Quasi-nested Clumped species loss
	quasiswap	Quasi-Clementsian	Random	Quasi-nested Clumped species loss
2010				
Coherence	Observed:	Abs = 195	Abs = 55	Abs = 29
	R1	251.6 ± 30.4	68.5 ± 14.7	57.9 ± 12.7
		P = 0.062	P = 0.359	**P = 0.023**
	quasiswap	239.8 ± 31.08	64.5 ± 13.5	54.3 ± 12.9
		P = 0.150	P = 0.480	**P = 0.0491***
Turnover	Observed:	Repl = 6088	Repl = 802	Repl = 486
	R1	6956 ± 1907	1426 ± 389	1056 ± 330
		P = 0.648	P = 0.109	P = 0.084
	quasiswap	6168 ± 1733	1134 ± 324	798 ± 285
		P = 0.963	P = 0.305	P = 0.274*
Boundary Clumping	Morisita's Index	2.534	3.453	2.536
		P = 0	**P = 0**	**P = 0**
		Df = 17	Df =8	Df = 6
Pattern	R1	Random	Random	Quasi-nested Clumped species loss
	quasiswap	Random	Random	Quasi-nested Clumped species loss

DISCUSSION

Our analysis found two main metacommunity patterns: random and quasi-structures. According to Simberloff (1983), random pattern is observed when species distribution among sites does not follow any pattern. However, one should bear in mind that by means of reciprocal averaging method, metacommunity structure is evaluated along a specific latent environmental gradient (Leibold & Mikkelson 2002) so a random pattern in this context only indicates that species distribution are independent of one another along that particular gradient (Dallas & Presley 2014). A quasi-structure is assigned when metacommunity exhibits a nonrandom pattern (i.e. significant coherence) but had a indistinguisible pattern of turnover (Presley et al. 2010). Advantages and disadvantages about different null models have been highlighted in previous works when coherence is analysed and some authors have recommended not to use very conservative models in order to asses correctly a truly coherent matrix (Presley et al. 2010). However, our discrepancies were related to the quasi structure type assigned (quasi-Clementsian *vs* quasi-nested). Although both patterns have been observed in dragonfly metacommunities (Bried et al. 2015), we decided to give more reliability to quasi-nested for two reasons: (a) model r1 constrains species richness of each site but assigns equiprobable occurrences for each species as Presley et al. (2010) recommeded and (b) A quasi-nested pattern was observed in Zygoptera species both in 1988 and 2010 without discordances between models, so we believe it is a robust pattern in present data (Table 4.2).

In a previous research of adult Odonata metacommunity structure, the presence of a random structure could be attributed to the inclusion of inmigrant species in the data set (Bried et al. 2015). When only resident species were considered, a Clementsian gradient pattern was found (Bried et al. 2015). This could not have affected our results, because in the present work species were recorded as larvae and were “resident” by definition. Nevertheless, species present in a single site can influence the reciprocal average ordination method (McCune et al. 2002; Dallas & Drake 2014; but see Heino et al. 2015). Thus, we tested if removing the species recorded at a single site would modify the patterns observed. The pattern observed for both1988 and 2010 was quasi-Clementsian. This fact did not change original results for 1988 but for 2010 did. Since the number of removed species was higher in 2010 (5) than in 1988 (2), we suspect that the change in observed pattern was probably caused by the size of the incidence matrix (Presley et al. 2010). This prevented us from similar tests for the Anisoptera and Zygoptera, since the incidence matrices became dangerously small after removing rare species.

Quasi-structures have been rarely reported in works focused on dragonflies as far as we know (McCauley et al. 2008; De Marco et al. 2015; but see Bried et al., 2015) although are known from other types of organisms (Kusch et al. 2005; Presley et al. 2012; Dallas & Presley 2014). Each quasi-structure is consistent with the conceptual patterns of Clementsian, evenly spaced, Gleasonian or nested distributions although their structuring forces are weaker than when turnover is significant (Presley et al. 2010). Nested structure is characterized by a predictable pattern of species loss among sites although multiple mechanisms may give rise to nested subset (Wright et al. 1998; Block et al. 2007). Nestedness can occur in odonates when species are filtered along gradients such as shading and water permanence (McCauley et al. 2008; De Marco et al. 2015). In the present study, boundary clumping was significantly positive so species loss was clumped (Table 4.2, Fig. 4.3). This specific pattern can be explained by habitat specialization (Presley et al. 2010).

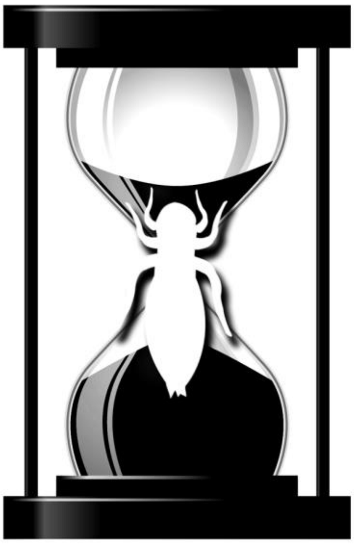
Habitat specialization has been related to dispersal limitations (McCauley 2007). Zygopterans have lower dispersal ability than anisopterans, so the former tend to disperse greatest distances and are more likely to colonize new habitats (McCauley 2007). Here, different metacommunity patterns were detected for anisopterans and zygopterans (Table 4.2). According to our results, we can suspect that zygopteran metacommunity pattern could be more influenced by the jointed effects of dispersal limitation and niche association than anisopterans.

In the studied metacommunity, the structure changed with time, for the whole data set, from a quasi-nested structure to a random pattern. However, the metacommunity structure for each suborder was more constant in time. The few studies available about temporal changes in metacommunity structure have mainly found stability (Keith et al. 2011; Bonthoux & Balent 2015). Moreover, when changes in the patterns have been detected, they have been related to subsets of species (e.g. native or non-native) rather than to all the species included in the study (Erős et al. 2014). We advance two non-exclusive hypotheses to account for the temporal change in metacommunity pattern: (a) the overall pattern observed is influenced by a change the dominance of anisopterans (6 in 1988, 11 in 2010) compared to zygopterans (9 in 1988, 11 in 2010) and/or (b) the change is due to a continual series of disturbance/re-colonisation events, (McCreadie et al. 2011; Dutra & De Marco 2015). This trend has been reported mainly in streams and other terrestrial habitats, where one non-random pattern (checkerboard) evolved to random one (McCreadie & Bedwell 2013). In our case, these two hypotheses make sense because in 2010 anisopterans were more abundant than zygopterans and they are likely more able to colonise new, even disturbed habitats (De Marco et al. 2015). Moreover, although we cannot know whether disturbance level of the sites changed after 22 years, re-colonisation events have been observed for dragonfly communities in restored habitats as well as sink-source dynamics (Crumrine et al. 2008; Chapter 6).

Although EMS is a useful tool to discriminate between different idealized patterns, we are aware that our results should be taken with caution. First, the analysis of the elements of meta-community structure not necessarily allows to disentangle the underlying processes. Indeed, the same patterns can result from different, even opposite processes (Gilpin & Diamond 1982; Ulrich & Gotelli 2007). As a consequence, further analyses are required to determine the gradient and the nature of the gradient along which a metacommunity is structured (Dallas & Presley 2014). Second, the analysis can be affected by the quality of the data. In this context, multispecies occupancy models allow a substantial improvement of the analysis, by taking into account imperfect detection (Mihaljevic et al. 2015).

In a nutshell, larval dragonfly metacommunities showed a quasi-nested pattern. However, this metacommunity structure was not stable in time and became random 22 years later. In addition, the metacommunity pattern of dragonfly larvae changed with depending on the suborder considered. While Zygoptera showed a quasi-nested pattern, Anisoptera had a random structure. Observed patterns could be driven by differences in dispersal ability and habitat specialization. These patterns were maintained after 22 years. In spite of matching with preview researchs, further analysis are required to identify the specific mechanisms associated with these patterns.

CAPÍTULO 5. TEMPORAL TURNOVER OF DRAGONFLY COMMUNITIES IN A MEDITERRANEAN ISLAND: COMPARISON OF TWO SURVEYS SEPARATED BY 22 YEARS.



INTRODUCTION

Understanding how biodiversity varies at several scales is a central theme in ecology (Mittelbach 2012; McGill et al. 2015). Such variation is usually estimated through beta diversity, which measures the variation in species composition among sites in a given area of interest (Whittaker 1960, 1972). Beta diversity and species turnover (MacArthur & Wilson 1967) have frequently been considered as interchangeable terms (see, however, Anderson et al. 2011). In recent years, beta diversity has received much empirical attention (Harrison et al. 1992; Koleff & Gaston 2002; Soininen et al. 2007a; Baeten et al. 2012), as indicated by several revisions for terrestrial (Rodríguez & Arita 2004; Overton et al. 2009) and aquatic environments (Witman et al. 2004; Heino & Soininen 2010; Korhonen et al. 2010). At the same time, theoretical aspects of beta diversity have been questioned (Koleff et al. 2003; Legendre et al. 2005; Tuomisto 2010; Anderson et al. 2011). Among the new theoretical developments, two complementary components of beta diversity have been distinguished: species replacement (some species are replaced by other species from site to site) and species richness differences (differences in composition across sites are due to species gain or loss) (Williams et al. 1999; Lennon et al. 2001; Baselga 2010; Carvalho et al. 2012).

In a metacommunity context, the study of beta diversity helps to understand how deterministic (environmental filtering, biotic interactions and interespecific trade-offs) and stochastic processes (ecological drift- i.e. stochasticity in birth, death, colonisation and extinction rates-, dispersal limitation or dispersal history) influence community assembly (Chase 2010; Chase & Myers 2011). Deterministic processes are related to niche theory (Chase & Leibold 2003) in which habitat heterogeneity mediates biological interactions and the environmental response of species. In addition, stochastic processes can vary the composition and diversity of local communities (Leibold et al. 2004; Legendre et al. 2005; Chase 2007).

Deterministic and stochastic processes can also produce changes over time within a local community (Pandit et al. 2009). However, temporal turnover has received less empirical attention due to the lack of long-term data from multiple sites (Shurin 2007; Angeler 2013). In a system with high environmental variability, high values of temporal turnover are expected. These high values would be mediated by species richness decreases and the role of biotic interactions in facilitating colonisation and extinction events (Shurin 2007; Pandit & Kolasa 2012). Temporal turnover has been shown to be negatively correlated to high species richness and stability (Krieger et al. 2003; Shurin 2007; Zamora et al. 2007; Pandit & Kolasa 2012).

Although compositional changes are inherent to natural communities (Vellend 2010; Pandit & Kolasa 2012; Hassall et al. 2012), they can be exarcerbated by human activities (Marvier et al. 2004; Donohue et al. 2009; Augestein et al. 2012). Thus, in addition to its ecological interest, quantification of beta diversity has been used for monitoring the effects that human activities have on biodiversity and for proposing conservation measures (Passy & Blanchet 2007; Overton et al. 2009). According to the prevalence of species replacement or the species richness components, and how they vary through time, different conservation measures can be considered (Angeler 2013). If the species richness component dominates, priority can be given to the sites with more species, while if the species replacement dominates, conservation measures should be focused on multiple sites (Angeler 2013).

Freshwater ecosystems are among the most studied habitats in which drivers of beta diversity have been investigated (Jeffries 1994; Wissinger et al. 2009; Suurkuka et al. 2011; Kuglerova et al. 2015). Their invertebrate communities often differ along environmental gradients (Welborn et al. 1996), fish predation pressure (Spencer et al. 1999) and the importance of dispersal (active and passive dispersers) (Wilbur 1997; Vanschoenwinkel et al. 2007). In a recent review, Heino (2011) pointed out that patterns of beta diversity are strongly scale-and organism-dependent (Soininen et al. 2007b). For instance, at large scale, spatial turnover is related to geographical distance for fish and phytoplankton communities while for zooplankton and stream invertebrates, both spatial distance and environmental dissimilarity are important (Cottenie & De Meester 2004; Angélibert et al. 2004; Thompson & Townsend 2006; Leprieur et al. 2009; Chase 2010).

Dragonfly communities can be found at many types of freshwater ecosystems (Corbet & Brooks 2008). Their taxonomy, distribution and main threats are well known (Clausnitzer & Jödicke 2006; Samways 2006; Bried & Mazzacano 2010; Dijkstra & Kalkman 2012) and the main determinants of their species richness at broad and local scales have been stablished (Heino 2001, 2002; Keil et al. 2008; Novelo-Gutiérrez & Gómez Anaya 2009; Campbell et al. 2010). However, knowledge of spatial turnover of their communities is limited (Wissinger et al. 2009; Juen & de Marco 2011; Florencio et al. 2014). Temporal turnover has only focused on successional dynamics (Moore 1991; Chovanec 1994; Chovanec & Raab 1997) or on changes driven by climate change (Flenner & Sahlén 2008; Bush et al. 2013; Cano & Carpintero 2014).

The main objective of the present study was to document temporal turnover and their environmental correlates for the Odonate fauna of Menorca (Balearic Islands, Spain), where historical information (García-Avilés et al. 1995) allows a comparison of two surveys separated by 22 years. Our specific questions were: (1) Has species richness and composition of the sites changed between surveys?, (2) Has the rarity rank of species changed between surveys?, (3) Did environmental factors changed between surveys?, (4) Did environmental factors influenced community structure and did this influence differed among surveys?, (5) What is the magnitude of temporal beta diversity and its two components, and (6) Is the magnitude of temporal beta diversity related to the extent of environmental change?

MATERIAL AND METHODS

Sampling sites and Odonata sampling

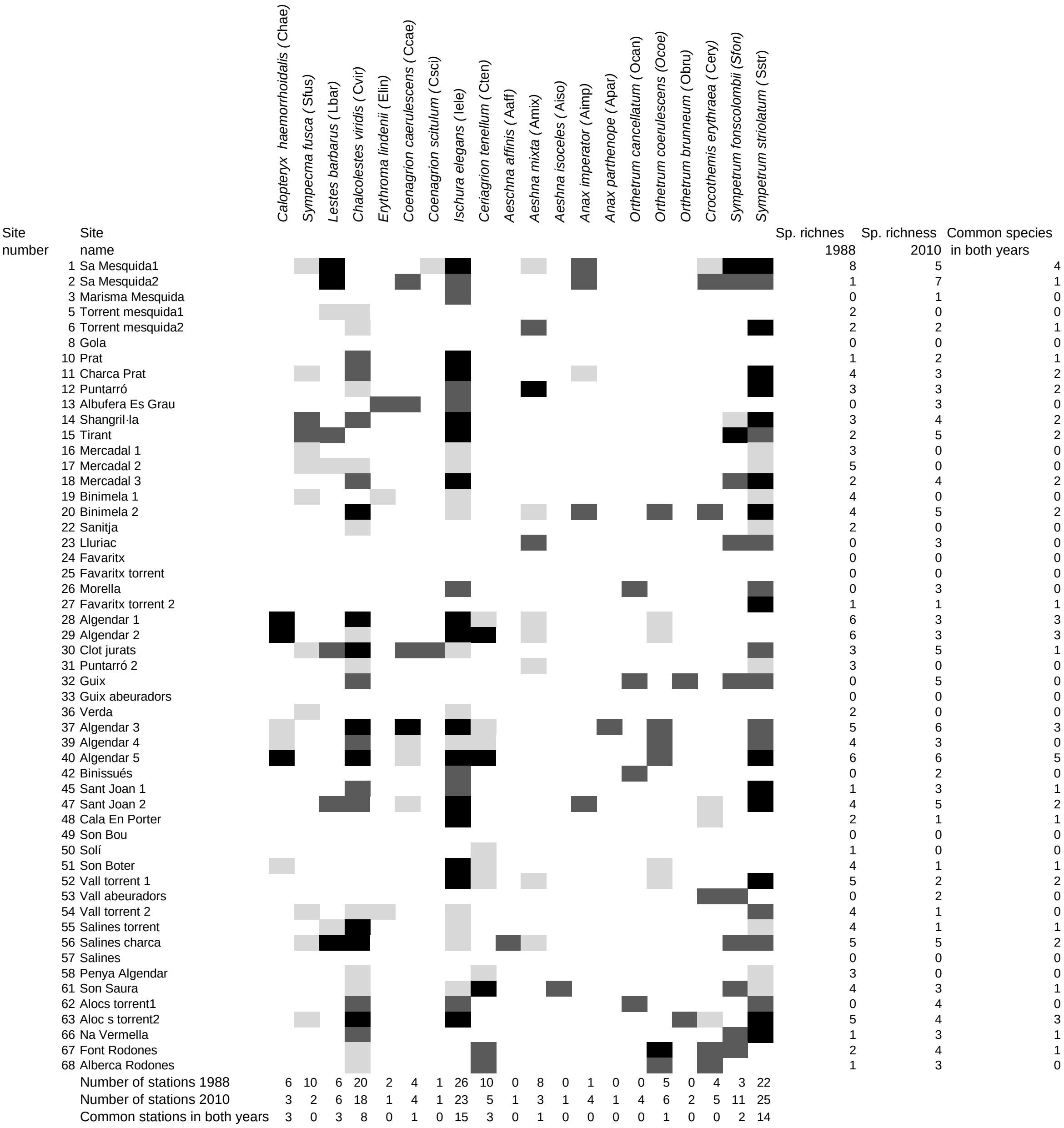
Sampling sites were chosen according to García-Avilés et al. (1995) and covered different freshwater habitats spreaded across the island (Fig. 4.1, Chapter 4). Only 54 of the 68 sites in García-Avilés et al. (1995) were resampled (see Chapter 4 for details). Due to their proximity and similar values for environmental variables, sites 9 and 10 (hereafter site 10) were joined for analysis (Table 5.1).

Details of field work and further identification of specimens were explained in Chapter 4. The present work used the same procedure of sampling as the one followed in the original sampling by García-Avilés et al. (1995). Nevertheless, rarefaction curves were calculated in order to test the completeness of inventories for each year (Jiménez-Valverde & Hortal 2003). Rarefaction curves were calculated using PAST (Hammer et al. 2001) and Statistica 7.0 was used for adjusting them to the Clench model (Jiménez-Valverde & Hortal 2003). The completeness of inventories ranged from 55 % to 100% for 1988 and from 74% to 91% for 2010 (Appendix 1).

The species regional pool was 15 species in 1988 (García-Avilés et al. 1995). Current checklist of Odonata in Menorca consists of 21 species (Chapter 3; Márquez-Rodriguez 2014), all of them found as both adults and larvae, i.e., proper resident species (Table 5.1). *L. depressa* and *A. cyanea* were not considered as a part of regional pool because these records were doubtful -in a single locality in the 1980s- and are probably misidentifications (Pons-Madrid 1984; Pons 1991). Three reasons could explain this discrepancy between both surveys: (a) species were present but undetected, (b) species were detected but remained unidentified due to their small size, or (c) species colonized Menorca after 1988. The last option seems unlikely. Intensive surveys can miss some species, especially when rare (Baixeras et al. 2006; Soler & Arlés 2007). This is the case of the five species present in

2010 but undetected in 1988. For example, adults of *A. affinis*, *A. isoceles* and *O. cancellatum* were recorded in 1987 (Ocharan 1987) but were not detected as larvae in the 1988 data set, probably due to their rarity. *A. parthenope* and *O. brunneum* were first reported in 1991 (Pons 1991) but they are also rare and were probably already present in 1988.

Table 5.1. Site per species matrix. Species presence at each site has been coded as light grey (1988), dark grey (2010) or black (both years). Species richness in 1988 and 2010 and the number of common species between years is indicated for each site. Species incidence in 1988 and 2010 and number or common sites occupied across years is indicated for each species.



Site number	Site name	*Calopteryx haemorrhoidalis* (Chae)	*Sympecma fusca* (Sfus)	*Lestes barbarus* (Lbar)	*Chalcolestes viridis* (Cvir)	*Erythroma lindenii* (Elin)	*Coenagrion caerulescens* (Ccae)	*Coenagrion scitulum* (Csci)	*Ischura elegans* (Iele)	*Ceriagrion tenellum* (Cten)	*Aeschna affinis* (Aaff)	*Aeshna mixta* (Amix)	*Aeshna isoceles* (Aiso)	*Anax imperator* (Aimp)	*Anax parthenope* (Apar)	*Orthetrum cancellatum* (Ocan)	*Orthetrum coerulescens* (Ocoe)	*Orthetrum brunneum* (Obru)	*Crocothemis erythraea* (Cery)	*Sympetrum fonscolombii* (Sfon)	*Sympetrum striolatum* (Sstr)	Sp. richnes 1988	Sp. richness 2010	Common species in both years
1	Sa Mesquida1		░	█				░	█			░		▓					░	█	█	8	5	4
2	Sa Mesquida2			█			▓		▓					▓					▓	▓	▓	1	7	1
3	Marisma Mesquida								▓													0	1	0
5	Torrent mesquida1			░	░																	2	0	0
6	Torrent mesquida2				░							▓									█	2	2	1
8	Gola																					0	0	0
10	Prat				▓				█													1	2	1
11	Charca Prat		░		▓				█					░							█	4	3	2
12	Puntarró				░				▓			█									█	3	3	2
13	Albufera Es Grau					▓	▓		▓													0	3	0
14	Shangril·la		▓		▓				█											░	█	3	4	2
15	Tirant		▓	▓					█											█	▓	2	5	2
16	Mercadal 1		░						░												░	3	0	0
17	Mercadal 2		░	░	░				░												░	5	0	0
18	Mercadal 3				▓				█											▓	█	2	4	2
19	Binimela 1		░			░			░												░	4	0	0
20	Binimela 2				█				░			░		▓			▓		▓		█	4	5	2
22	Sanitja				░																░	2	0	0
23	Lluriac											▓								▓	▓	0	3	0
24	Favaritx																					0	0	0
25	Favaritx torrent																					0	0	0
26	Morella								▓							▓					▓	0	3	0
27	Favaritx torrent 2																				█	1	1	1
28	Algendar 1	█			█				█	░		░					░					6	3	3
29	Algendar 2	█			░				█	█		░					░					6	3	3
30	Clot jurats		░	▓	█		▓	▓	░												▓	3	5	1
31	Puntarró 2				░							░									░	3	0	0
32	Guix				▓											▓		▓		▓	▓	0	5	0
33	Guix abeuradors																					0	0	0
36	Verda		░						░													2	0	0
37	Algendar 3	░			█		█		█	░					▓		▓				▓	5	6	3
39	Algendar 4	░			▓		░		░	░							▓				▓	4	3	0
40	Algendar 5	█			█		░		█	█							▓				█	6	6	5
42	Binissués								▓							▓						0	2	0
45	Sant Joan 1				▓				▓												█	1	3	1
47	Sant Joan 2			▓	▓		░		█					▓					░		█	4	5	2
48	Cala En Porter								█										░			2	1	1
49	Son Bou																					0	0	0
50	Solí									░												1	0	0
51	Son Boter	░							█	░							░					4	1	1
52	Vall torrent 1								█	░		░					░				█	5	2	2
53	Vall abeuradors																		▓	▓		0	2	0
54	Vall torrent 2		░		░	░			░												▓	4	1	0
55	Salines torrent			░	█				░												░	4	1	1
56	Salines charca		░	█	█				░		▓	░								▓	▓	5	5	2
57	Salines																					0	0	0
58	Penya Algendar				░					░											░	3	0	0
61	Son Saura				░				░	█			▓							▓	░	4	3	1
62	Alocs torrent1				▓				▓							▓					▓	0	4	0
63	Aloc s torrent2		░		█				█									▓	░		█	5	4	3
66	Na Vermella				▓															▓	█	1	3	1
67	Font Rodones				░					▓							█		▓	▓		2	4	1
68	Alberca Rodones				░					▓							▓		▓			1	3	0
	Number of stations 1988	6	10	6	20	2	4	1	26	10	0	8	0	1	0	0	5	0	4	3	22			
	Number of stations 2010	3	2	6	18	1	4	1	23	5	1	3	1	4	1	4	6	2	5	11	25			
	Common stations in both years	3	0	3	8	0	1	0	15	3	0	1	0	0	0	0	1	0	0	2	14			

Habitat characterization

At each site, water temperature (ºC), pH, conductivity (mS/cm), total dissolved solids (mg/l) and dissolved oxygen (mg/l,) were measured with a multiparametric probe Hanna HI-9829. The three first variables were measured in 1988 too (García-Avilés et al. 1995). Water depth was measured with a tape (cm). This variable was measured at the sampling point whereas in García-Avilés et al. (1995) an average value was estimated for each site. Both measures were positively correlated ($R_s = 0.48$, $p < 0.001$) and no significant differences were found between these two measures ($t = 1.41$, $p = 0.16$, $n = 49$). Moreover, distance to the sea and altitude were calculated and presence/absence of aquatic vegetation and organic matter was scored. Sites were coded according to bottom (rock, gravel, sand and silt) and habitat types (stream, pond, small man-made pond, marsh and wetland (hereafter wetlands) or spring) following the terminology of García-Avilés et al. (1995).

Data analysis

To test wether species richness differed among freshwater habitats, a Welch F test was used, due to heteroscedasticity. For each surveyed year, the median number of species per site was compared between sites occupied in one year and sites occupied in both years using a Mann Withney test. A rarity assessment according to the 25% criterium (Gaston 1994), i.e., those species representing the 25% of species showing the smallest incidence and/or abundance, was carried out for each year separately. Species average abundance was calculated and log transformed.

The analysis performed to compare the structure of the dragonfly communities as well as their relation to environmental changes between two surveys (1988 and 2010) were done by multivariate analysis (Quinn & Keough 2002) with PAST 3.02 (Hammer et al. 2001). Temporal variability in dragonfly community composition was quantified using a Non Metric Dimensional Scaling ordination (NMDS), applying the Bray-Curtis dissimilarity measure to the species abundance of each site at the two surveys. Only sites occupied in 1988 and 2010 were included in this analysis. In addition, a one-way Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson & Walsh 2013) was used to test whether there were differences between years among sites regarding their dragonfly communities. Species matrix used in this analysis consisted of relative abundance of each species per year and the Bray-Curtis distance was chosen. Moreover, a Similarity Percentage test (SIMPER) was performed to detect which species had the highest contribution to these differences. In these analyses, sites occupied at least in one of the sampling years were included (1988, n = 39; 2010, n = 38). Only species contributing 2% or more to the total dissimilarity were considered in the interpretation of the SIMPER.

Variability in environmental variables across habitats and years was studied in a similar way to variability in dragonfly community composition, with minor differences. Sites 24, 25, 39 and 52 did not have environmental measurements in 2010 so they were excluded from some tests. First, continuous variables (i.e., water temperature, water depth, conductivity and pH) were normalized to mean zero and unit standard deviation. Then, a NMDS was carried out using the Euclidean dissimilarity index. This analysis included the 49 sites for which environmental variables were measured on both years. Afterwards, a two-way PERMANOVA and a SIMPER test were performed to test whether these environmental variables showed differences between years and habitats. Euclidean distance was chosen for these tests. In these analyses, all sites with environmental data (53 in 1988 and 49 in 2010) were considered.

To test whether values of environmental variables were different between sites with or without species a one-way PERMANOVA was performed for each year separately. Then, a SIMPER test was used to find out which variable contributed to these differences to a larger extent. Euclidean distance was chosen for these tests. In these analyses, all sites with environmental data (53 in 1988 and 49 in 2010) were considered. Occupancy status for each site was scored in one of four categories as follows: unoccupied in both years, occupied in

1988 only, occupied in 2010 only, and occupied in both years. To test whether environmental change differed among sites depending on their occupancy status, the Euclidean distance was computed for each site between 1988 and 2010 and was compared using a one-way ANOVA.

To study which variables influenced Odonata assemblages, a Canonical Correspondence Analysis (CCA) was performed with Canoco 4.5 (Lepš & Šmilauer 2003) for each year separately. In this analysis all variables used for habitat characterization were included: water temperature, pH, conductivity, total dissolved solids, dissolved oxygen, distance to the sea, altitude, presence/absence of aquatic vegetation and organic matter score. In 2010, vegetation was not included because it was highly correlated with habitat type. Sites were coded according to substrate (rock, gravel, sand and silt) and habitat types (stream, pond, small man-made pond, wetland or spring). Quantitative environmental variables were $\log_{10} + 1$ transformed due to their different measurement scales. Substrate and habitat type were coded as dummy variables. Significance of each variable was determined using automatic forward selection based on a Monte Carlo resampling procedure with 499 permutations. CCA included 39 sites and 15 species in 1988 and 36 sites and 20 species in 2010. Species abundance was squared root transformed. Downweighthing of rare species was applied and species present at a single site were included as passive species (*C. scitulum*, *A. imperator* in 1988, *A. affinis*, *A. isoceles* and *A. parthenope* in 2010). In 2010, site 53 was included as a passive sample.

To quantify spatial and temporal beta diversity as well as the relative importance of species replacement and species richness differences in beta diversity, we followed the approach of Carvalho et al. (2012, 2013) using the BAT package (Cardoso et al. 2015) of R 3.1.0. BAT calculates temporal or spatial beta diversity (B_{cc}) using the Jaccard index. Values of B_{cc} for pairwise comparisons ranged from 0 (identical communities) to 1 (completely different communities). In addition, BAT performs a partition into two additive components: species replacement (B_{-3}) and species richness differences (B_{rich}) (Carvalho et al. 2013).

Since dispersal ability is different between Anisoptera and Zygoptera species (Angelibert & Gianni 2003), values of spatial turnover in Zygoptera (low dispersal ability) are expected to be higher than in Anisoptera (Juen & De Marco 2011). Spatial beta diversity was calculated for 1988 and 2010 separately, in two ways: (1) including all the sites with recorded species for each year (39 sites in 1988, 38 sites in 2010) and (2) taking separately Anisoptera and Zygoptera species to calculate spatial turnover for each year. Temporal beta diversity could be only calculated for sites occupied in both surveys and all species were included. Kruskal-Wallis analysis was used to test whether values of temporal beta diversity were different with regard to habitat type. Spearman correlation was done in order to test whether temporal beta diversity values were related to the Euclidean distance in environmental variables for a given site across surveys. Spearman correlation was done in order to test whether temporal beta diversity values were related to the species richness in 1988. These analyses were performed with PAST 3.02.

RESULTS

Odonata species richness, site occupancy and rarity

Overall, 15 species (9 Zygoptera and 6 Anisoptera) were recorded in 1988 and 20 (9 Zygoptera and 11 Anisoptera) in 2010 (Table 5.1). In 1988, the number of species per site ranged from zero to eight (mean ± SD = 3.28 ± 1.73, n = 40 occupied sites). In 2010, the number of species recorded per site ranged from zero to seven (3.26 ± 1.62, n = 38 occupied sites). Odonata were found in all freshwater habitats included in the study (Fig. 5.1). Significant differences in species richness among habitats were observed only in 1988 (Welch test; 1988: $F_{5.7} = 14.96$, $p = 0.003$; 2010: $F_{5.2} = 0.7312$, $p = 0.607$). In 1988, streams had the highest species richness and wetlands the lowest one (Fig. 5.1).

Six sites were unoccupied in both surveys, and 30 sites were occupied in both surveys. The remaining sites changed their occupancy status from 1988 to 2010, eight becoming occupied and nine becoming unoccupied. No significant differences were found in the median species richness for sites occupied only in one year or in both years (Mann-Whitney test; sites occupied only in 1988 (n = 9) *vs* sites occupied in both years (n = 30): Z = -0.898, p = 0.369; sites occupied only in 2010 (n = 8) *vs* sites occupied in both years (n = 30): Z = -0.713, p = 0.476).

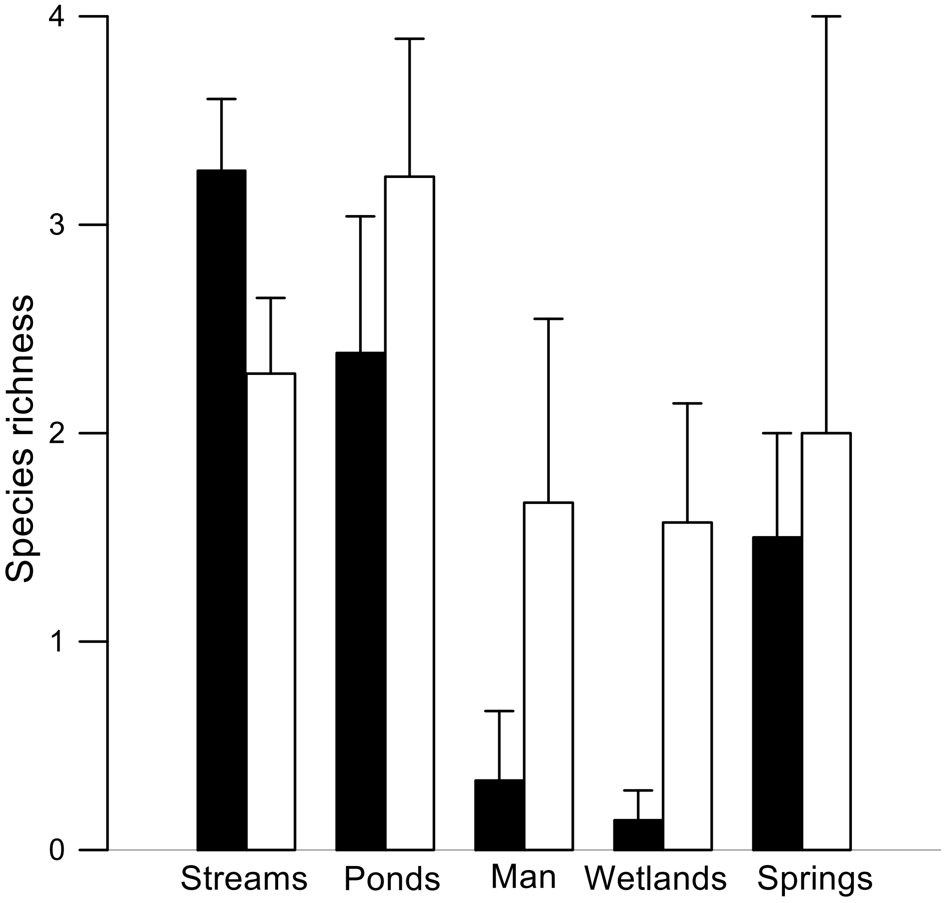


Fig. 5.1. Mean number of species per habitat in 1988 (black bars) and 2010 (white bars). Error bars indicate standard error. Man = small man-made ponds.

In 1988, six species were common, one was little abundant, one had low incidence and seven were both little abundant and had low incidence (Fig. 5.2a). In 2010, four species were common, one had low incidence and ten were both little abundant and had low incidence (Fig. 5.2b). In general, species recorded for the first time in 2010 had a low incidence and abundance (Fig. 5.2b). Nine of 15 species showed changes in their rarity status: (a) three species common in 1988 became rare in 2010, (b) one species rare in 1988 became common in 2010, (c) three species having both low abundance and incidence in 1988 remained rare in 2010 but only due to low incidence, and (d) two species having either low abundance or incidence in 1988 had both low abundance and low incidence in 2010.

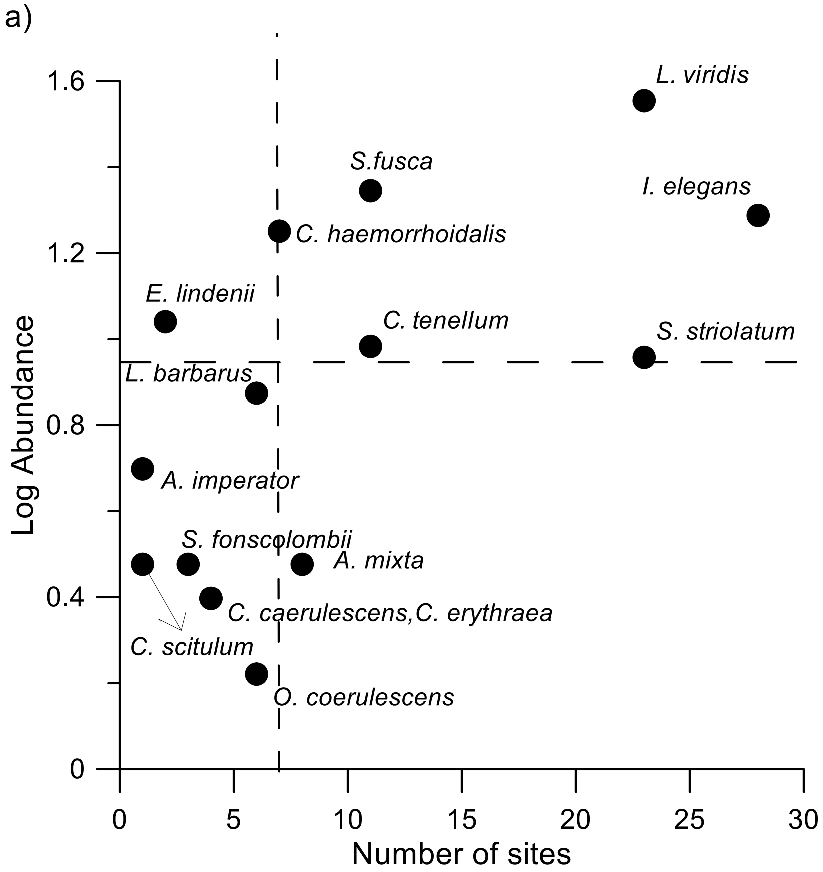


Fig. 5.2. Rarity of species according to Gaston (1994) in 1988 (a) and in 2010 (b) Species not recorded in 1988 are shown in red.

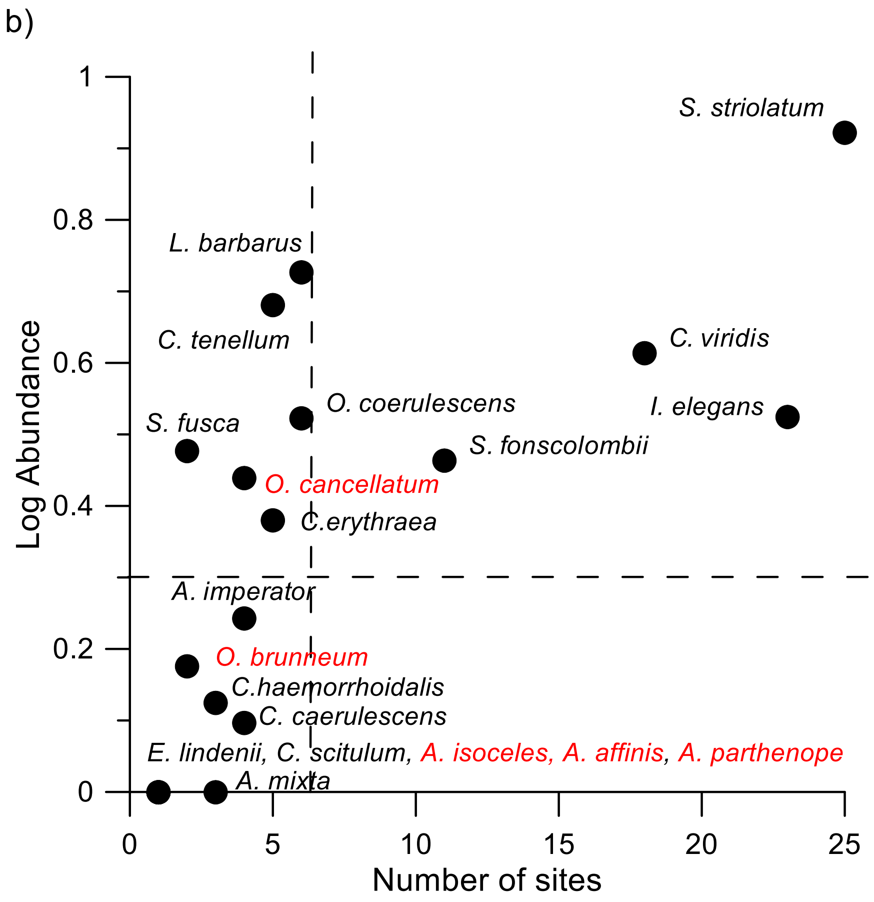


Fig. 5.2. (Cont.)

Changes in dragonfly assemblage composition

The NMDS yielded an ordination with three axes that explained 61% of the total variance (29.8, 18.1 and 13.2%, respectively; stress = 0.197) (Fig. 5.3). According to the NMDS plot (Fig. 5.3), most of the sites experienced changes in their assemblages between 1988 and 2010. One-way PERMANOVA revealed significant changes in assemblage composition between 1988 and 2010 ($F_{1,\ 75}$ = 2.253, p = 0.013). Changes were mainly due to the variation in abundance or occupancy of 11 species which explained 94.21% of the dissimilarity (Table 5.2). Six of them increased in abundance (including a newly appearing species) and four decreased. One species did not change its abundance between years but decreased in occupancy (Table 5.2).

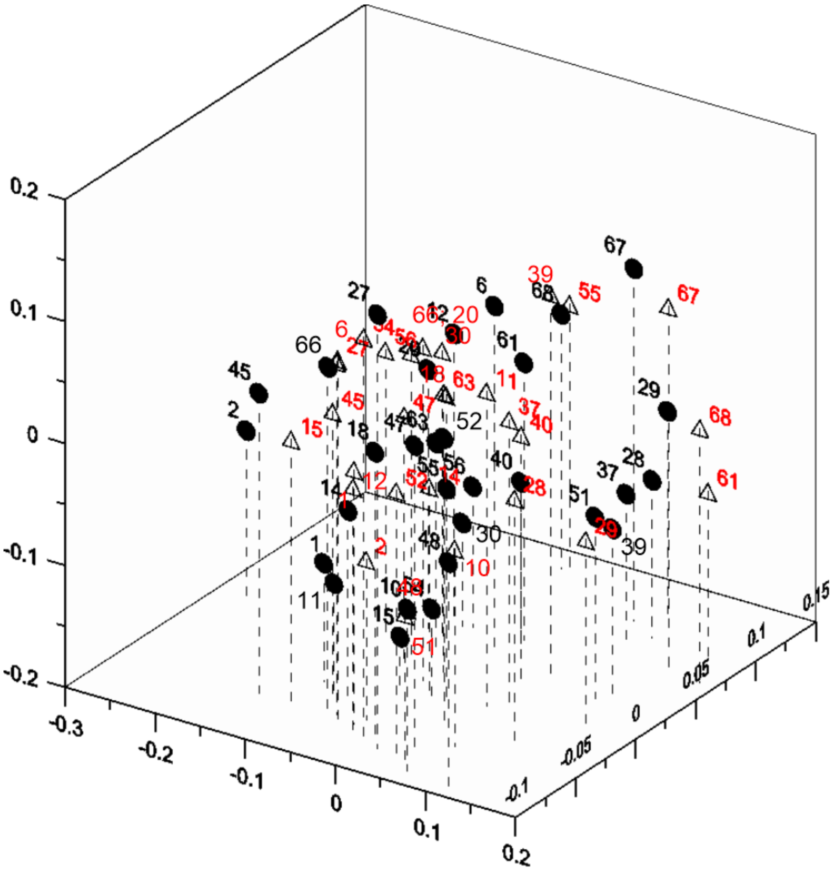


Fig. 5.3. NMDS ordination of the abundance of dragonflies in those sites where species were recorded in both years. Black numbers and dots: 1988; open triangles and red numbers: 2010. Numbers refer to sampling sites (Table 5.1).

Table 5.2. Results of the SIMPER analysis for differences between assemblages between 1988 and 2010. In bold, maximum values per species in each year.

Species	Average dissimilarity	Contribution %	Mean abundance 1988	Mean abundance 2010
Sympetrum striolatum	20.14	24.09	0.0035	**0.0105**
Ischnura elegans	17.46	20.88	**0.0084**	0.0039
Chalcolestes viridis	13.42	16.05	**0.0047**	0.0037
Ceriagrion tenellum	5.58	6.676	0.0012	0.0012
Sympecma fusca	4.43	5.299	**0.0040**	0.0003
Calopteryx haemorrhoidalis	4.20	5.025	**0.0016**	0.0002
Lestes barbarus	3.25	3.888	0.0008	**0.0016**
Sympetrum fonscolombii	3.17	3.796	0.0002	**0.0016**
Orthetrum coerulescens	3.15	3.768	0.0001	**0.0010**
Orthetrum cancellatum	2.01	2.406	0	**0.0006**
Crocotemis erythraea	1.94	2.326	0.0002	**0.0006**

Spatiotemporal changes in environmental variables

The NMDS yielded an ordination with two axes explaining 93% of the total variance (65% and 28%, respectively; stress= 0.169). According to the NMDS plot (Fig. 5.4), the habitats where changes were greater were small man-made ponds, wetlands and a few stream sites.

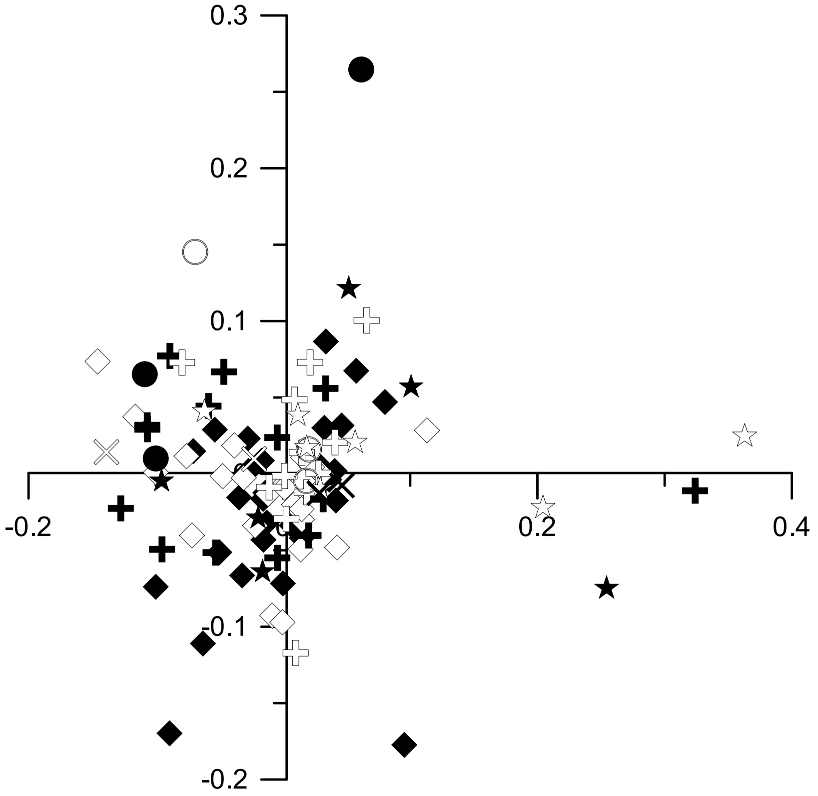


Fig. 5.4. NMDS ordination of sites according to their environmental variables. Black symbols = 1988; Empty symbols = 2010. Diamonds: streams; crosses: ponds; circles: small man-made ponds; stars: wetlands; crosses x: springs.

The two-way PERMANOVA indicated significant differences in environmental variables between habitats ($F_{4, 92}$ = 1.594, p = 0.004) and years ($F_{1, 92}$ = 1.402, p = 0.032), as well as their interaction ($F_{4, 92}$ = -7.100, p = 0.005). SIMPER analysis identified all four environmental variables as contributing > 15% variation to spatiotemporal changes (Table 5.3).

Conductivity was highest in small man-made ponds in both years and decreased in streams in 2010 (Table 5.3). Water depth was higher in wetlands in 1988 and decreased in ponds and wetlands in 2010 (Table 5.3). Most changes between years and habitats involved temperature and pH. Temperature was highest in small man-made ponds and springs in 1988 but in ponds and wetlands in 2010 (Table 5.3). Temperature decreased in ponds and springs in 2010 and increased in the other habitats (Table 5.3). pH values were highest in streams and wetlands in 1988 but in wetlands and springs in 2010 (Table 5.3). pH values decreased in streams and small man-made ponds in 2010 and increased in the other habitats (Table 5.3).

One-way PERMANOVA detected significant differences in environmental variables among occupied and unoccupied stations for each year ($F_{1, 51}$ = 3.648, p = 0.006 for 1988; $F_{1, 47}$ = 2.811, p = 0.046 for 2010) especially in 2010 (Table 5.4). SIMPER test revealed that these differences were mainly due to conductivity values, specially in 2010 (Table 5.4).

Table 5.3. Results of the SIMPER analysis for environmental differences between 1988 and 2010 regarding to habitat type. In bold, clearly positive values of each variable within a year. Man = small man-made pond. Wet= wetland.

			Mean value									
			1988					2010				
Variable	Average dissimilarity	Contribution %	Stream	Pond	Man	Wet	Spring	Stream	Pond	Man	Wet	Spring
Conductivity	2.20	29.25	0.195	-0.215	**0.735**	-0.248	-0.194	-0.235	-0.167	**1.270**	-0.405	-0.348
Temperature	2.08	27.73	-0.231	0.082	**0.331**	-0.343	**0.737**	0.403	-0.426	**0.850**	**0.659**	-1.050
pH	2.00	26.69	**0.503**	-0.285	0.120	**0.562**	-1.040	0.002	0.095	-0.290	**0.821**	**0.986**
Water depth	1.22	16.33	-0.233	0.068	-0.117	**0.990**	-0.459	-0.527	-0.525	-0.526	-0.527	-0.528

Table 5.4. Results of the SIMPER analysis for abiotic differences between occupied and unoccupied sites for each year. In bold, clearly positive values of each variable within a year. Mean ± SD is indicated for recorded values of each variable. O = occupied sites; U =unoccupied sites.

	1988						2010					
			Mean abundance						Mean abundance			
					Mean ± SD						Mean ± SD	
Variable	Average dissimilarity	Contribution %	O	U	O	U	Average dissimilarity	Contribution %	O	U	O	U
Conductivity	3.790	37.89	-0.196	**0.546**	2076 ± 3026	3287 ± 8031	3.946	50.02	-0.214	**0.661**	3036 ± 330	11479 ± 17630
Temperature	2.331	23.30	-0.006	**0.121**	13.8 ± 5.9	14.6 ± 8.2	2.027	25.69	**0.068**	-0.210	16.7 ± 4.2	15.5 ± 4.4
pH	2.205	22.05	-0.207	**0.534**	7.9 ± 0.8	8 ± 0.7	1.916	24.28	**0.057**	-0.175	8.1 ± 1.0	7.8 ± 0.9
Water depth	1.676	16.76	**0.128**	-0.357	40.4± 40.7	24.1± 17.5	8.925×10^{-6}	0.0001	-0.526	-0.526	31.8 ± 19.5	32.8 ± 22.4

Abiotic variables influencing Odonata assemblages

In 1988, the ordination was almost significant ($F = 1.362$, $p = 0.058$) and the first ordination axis was statistically significant ($F = 3.893$, $p = 0.026$). The eigenvalue for the first axis was 0.601 and 0.375 for the second axis. The two axes accounted for 49.1 %of the total variance. In 1988, distance to sea ($F = 2.52$, $p = 0.010$), altitude ($F = 2.36$, $p = 0.022$) and habitat (ponds) ($F = 3.43$, $p < 0.01$) significantly influenced the ordination of species and sites (Fig. 5.5a).

In 2010, the significance of the ordination was statistically significant ($F = 1.327$, $p = 0.024$) as well as the first ordination axis ($F = 3.893$, $p = 0.026$). The eigenvalue for the first axis was 0.467 and 0.240 for the second axis. The two axes accounted for 43.7% of the total variance. Water temperature ($F = 2.47$, $p < 0.01$) and habitat (small man-made ponds) ($F = 2.75$, 0.026) significantly influenced the ordination of species and sites (Fig. 5.5b).

Spatial and temporal beta diversity

Temporal beta diversity ranged from 0 (1 site) to 1 (19 sites) (0.78 ± 0.24). 92% of sites had turnover values ≥ 0.5. Contribution of species replacement component was lower (0.19) than species richness component (0.59). These values were not significantly different among habitat types (Kruskal-Wallis test: $H = 7.049$, $p = 0.106$), and no correlation was found between values of temporal turnover and Euclidean distance of the environmental variables ($R_s = -0.097$, $p = 0.522$, $n = 46$). Values of temporal turnover were significantly negatively correlated to species richness of the sites in 1988 ($R_s = -0.454$, $p = 0.001$, $n = 48$).

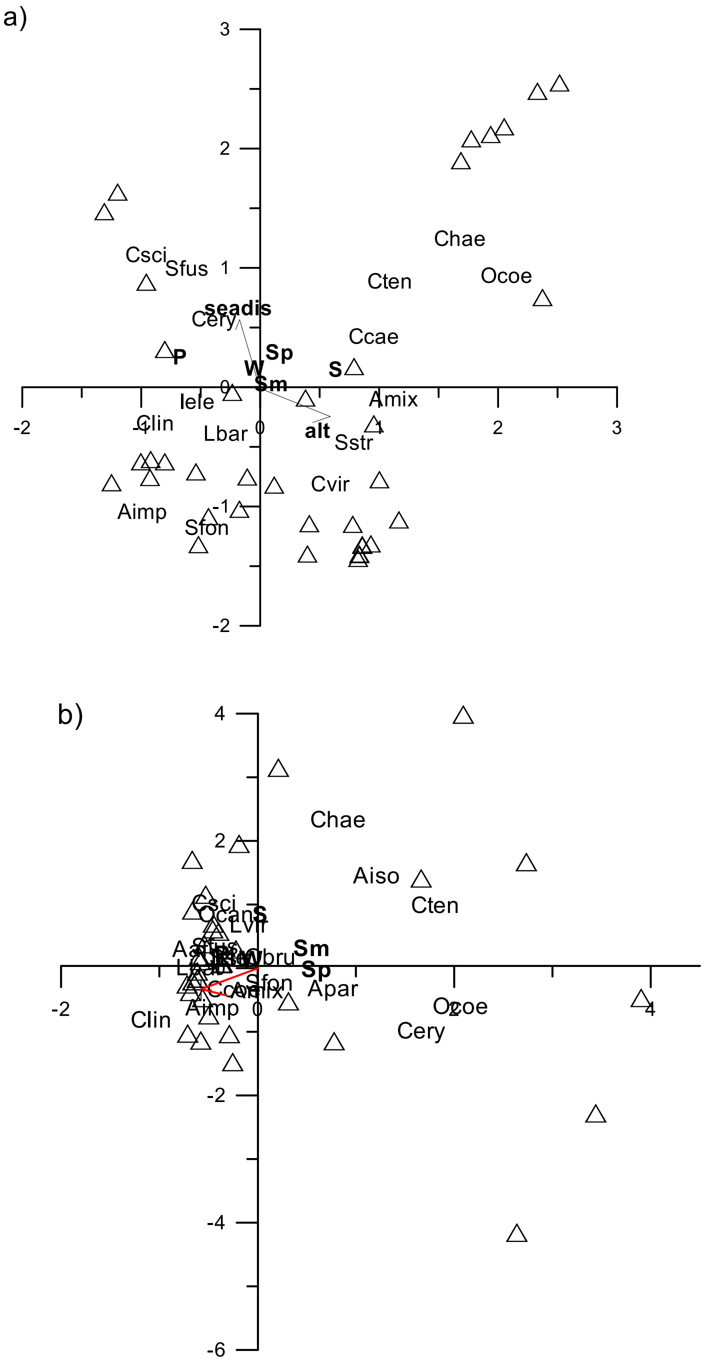


Fig. 5.5. CCA triplot of dragonfly species, sites and environmental variables (arrows) in 1988 (a) and 2010 (b). Habitat types were shortcuts (S = stream, P = pond, Sm = small man-made pond, W = wetland, Sp = spring). For the meaning of species abbreviations see Table 5.1. Seadis (sea distance) and alt (altitude). In 2010, temperature was represented by a red arrow.

Spatial beta diversity values were high and very similar in both years for all the Odonata. Both components of beta diversity had a similar magnitude (Table 5.5). Total spatial turnover were similar for Zygoptera and Anisoptera (Table 5.5). The contribution of each component to spatial diversity was similar in Zygoptera. In Anisoptera, the replacement component was slightly higher than the species richness component (Table 5.5).

Table 5.5. Mean ± SD spatial beta diversity in 1988 and 2010 for all Odonata species and for Anisoptera and Zygoptera separately. Total beta diversity and their two components, species replacement and species richness, are indicated. For each analysis number of sites (n) and number of species (spp.) are shown.

	Total	Species replacement	Species richness	n / spp.
1988				
All species	0.766 ± 2.705	0.398 ± 1.404	0.368 ± 1.300	39/15
Anisoptera	0.614 ± 7.183	0.361 ± 4.220	0.253 ± 2.964	27/6
Zygoptera	0.701 ± 6.137	0.326 ± 2.853	0.375 ± 3.284	36/9
2010				
All species	0.781 ± 1.523	0.409 ± 0.798	0.372 ± 0.726	38/20
Anisoptera	0.670 ± 2.650	0.375 ± 1.483	0.295 ± 1.167	30/11
Zygoptera	0.668 ± 4.600	0.332 ± 2.287	0.336 ± 2.313	32/9

DISCUSSION

Influence of abiotic variables on species richness and dragonfly assemblages

Freshwater habitats in Menorca showed environmental heterogeneity between sites and years. Across sites, differences in conductivity could be influenced by temperature changes or by the increase of N, P or Na concentrations (Carchini & Rota 1985; Carchini et al. 2007). Moreover, high conductivity was observed at sites close to the sea with high salinity (Javier García Avilés, pers. comm.). In turn, differences in water temperature could be related to water depth, because temperature was higher in temporary or small sites. Differences in pH are often related to substrate type and in Menorca it could differ between northern, siliceous and southern, calcareous sites. Nevertheless, information for explaining the temporal changes in each variable was not available. The highest mean values of conductivity in 2010 could be due to salt water intrusion into freshwater aquifers reported in recent years as well as to the excess of pesticides (*www.obsam.cat*). The highest mean water temperature is probably correlated to the lowest depth in 2010. Temporal differences in water depth levels were probably due to differences in the distribution of rainfall for each year rather than the amount of rainfall recorded for each year (*www.obsam.cat)*.

The number of abiotic variables which were quantified in the present study was very low and this limited our ability to detect environmental changes. Other local abiotic variables such as temporariness, presence of vegetation (Carchini et al. 2003; Hinden et al. 2005; Balzan 2012), biotic local factors such as mechanisms of coexistence of similar species (Johansson 1978; Johnson et al. 1985; Morin 2008) and the effect of fish and exotic species (Maezono & Miyashita 2003, 2004; Carchini et al. 2007), or regional factors such as the degree of isolation of the sites, could have influenced the occupancy status of the sites studied.

Unoccupied sites had mainly high conductivity. These high values may be related to the distance to sea, although unoccupied sites were located from 100 m to 7 km distance from the sea. High values of conductivity do not seem to be tolerated by dragonflies or other macroinvertebrates (Hinden et al. 2005). The same trend is observed with acid conditions (Oertli et al. 2001; Hinden et al. 2005; Florencio et al. 2014). Other abiotic variables, such as water depth and water temperature also differed between unoccupied and occupied sites and have been previously found to influence Odonata presence (Corbet & Broooks 2008). Water depth has been correlated to species richness (Hinden et al. 2005; Carchini et al. 2007). Low water depth usually means a higher water temperature, the effect of which on larval development depends on the range of temperatures achieved (Johansson 2000; Corbet & Brooks 2008). Nevertheless, the magnitude of change for these variables was low and their actual influence is not so clear.

Dragonfly assemblages were affected by different abiotic variables in each studied year: in 1988 altitude, distance to sea and habitat were significant whereas in 2010, only the water temperature and habitat were. The fact that the influence of abiotic variables changes over the time has been previously reported (Balzan 2012). Distance to the sea may involve either certain tolerance to salinity or to effects of salt spray. However this variable has not been highlighted in a previous study (Florencio et al. 2014). Altitude may have been related to inland areas, far from the sea. Water temperature is not considered to directly affect dragonfly species assembly, but indirectly due to its higher values in temporary waters (Schindler et al. 2003; Carchini et al. 2007). Ordination of the species in 1988 allowed to distinguish Mediterranean species into lentic (left) or lotic (right) species (Fig. 5.5a) (Baixeras et al. 2006; Lockwood & Oliver 2007; Sato & Riddiford 2007; Sánchez et al. 2009). However, in 2010 only some of the lotic species and species related to small-man made ponds were clearly distinguished (Fig. 5.5b). In Menorca, streams are temporary and when rainfall decreases most of them are reduced to small, isolated ponds along their channel. Therefore, the duration of the period with continuous flow probably influences dragonfly assemblages. Similar results have been reported for macroinvertebrate communities in Majorca (Álvarez & Pardo 2007).

Changes in assemblage composition, beta diversity and rarity

Three results indicate that Menorcan dragonfly communities are spatial and temporally dynamic. First, both spatial turnover for each year and average temporal turnover were large. Second, differences between assemblages of 1988 and 2010 were due to changes in the relative abundances of 11 of the 20 of species recorded. Third, many species modified their rarity status among survey years.

Present values of spatial and temporal beta diversity were slighty higher than whose obtained for adult assemblages of Banyoles wetland (Chapter 6) and other adult dragonfly communities (Juen & De Marco 2011) (Chapter 6). Moreover, they were also higher than those reported for macroinvertebrate communities (Florencio et al. 2014). Our high values could be related to the large area covered and the distance between some of the sites, but no to the species pool (Florencio et al. 2014). By contrast with the study of adult assemblages (Chapter 6), both components (species replacement and species richness differences) of spatial beta diversity were similar. For the temporal beta diversity, species richness differences was the prevalent component to temporal turnover, situation that has not been observed when adult assemblages are compared year to year (Chapter 6). Partition of spatial beta diversity for macroinvertebrates in Doñana (Florencio et al. 2014) has revealed a prevalent role of species replacement component.

Most of the species that make up the regional pool were rare from a distribution and abundance viewpoint whatever the year considered. Changes in dragonfly abundance could have been due to intraguild predation and competition (Pierce et al.

1985; Wissinger 1989; Suutari et al. 2004). Dragonfly fauna in Mediterranean islands consists of euryoecious species (Ahijado Guzmán 2013). All of the species recorded in Menorca may be considered euryoecious except for those associated to streams (Fig. 5.5a) which in addition became rare (*C. tenellum* and *C. haemorrhoidalis*) (Fig. 5.2). On the contrary, species capable of breeding in many habitats, even temporary ones (i.e. species with high activity and fast growth) (McCauley 2008) increased their prevalence and abundance like in the case of *S. fonscolombii* (Fig. 5.2). A similar trend was reported by Domingo (2002) after studying odonate records covering 100 years.

Beta diversity drivers

Short and long term changes in dragonfly community composition have been documented, but not quantified, and have been traditionally related to environmental features (Domingo 2002; Kadoya et al. 2004; Flenner & Sahlén 2008). Nevertheless, no relationship was found between the sites that gained or lost species and their environmental change, estimated as Euclidean distances in environmental variables. If deterministic factors were dominant in temporal turnover, we could expect that the more habitat changes occur the more temporal turnover would occur (Shurin 2007) but our results do not support this hypothesis. Moreover, temporal turnover significantly decreased as the number of species at each station in 1988 increased, so stochastic factors instead of deterministic factors could be more important. Moreover, species richness in 1988 did not influence in species richness of 2010, thus reinforcing our hypothesis.

In metacommunities, distance among sites is related to spatial correlation but also can stress dispersal limitations (Florencio et al. 2014). Dispersal limitation did not seem to have an important role since spatial turnover values were quite similar for Anisoptera and Zygoptera in both years. This result disagrees with those reported for other dragonfly communities (Juen & De Marco 2011). Changes in the vicinity of the sites could have affected temporal turnover too (Flenner & Sahlén 2008). Differences in land use around sites were tested in a preliminary analysis and there were minimal (*www.obsam.cat*). However, quality of riparian forest of most of the streams in Menorca has been classified as low due to farming activities, methods of mechanical cleaning and the presence of invasive plants (*www.obsam.cat*). In addition, the effect of connectivity, or characteristics of the organisms (Korhanen et al. 2010) remained unknown at present work.

Implications for conservation

In islands, where biota is poorer than in the mainland and could hold high number of endemic species (Whittaker 2002), extinction events caused by human causes is specially worrying (Mayumi & Isamu 2010 but see Samways et al. 2011) although in Mediterranean area, endemic species of Odonata in islands range from 0 to 2 (Ahijado Guzmán 2013). Within the Mediterranean region dragonfly communities are increasingly threatened by habitat loss and degradation (Riservato et al. 2009). In the Maltesse archipelago, species adittion but also extinctions have occurred (Balzan 2012). The situation in Menorca seems far more favourable. Changes in odonate fauna in Menorca do not indicate important threats and after 22 years the species list has even increased.

None of the two components of turnover showed a clear dominancy in their temporal change. Although information about the intermediate years between 1988 and 2010 is not available, this trend may indicate two possible scenarios according to Angeler (2013): dragonfly metacommunity dynamic is unpredictable or the species involved are resilient. This last situation implies temporal stability and demands little management (Angeler 2013). Similar results have been reported for the main Mediterranen islands due to the predominance of generalist species (Ahijado Guzmán 2013). In spite of this, we suggest special attention for enhancing the dynamism of these communities, that is, keep the network of freshwater habitats and guarantee that they are well-connected (Crumrine et al. 2008; Picazo et al. 2012; Florencio et al. 2014).

To conclude, in Menorca all of the freshwater habitats hosted dragonfly communities. Dragonfly communities have shown to be highly dynamic. After 22 years, local and regional composition has changed as well as the rarity status of the species. Stochastic instead of deterministic factors could be more important in driving metacommunity structure because changes in water physicochemical properties in all freshwater habitats were not correlated to temporal turnover. Moreover, no relationship was found between species richness in 1988 and species richness in 2010 although sites with high species richness recorded low values of turnover. Nevertheless, unmeasured biotic factors and environmental variables could also have an important role in temporal turnover. Spatial turnover was similar for Anisoptera and Zygoptera so dispersal limitations were not observed. In order to conserve dragonfly metacommunity is important to keep its dynamism, which requires a wide range of freshwater habitats well-connected each other.

Appendix 1. Parameter values of the rarefaction curves for each site and year. Adjustment to the model was indicated by R^2. S: species number (expected and observed). See Table 5.1 for site numbers.

1988	**R^2**	**S_{exp}**	**S_{obs}**	**Inventory completeness (%)**	**Slope**
1	0.973	9.341	8	85.6	0.0068
11	0.969	2.589	4	154.4	0.0006
12	0.940	3.245	3	92.4	0.0142
14	0.994	3.153	3	95.1	0.0031
15	0.933	2.084	2	95.9	0.0013
16	0.991	3.435	3	87.3	0.0156
17	0.998	5.834	5	85.7	0.0181
19	0.971	4.890	4	81.8	0.0408
20	0.934	4.106	4	97.4	0.0053
22	0.934	2.087	2	95.8	0.0012
28	0.956	7.486	6	80.2	0.0291
29	0.972	10.861	6	55.2	0.0730
30	0.948	3.065	3	97.9	0.0009
31	0.999	3.353	3	89.5	0.0139
34	0.979	3.342	3	89.8	0.0211
36	0.888	2.027	2	98.7	0.0001
37	0.980	5.679	5	88.0	0.0114
40	0.957	6.431	6	93.3	0.0129
54	0.950	4.455	4	89.8	0.0223
55	0.994	4.201	4	95.2	0.0035
56	0.965	5.357	5	93.3	0.0083
58	0.981	3.152	3	95.2	0.0012
61	0.974	5.662	4	70.6	0.0773
63	0.990	5.400	5	92.6	0.0047
2010					
1	0.999	6.436	5	77.7	0.0607
2	0.996	8.889	7	78.7	0.0470
12	0.986	3.378	3	88.8	0.0247
14	0.998	4.959	4	80.7	0.0439
15	0.971	6.275	5	79.7	0.0270
20	0.929	5.769	5	86.7	0.0281
23	0.986	3.295	3	91.0	0.0203
30	0.978	6.665	5	75.0	0.0688
40	0.996	8.046	6	74.6	0.0650
45	0.866	3.625	3	82.8	0.0261
47	0.984	5.611	5	89.1	0.0141
56	0.988	5.552	5	90.1	0.0141
63	0.998	4.904	4	81.6	0.0378

CAPÍTULO 6. SPATIOTEMPORAL DYNAMICS OF DRAGONFLY COMMUNITIES IN CREATED HABITATS: STABILITY IN SPECIES RICHNESS, BUT HIGH TURNOVER IN SPECIES COMPOSITION.

INTRODUCTION

Human activities are substantially altering survival, reproduction and dispersal of many species (Hooper et al. 2012) due to habitat modification or destruction (Ehrlich 1988; Tilman et al. 1997), introduction of non-native species (Vitousek et al. 1996; Marvier et al. 2004) and climate change (Root et al. 2003; Pounds et al. 1999; Parmesan 2006). This situation is especially true for aquatic ecosystems (Boyland & McLean 1997; Ricchiardi & Rasmussen 1999; Sala et al. 2000; Wall et al. 2001; Malmqvist & Rundle 2002; Covich et al. 2004; Darwall & Vie 2005; Naiman et al. 2006; Woodward et al. 2010) where biodiversity has declined, as a whole, faster than terrestrial or marine biodiversity over the past 30 years (Jenkins 2003). This is worrying because inland waters and freshwater biodiversity are a valuable natural resource, so their conservation and management are critical to human interests (Covich et al. 2004; Dudgeon et al. 2006; Sligenberg et al. 2009). Therefore, considerable effort has been put into reducing the impacts in or near wetlands, compensating for additional losses and restoring or replacing wetlands destroyed by means of habitat creation (Kusler & Kentula 1990; Zedler & Kercher 2005). These actions have been partially motivated by an interest in stopping habitat loss for some groups of organisms such as macroinvertebrates, plants, fishes, amphibians or birds (Brown et al. 1997; Pfadenhauer & Grootjans 1999; Pokorný & Hauser 2002; Porej & Hetherington 2005; Ma et al. 2010).

In addition to its practical motivations, wetland creation provides a valuable opportunity to test ecological theories related to community assembly and dynamics (Zedler 2000; Anderson 2007). For example, created wetlands allow to study the dispersal, abiotic and biotic filters (Holyoak et al. 2005) that influence which species from the regional pool are able to establish local populations in the new habitat (Allen et al. 2011). They are also ideal to explore successional trajectories (Solimini et al. 2003; Hapner et al. 2011) and their departure from the convergence expected by traditional succession theory (Moral 2007; Matthews & Spyreas 2010; Ruhi et al. 2013). Successional dynamics, in turn, allows quantitative analysis of persistence (sensu Connell & Sousa 1983) or turnover in species composition (Whittakker 1960, 1972; Carey et al. 2006; Anderson et al. 2011; McGill et al. 2015), as well as its two components: species richness differences and species replacement (Williams et al. 1999; Lennon et al. 2001; Baselga 2010; Carvalho et al. 2012). Finally, it allows to test whether apparent stability in species number hides a turnover in species identity, following a "compensatory dynamics", "community-level density dependence" (Houlahan et al. 2007; González & Loreau 2009; Tanner et al. 2009) or "zero-sum dynamics" (Hubbell 2001; Ernest et al. 2008). All these issues are of longstanding theoretical interest, but also enlighten conservation and restoration practices (Zedler 2000; Heino & Soininen 2010; Angeler 2013; Hassall et al. 2012).

Dragonflies are among the target groups for wetland creation (Steytler & Samways 1995; Chovanec & Raab 1997; Oertli 2008). The reason is their high sensitivity to environmental changes in most freshwater ecosystems (Stewart & Samways 1998; Sahlén & Ekkestube 2001; Kadoya et al. 2008a; Reece & McIntire 2009) and the fact that their diversity has been negatively affected by introduction of invasive species (Samways & Steytler 1996), changes in agricultural practices (Maezono & Miyashita 2004; Kadoya et al. 2008a), urban development (Primack et al. 2000) or water pollution (D'Amico et al. 2004; Harabiš et al. 2013).

Dragonfly assemblages are certainly dynamic (Osborn & Samways 1996; Morris et al*.* 2006). In created wetlands, studies of this community dynamic has focused on successional trajectories. Pioneer, developmental, climax and senescent succesional stages have been described by Moore (1991) and Chovanec & Raab (1997). Nevertheless, convergence to a single, common assemblage does not always occur (Osborn & Samways 1996; Moore 2001). Variability between assemblages has been related to environmental factors (Osborn & Samways 1996; Moore 2001; Such &

Samways 2005) rather than to biotic interactions (Osborn & Samways 1996). Dragonflies are fast colonisers (Steytler & Samways 1995; Suhling et al. 2004; Morris et al. 2006; Williams et al. 2008; Harabiš & Dolný 2012) if source habitats in the vicinity exist (Moore 1991) and both directed and chance movements of adult dragonflies have been documented (Gibbons et al. 2002; Bernath et al. 2002; Carchini et al. 2003; Kadoya et al. 2004). Species recovery at a restoration site follows the regional order of prevalence of the species (Kadoya et al. 2008a). Despite this dynamism, beta diversity of dragonfly communities has received uneven attention. On one hand, spatial turnover has been related to hydroperiod and area (Wissinger et al. 2009; Florencio et al. 2014) but also to dispersal ability (Juen & de Marco 2011). This suggests that even homogenous habitats can present high values of beta diversity. On the other hand, temporal turnover has focused on changes driven by climate change (Flenner & Sahlén 2008; Bush et al. 2013). Nevertheless, a proper temporal turnover has not been quantified for dragonfly communities.

Oertli (2008) remarked that creation of new water bodies such as ponds is a frequent restoration measure which benefits dragonfly diversity in the short term. DBI is an index that allows to assess the increase in dragonfly value in a given habitat, by hosting rarer, more sensible or threatened species. Indeed, DBI has been used for rapid assessment for evaluating early warning of ecosystems degradation (Simaika & Samways 2009a), selecting biodiversity hotspots for dragonflies (Simaika & Samways 2009b) and determining the effectiveness of management and restoration actions (Harabiš et al. 2013). Nevertheless, despite its potential utility, DBI i has not been used in a context of habitat creation.

In the present study, we compared the dragonfly assemblage dynamics of created semi-permanent lagoons with those of a stable karstic lake nearby. Our main goals were: (1) To check if a successional trajectory was discernible in the assembly process in the lagoons, (2) to assess the presence of divergent, stochastic or convergent trajectories in the dragonfly assemblages across lagoons, (3) to compare beta biodiversity between sites and over time and to asses whether species richness differences or species replacement were more important for beta diversity, and (4) to assess whether dragonfly diversity has been enhanced by creating new lagoons.

MATERIAL AND METHODS

Sampling sites

Field work was carried out in Banyoles wetland that is formed by karstic lake of Banyoles and over 70 much smaller satellite lakes and springs of varying sizes and depths (see Chapter 2 for details). As a part of a LIFE project (LIFE03 NAT/E/000067), five new shallow semi-permanent lagoons were dug in 2005 to the NE of the lake to restore part of the floodplain and marshy habitats that once surrounded the lake: Llacuna de L'Artiga (1.97 ha), Llacuna d'en Margarit (1.23 ha), Llacuna de l'Aulina (1 ha), Bassa de la Déu (1.20 ha) and Llacuna dels Amaradors (0.32 ha) (hereafter, Artiga, Margarit, Can Morgat and Amaradors, respectively; l'Aulina was not monitored) (Fig. 6.1). These lagoons are of similar depth (max. 2 m) and have a similar hydroperiod (annual fluctuations from bankful to almost dry depending on rainfall and sluice management). The surrounding land is occupied by cropland (cereal and fodder crops) and Mediterranean woodland. The predominant vegetation of the lagoons varies from *Typha angustifolia* in Artiga, through a mix of *T. angustifolia* and *Phragmites australis* in Margarit to *P. australis* in Can Morgat and Amaradors. Distance from the main lake ranges from 375 m for Artiga, through 320 m for Margarit and 250 m for Can Morgat to 60 m for Amaradors.

Sampling protocol

A second LIFE project (LIFE08 NAT/E/000078) awarded in 2007 included a monitoring programme for Odonata that covered the main lake and the new lagoons dug in 2005. The sampling protocol followed the SLIC (*Seguiment de Libèl·lules de Catalunya*) methodology devised to monitor the Odonata of the Banyoles site and developed by the *Oxygastra* Catalonian Odonata Recording Group (OCORG). SLIC is partially based on the well-known butterfly walks (Pollard 1977). Observers conducted counts of adult insects (species and number of individuals) along linear transects of varying lengths (Fig. 1) that were walked at a steady pace, stopping only to identify species whenever necessary. A net was used occasionally to confirm the identification of certain problematic individuals (e.g. *Coenagrion* spp. and *Sympetrum* spp.), which were released after identification. Data collection was performed between 11.00 and 17.00 (local time) (Schlinder et al. 2003) on warm and windless days (Sato & Riddiford, 2007). In addition, given the impossibility of accessing some of the lakeside habitats, point counts were added consisting of 5-minute naked-eye counting sessions from a fixed point (e.g. observation platforms on the lake shore) of all adult Odonata detected by the observer (binoculars were only used to confirm identifications, not to search). Both lake and created lagoons were surveyed using transects and point counts except for Margarit, where only one point count was carried out. The number of sampling sites was 16 (Fig. 6.1): seven sites in the new lagoons (four points counts and three transects) and nine sites in the lake Banyoles, with three points counts and one transect in the North zone and four point counts and one transect in the South zone. All counts (excepting a few initial ones) were carried out by one of the authors (M. L.).

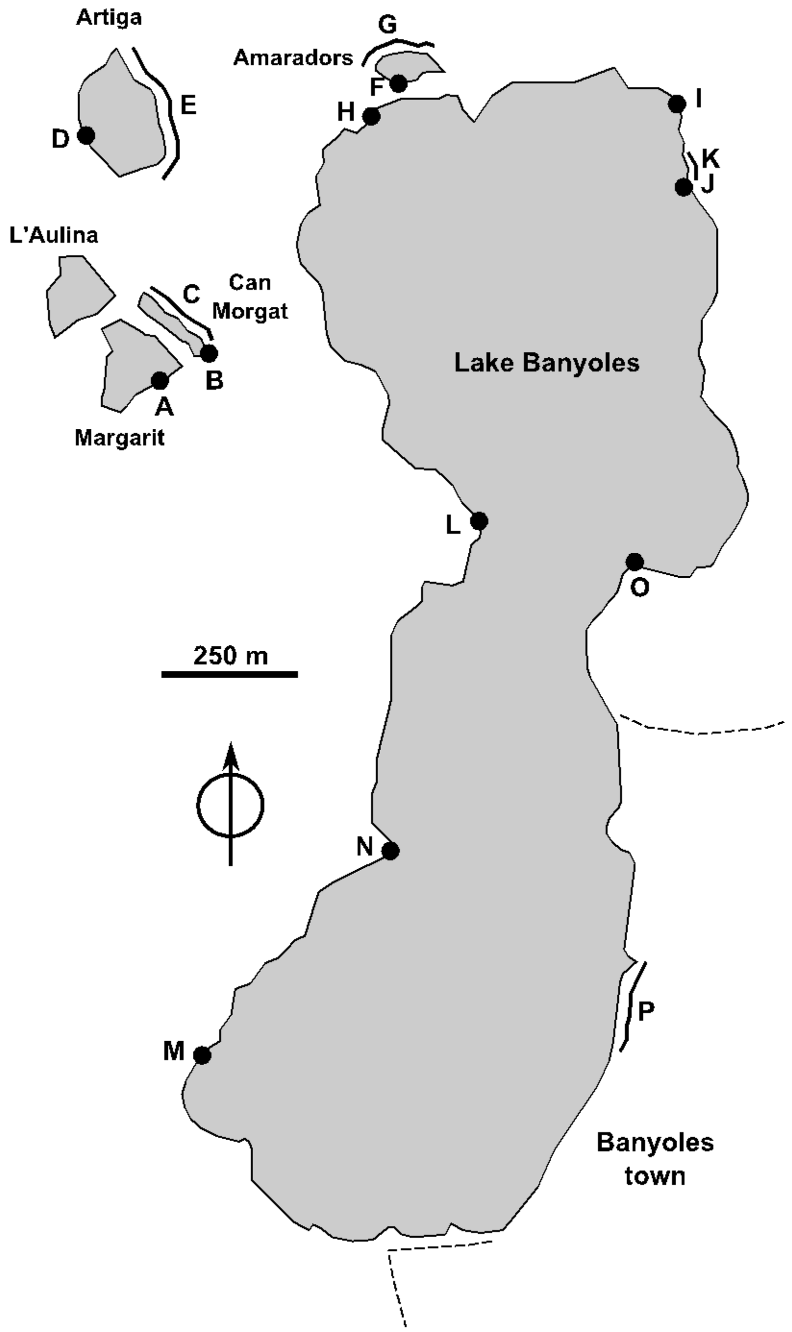


Fig. 6.1. Study area, indicating the counting points (dots) and the SLIC transects (lines). A-G are sampling sites in the created lagoons, H-K are sampling sites in the North zone of the lake and L-P are sampling sites in the South zone of the lake. Transect lengths are 123 m (C), 209 m (E), 90 m (G), 70 m (K) and 150 m (P). Dashed lines indicate the village limits of Banyoles town.

By contrast to Osborn & Samways (1996), both males and females were counted. This did not greatly change our results. During the studied period, females were recorded in all created lagoons and the South zone of the lake. Their addition only slightly increased richness by 1 to 1.4 species in the lagoons and by 1 to 2 species in the South zone of the lake.

Given the phenology of most species, counts were conducted in April-October with at least 7 days between successive counts (Carchini et al. 2003). Sites were surveyed 14 times per year. Annual abundance for a species at a site were calculated by summing the total number of individuals recorded, separately for transects and point counts. For the four new lagoons, counts between 2007 and 2013 were included in analyses. For lake Banyoles, where five sites were surveyed from 2008 onwards, only data between 2008 and 2013 were considered. Odonata species nomenclature follows Dijkstra & Kalkman (2012).

Dragonfly biotic index

A modification of the Dragonfly Biotic Index (DBI) focused on adults and introduced by Simaika & Samways (2009a) was calculated for the lake and for the created lagoons per studied year. DBI estimates the odonatological value of a site (Harabiš & Dolný 2012) by scoring in a scale from 0 to 3 three atributes of Odonata species present at a site: distribution, threats and sensitivity to habitat changes for each species. Thus, DBI scores per species ranged from 0 to 9. DBI applicability has been confirmed in different geographical areas and for different types of water bodies provided that information about the three attributes are available (Rosset et al. 2013).

In the present work, distribution scores were calculated using the number of 50 x 50 km squares occupied in the Mediterranean basin, taken from Boudot et al. (2009) and the number of 10 x 10 km squares occupied in Catalonia (OCORG unpublished data) (Table 6.1). Both estimates of distribution showed a weak positive correlation (r = 0.329; p = 0.040). Threat levels were taken from the European Red List (Kalkman et al. 2010) and the same criterion to assign scores described by Simaika & Samways (2009a) was followed (Table 6.1). Sensitivity to habitat changes was estimated using information about the tolerance of the different species to eutrophyc and altered habitats, taken from Baixeras et al. (2006) and Lockwood & Oliver (2007) (Table 1). For each site, total DBI was calculated as the sum of the scores of all the species present for any given year (Simaika & Samways 2012).

Data analysis

For each species, number of years present, incidence and abundance were calculated separately for the created lagoons as a whole and for lake Banyoles. Number of years present was calculated as the number of years in which each species was recorded. Incidence was calculated as the number of sites in which each species was recorded, considering the whole study period. Abundance was calculated as the average across years of the ratio of the annual number of individuals of each species between the number of sites occupied by that species in that year. Correlation between incidence, distribution and abundance was tested using a nonparametric Spearman correlation. Moreover, for each species recorded at the created lagoons the year of first appearance and the year in which it made its latest colonization of a lagoon were indicated.

To study the spatiotemporal variability in dragonfly community composition a Non Metric Multidimensional Scaling (NMDS) ordination (Quinn & Keough 2002) was carried out in PAST 3.02 (Hammer et al. 2001), using the Bray-Curtis disimmilarity of the yearly counts of species at each site. Point counts and transects were coded separately for this analysis.

Table 6.1. Criteria used to assign scores to the three components of the Dragonfly Biotic Index (DBI). In the distribution criterium, the range of 50 x 50 km squares occupied in the Mediterranean basin (Md) or of 10 x 10 km squares in Catalonia (Ct) are indicated in brackets. See text for details about references utilised to assign scores.

Score	Criterium variable		
	Distribution	Threat	Sensitivity
0	Common in Mediterranean basin and in Catalonia (501-997 Md; 113-224 Ct).	Least concern	Not sensitive and not associated to any specific habitat
1	Common in Mediterranean basin / Rare in Catalonia (501-997 Md ; 1-112 Ct)	Near threatened	Low sensitivity to habitat change. It may occur in artificial water bodies
2	Rare in Mediterranean basin/ Common in Catalonia (1-500 Md; 113-224 Ct)	Vulnerable	Medium sensitivity to habitat disturbation although it shows preference by running and oxygenated water
3	Rare in Mediterranean basin and Catalonia (1-500 Md; 1-112 Ct).	Endangered or Critically endangered	Extremely sensitive to habitat change (loss of vegetation or water pollution)

To further study temporal patterns of community change at each site, we utilized the method described by Collins et al. (2000). In short, this analysis regresses the Euclidean dissimilarity in community composition of a given site at increasing time lags. This allows to discriminate among three patterns of community dynamics: stochastic (no significant linear regression), directional (significantly positive -divergence- or negative -convergence- linear regression) or cyclical (significant quadratic regression) (Collins et al. 2000). Euclidean distances of the abundance matrix data for each site were obtained with PAST 3.02 and linear and quadratic regressions of Euclidean distances as a function of the square root of the time lag were performed using R software (R Core Team 2014).

To quantify spatial and temporal beta diversity as well as the relative importance of species replacement and species richness differences in beta diversity, we followed the approach of Carvalho et al. (2012, 2013) using the BAT package (Cardoso et al. 2015) of R 3.1.0. BAT calculates temporal or spatial beta diversity (B_{cc}) using the Jaccard index. Values of B_{cc} for pairwise comparisons range from 0 (identical communities) to 1 (completely different communities). In addition, BAT performs a partition into two additive components: species replacement (B_{-3}) and species richness differences (B_{rich}) (Carvalho et al. 2013).

Temporal variation in the DBI index for the lake and the created lagoons was explored using nonparametric Spearman correlation. The DBI index for the lake and the created lagoons was compared using a paired samples t-test.

RESULTS

Species richness and description of the dragonfly community

Overall, 40 Odonata species, 16 Zygoptera and 24 Anisoptera, were recorded in lake Banyoles and the four created lagoons (Table 6.2). Of these species, 32 were recorded at the lake and 38 at the created lagoons, from which 23 were recorded at least once in all the created lagoons (Table 6.2). Eight species were exclusive from the created lagoons and two from the lake (Table 6.2). The number of species which took part in the dragonfly community at each site at least on one year was higher for the created lagoons than for the lake (Table 6.2). The number of species recorded per site and year ranged 6-23 for the created lagoons and 2-19 for the lake (Fig. 6.2). At the created lagoons, total number of species per site increased significantly with time for Margarit ($R_s = 0.764$, $p = 0.046$, $n = 7$) and Artiga ($R_s = 0.847$, $p = 0.016$, $n = 7$), but not for the other two lagoons ($p > 0.644$) (Fig. 6.2). Total number of species did not change with time in either zone of the lake Banyoles ($p > 0.355$) (Fig. 6.2).

In general, most species were detected three or more years and in more than half of the sampling sites (Fig. 6.3). Average abundance was higher at the created lagoons compared with the lake (Fig. 6.3). The most abundant species differed between the created lagoons and the lake. In the lake Banyoles the most abundant species was *T. annulata* whereas at the created lagoons was *S. striolatum* (Fig. 6.3). In both habitats, species incidence, number of years present and abundance were significantly positively correlated (Table 6.3).

Table 6.2. Species list of lake Banyoles and created lagoons. Species names were shortened by the first letter of genus and three first letters of species name.

	Created lagoons							Lake Banyoles									Sampling	First	Last
Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	sites	colonisation	colonisation
Aeshna cyanea (Acya*)*		■	■				■	■			■	■	■				7	2007	2013
Aeshna isoceles (Aiso*)*	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	16	2007	2009
Aeshna mixta (Amix*)*	■	■	■	■	■	■	■	■	■	■	■	■	■	■			14	2007	2009
Anax ephippiger (Aeph*)*				■	■	■	■		■							■	6	2008	2009
Anax imperator (Aimp*)*	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	16	2007	2007
Anax parthenope (Apar*)*	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	16	2007	2011
Calopteryx haemorrhoidalis (Chae*)*	■	■	■	■	■	■	■	■	■	■		■	■	■			13	2007	2011
Calopteryx xanthostoma (Cxan*)*		■		■				■							■		4	2011	2013
Ceriagrion tenellum (Cten*)*		■	■			■	■				■	■	■	■	■		9	2007	2012
Coenagrion puella (Cpue*)*	■	■	■	■	■	■	■	■	■		■	■	■	■	■		14	2008	2011
Crocothemis erythraea (Cery*)*	■	■	■	■	■	■	■		■	■	■	■	■	■		■	14	2007	2009
Enallagma cyathigerum (Ecya*)*		■	■	■	■					■							5	2007	2011
Erythromma lindenii (Elin*)*	■	■	■	■	■		■	■	■	■	■		■	■	■	■	14	2007	2008
Erythromma viridulum (Evir*)*	■	■	■	■	■												5	2007	2010
Gomphus pulchellus (Gpul*)*					■												1	2011	2011
Ischnura elegans (Iele*)*	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	16	2007	2008
Ischnura graellsii (Igra*)*											■						1		
Ischnura pumilio (Ipum*)*															■		1		
Lestes barbarus (Lbar*)*							■										1	2012	2012
Chalcolestes viridis (Cvir*)*	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	15	2007	2011
Libellula depressa (Ldep*)*		■	■				■			■							4	2007	2013
Libellula fulva (Lful)	■	■		■		■	■	■	■	■	■	■	■	■	■	■	14	2007	2011
Libellula quadrimaculata (Lqua*)*					■	■	■										3	2008	2010
Onychogomphus forcipatus (Ofor*)*				■	■				■					■	■		5	2007	2013
Onychogomphus uncatus (Ounc*)*					■												1	2007	2007
Orthetrum brunneum (Obru*)*	■	■	■	■	■		■				■						7	2007	2009
Orthetrum cancellatum (Ocan*)*	■	■	■	■	■	■	■		■	■	■	■	■	■	■		14	2007	2007
Orthetrum coerulescens (Ocoe*)*	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	15	2007	2013
Oxygastra curtisii (Ocur*)*	■	■		■	■		■	■	■	■	■	■	■	■	■	■	14	2008	2012
Platycnemis acutipennis (Pacu*)*		■		■		■	■	■	■	■	■	■	■	■	■		12	2007	2011
Platycnemis latipes (Plat*)*	■	■	■	■		■	■	■	■	■		■	■	■	■		13	2008	2011
Pyrrhosoma nymphula (Pnym*)*						■					■						2	2008	2008
Selysiothemis nigra (Snig*)*	■	■	■	■	■		■	■	■	■	■	■	■	■	■		14	2007	2010
Sympecma fusca (Sfus)	■	■	■	■	■		■		■	■	■	■			■	■	12	2008	2010
Sympetrum fonscolombii (Sfon*)*	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	16	2007	2007
Sympetrum meridionale (Smer*)*			■	■	■		■										4	2009	2012
Sympetrum sanguineum (Ssan*)*					■		■										2	2010	2013
Sympetrum sinaiticum (Ssin*)*							■										1	2013	2013
Sympetrum striolatum (Sstr*)*	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	16	2007	2007
Trithemis annulata (Tann*)*	■	■	■		■	■	■	■	■	■	■	■	■	■	■	■	15	2007	2012
Species (total)	22	28	25	27	28	21	31	20	23	22	24	22	22	22	20	15			

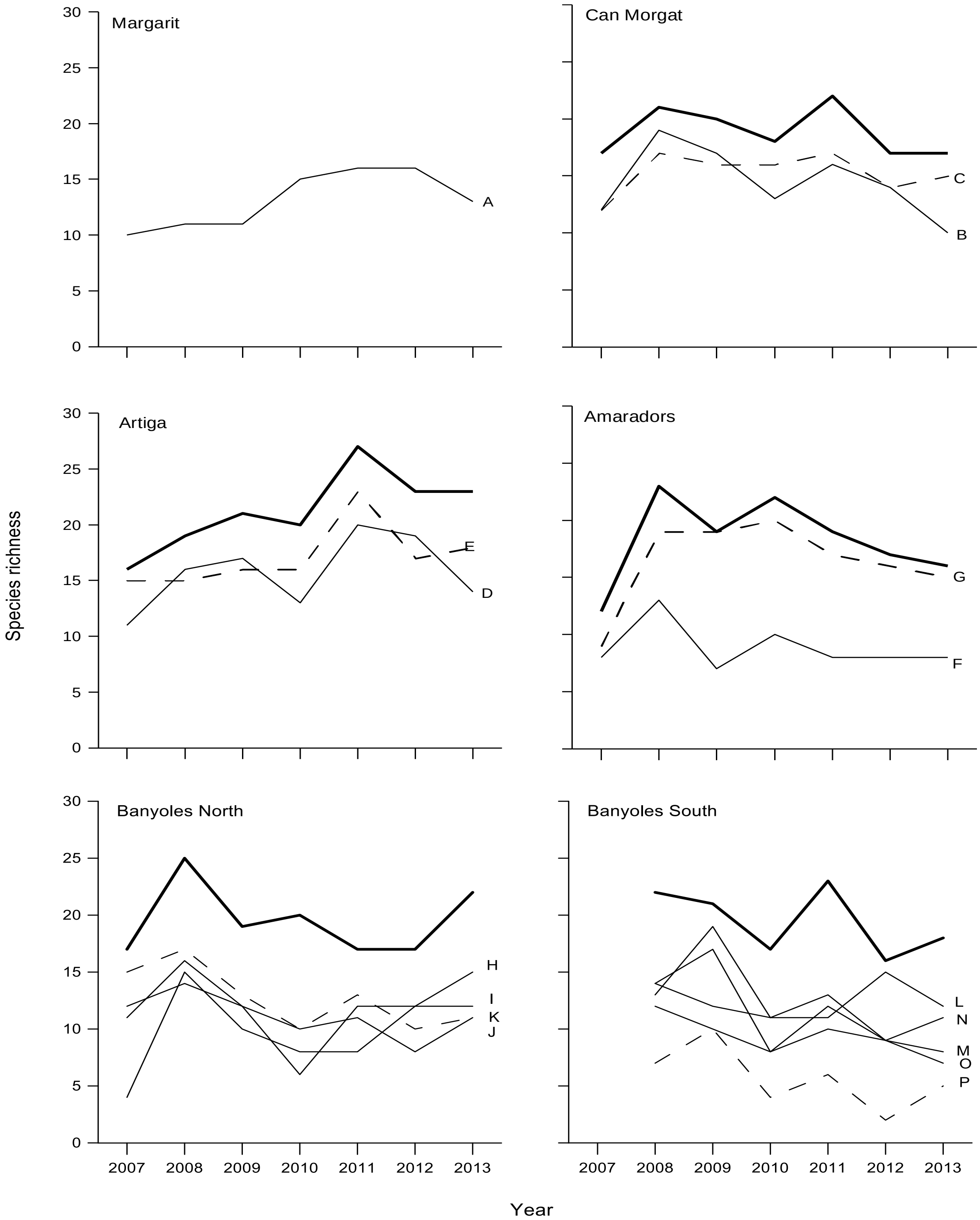


Fig. 6.2. Number of species per year recorded at each created lagoon and in the two zones of lake Banyoles. The solid thick line represents the total number of species, the dashed line the species counted in transects and the solid thin line the species counted in point counts.

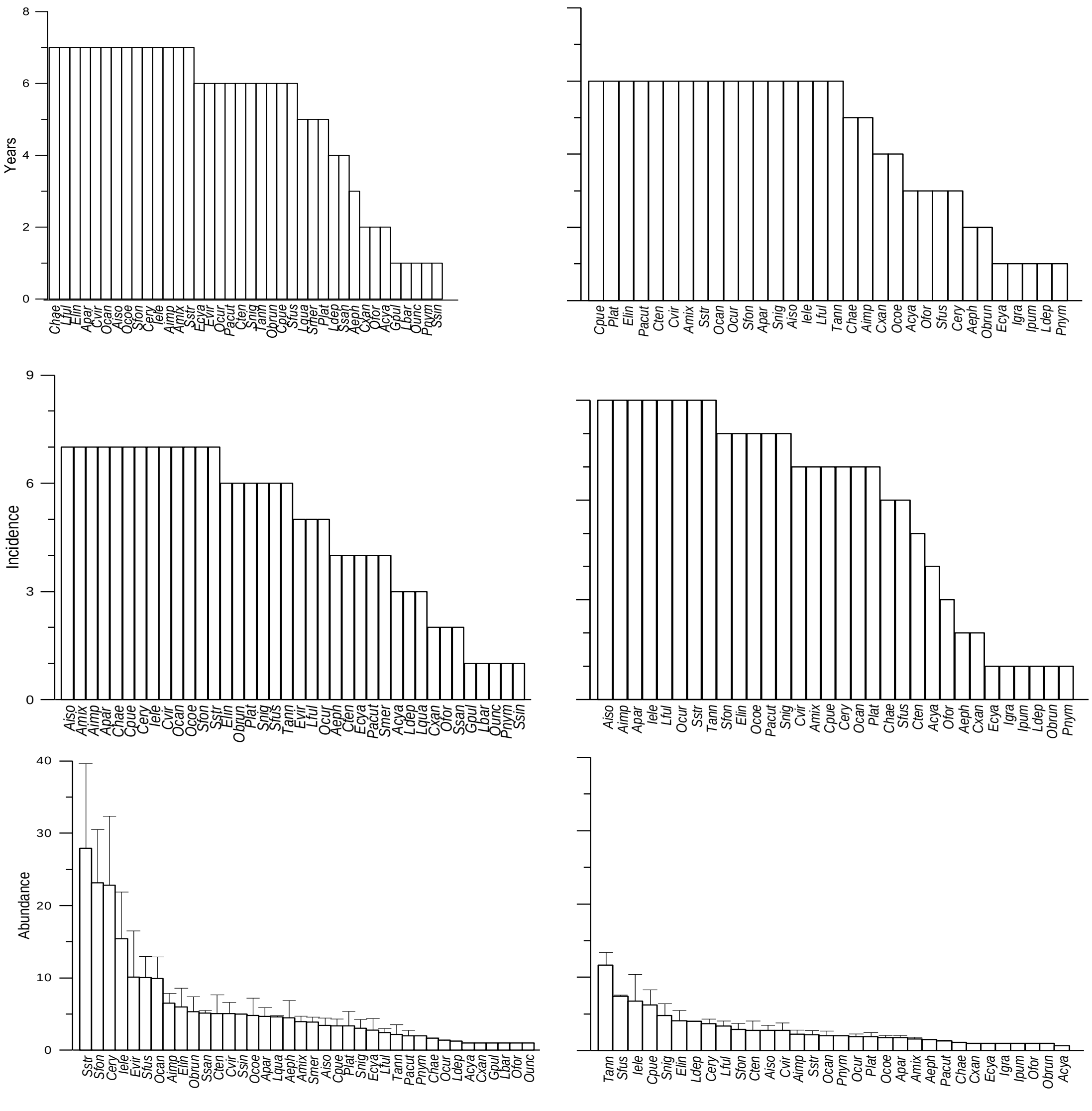


Fig. 6.3. Number of years present, incidence and mean abundance at the created lagoons (left) and lake Banyoles (right). Error bars indicate the standard error. Species abbreviations are in Table 6.2.

Table 6.3. Spearman correlation coefficient (R_s) and significance (p) of the relationships between number of years present, species incidence (number of sampling sites) and average abundance of each dragonfly species, in the created lagoons (above the diagonal) and in the lake Banyoles (below the diagonal).

	Number of years present	Incidence	Abundance
Number of years present		$R_s = 0.919$ $p < 0.001$	$R_s = 0.610$ $p < 0.001$
Incidence	$R_s= 0.801$ $p < 0.001$		$R_s = 0.597$ $p < 0.001$
Abundance	$R_s= 0.476$ $p = 0.006$	$R_s = 0.514$ $p = 0.003$	

Spatiotemporal variation in dragonfly community composition and assembly

Colonisation of the created lagoons was fast; 32 of the 38 species recorded (84%) appeared in the two first years of the study, i.e., 2-3 years after the creation of the lagoons (table 6.2). Species first appearing after the third year (2008) were mainly species with a small distribution range in Catalonia (Fig.6.4). In the lake Banyoles, all species but two were recorded already in the two first years of monitoring. At the created lagoons, it took up to six years to reach their final occupancy for those species recorded in more than one sampling site. Six species reached their final occupancy already in their first year of appearance (Table 6.2).

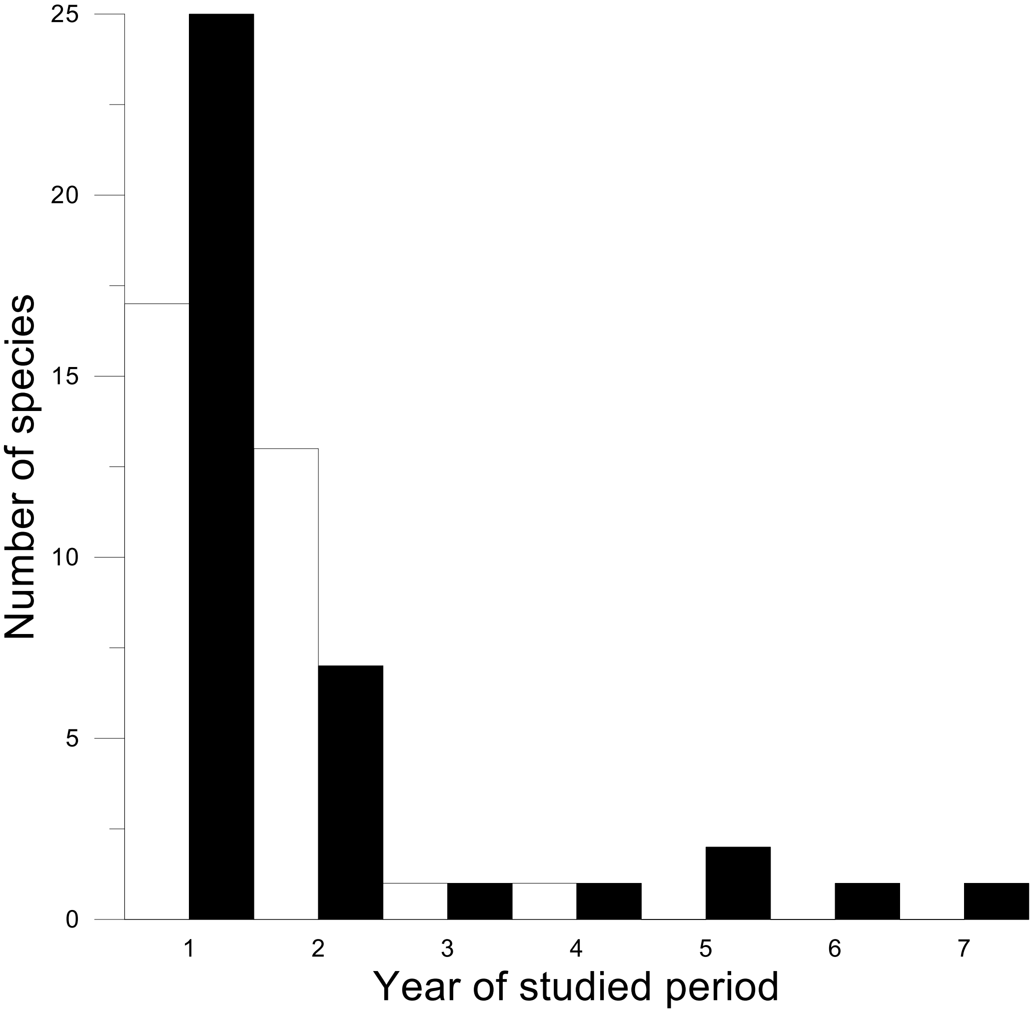


Fig. 6.4. Number of species recorded at the created lagoons for each studied year in relation to their distribution (number of 10 x 10 km squares occupied) in Catalonia. White bars: 1-56 squares, light grey bars: 57-112 squares, dark grey bars: 113-168 squares, black bars: 169-224 squares.

The NMDS analysis yielded an ordination with three axes that explained 85.5% of the total variance, with a stress value of 0.142. The three axes explained 60.4, 13.8 and 11.3% of the variance, respectively. Three patterns were clear from this analysis. First, the ordination separated the lagoons from the lake samples along the first axis, excepting the transect K in the North zone of the lake, that overlapped with the lagoon samples (Fig. 6.5). Second, in general, lagoons showed more dissimilarity in species composition than lake samples, as indicated by their larger scatter in the ordination plot (Fig. 6.5). Third, samples were grouped by site, rather than by year, indicating no clear temporal convergence in species composition (Fig. 6.5).

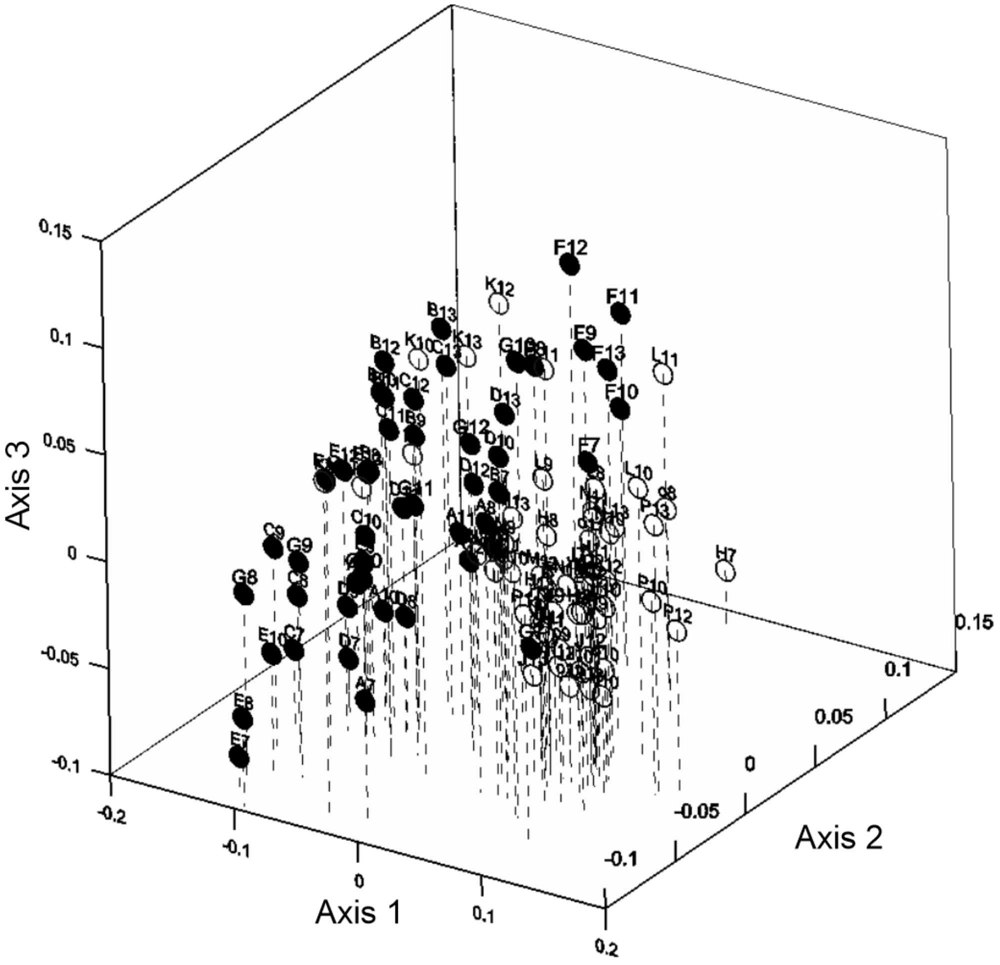


Fig. 6.5. NMDS ordination plot of sampling sites according to species composition and abundance. Created lagoons (A-G) are represented by filled symbols and lake Banyoles (H-K, North zone and L-P, South zone) with open symbols. The number by each letter indicates the study year.

In general, dragonfly assemblages showed stochastic temporal variation, indicated by a non significant regression of Euclidean distance between samples versus time lag. A divergent temporal trend was found only for site N in the South zone of lake Banyoles ($F_{1,\ 13}$ = 4.65, p = 0.050) and in the transect C in Can Morgat ($F_{1,\ 19}$ = 8.824, p = 0.008).

Beta diversity measurements

In general, total values of spatial beta diversity were higher at lake Banyoles sites (mean ± SD = 0.614 ± 0.014) than at the created lagoons (0.535 ± 0.007) (Fig. 6.6). Species replacement was the most important component in both cases (64.49 % for lake Banyoles, 61.47% for the created lagoons) (Fig. 6.6).

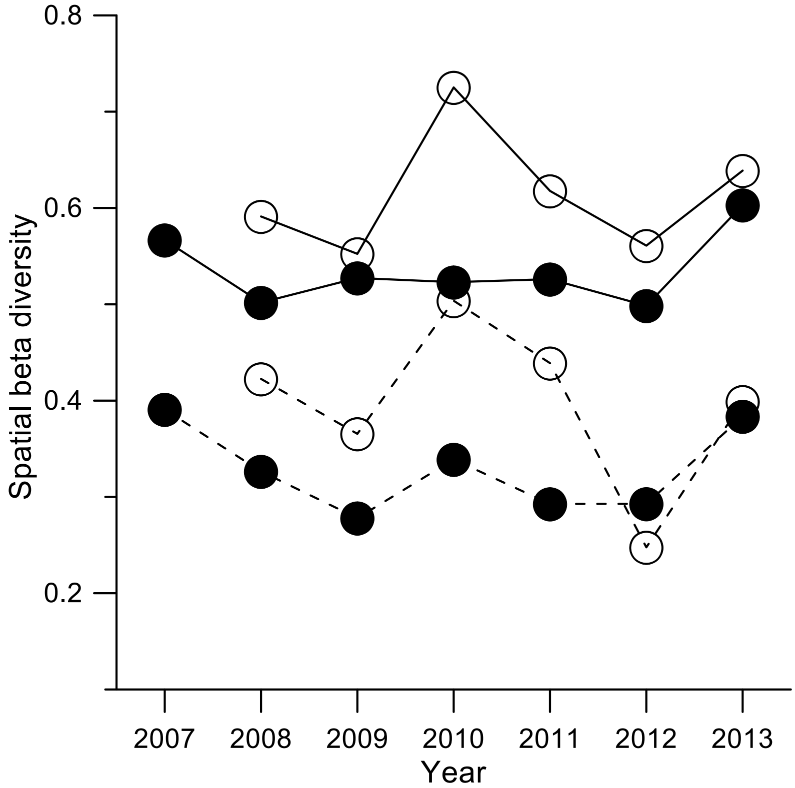


Fig. 6.6. Spatial beta diversity for each study year in the created lagoons (filled circles) and the lake Banyoles (open circles). Solid lines: Total beta diversity. Dashed lines: species replacement contribution to total beta diversity. Error bars are ommited because standard deviation did not exceed symbol size.

Temporal beta diversity was higher for lake Banyoles sites (0.554 ± 0.005) than for the created lagoons (0.480 ± 0.065) (Fig. 6.7). The species replacement component was more important both in the lake (59.96%) and in the created lagoons (66.78%) (Fig. 6.7).

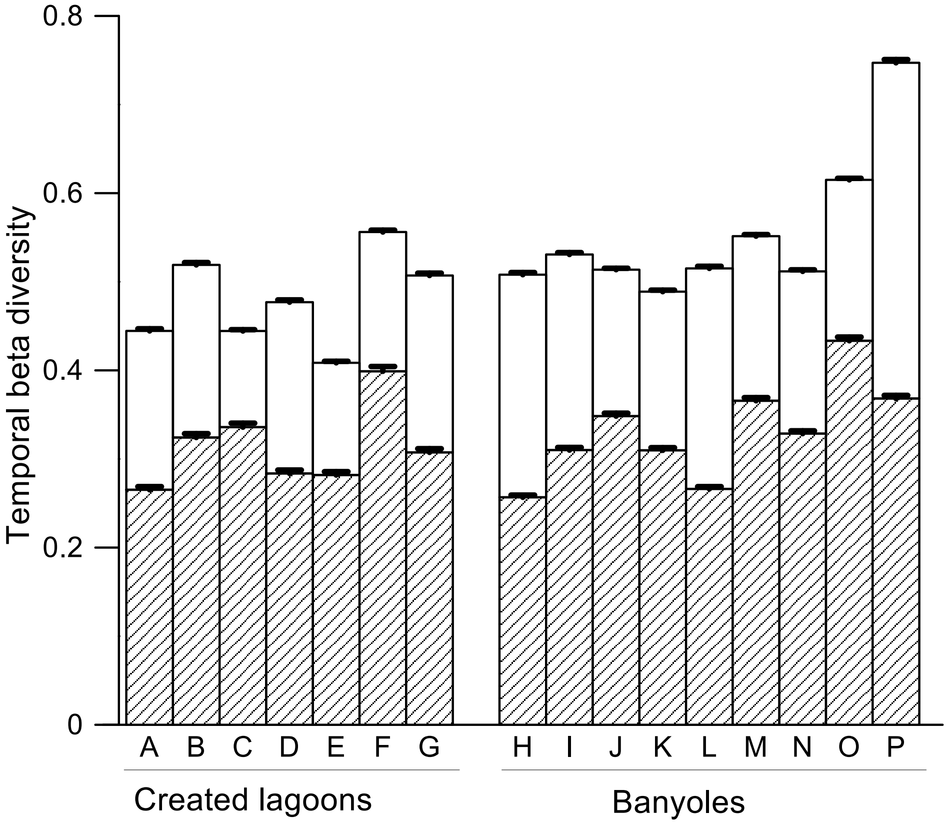


Fig. 6.7. Temporal beta diversity in the created lagoons and in the lake Banyoles samples. White bars: total beta diversity; hatched bars: species replacement contribution to total beta diversity. Error bars indicate the standard deviation.

Dragonfly Biotic Index

DBI did not increase with time for lake Banyoles ($R_s = -0.232$, $p = 0.658$) but it did for the created lagoons ($R_s = 0.841$, $p = 0.036$) (Table 6.4). DBI values per year were significantly higher for the created lagoons than for the lake ($t_5 = -2.907$, $p = 0.034$) (Table 6.4).

Table 6.4. Annual DBI values for lake Banyoles and the created lagoons.

Year	Lake Banyoles	Created lagoons
2008	58	54
2009	42	51
2010	49	55
2011	53	66
2012	42	55
2013	50	69
Mean ± SD	49.0 ± 6.3	58.3 ± 7.7

DISCUSSION

Dragonfly succession and assembly composition

Colonisation and assembly of new communities was fast at the created lagoons. A fast colonisation of the created lagoons was expected because dragonflies are considered to be a pioneer group within freshwater invertebrate communities (Moore 2002; Foote & Hornung 2005; Leitão et al. 2007) and some species can colonise a new pond on the same day it has been set up (Shuling et al. 2004). This contrasts with other aquatic insects such as beetles (Ruhí et al. 2009). Colonisation speed depends, among other factors, on the availability of colonists in the vicinity (Moore 1991) and on the connectance (Gee et al. 1997; Fairchild et al. 2000). The most likely source of colonists in this case was the lake Banyoles. Nevertheless, the presence at the created lagoons of dragonfly species not shared with the lake Banyoles suggests that other nearby habitats, such as streams, rivers and drainages channels were also a source of colonists. Regarding connectance, it is remarkable that the few species that colonized the lagoons after the third year of lagoon creation (i.e. after 2008) were regionally rare (Kadoya et al. 2008a).

Unlike has been reported in previous studies of Odonata (Moore 1991; Chovanec 1994) in this work no clear successional dynamics was present in the created lagoons. One possibility is that succession was so fast that it was missed because monitoring started two years after the lagoon creation. However, other short term studies monitoring for a few months to two years since pond creation did not find a succession either (Steytler & Samways 1995; Osborn & Samways 1996; Chovanec & Raab 1997; Kadoya et al. 2004). In addition, when successional change has been observed, it lasted over five years (Moore 1991; Chovanec 1994).

Successional changes also include a yearly increase of species number (Moore 1991; Chovanec 1994). The number of species quickly levelled off in most lagoons, as well as in the Lake Banyoles. This is consistent with a regulation by compensatory dynamics of dragonfly assemblies even a few years after the stablishment of the assembly. Vinebrooke et al. (2003) highlighted that compensatory species dynamics are apparent in species-rich groups of fast-growing and widely dispersing organisms and González & Loreau (2009) related the stability of the community to the diversity of responses to environmental changes. Unfortunately, information was not available in the present study to address the underlying causes of this finding.

Temporal trends in the dragonfly community and beta diversity measurements

Divergent successional trajectories have been documented in ponds (Osborn & Samways 1996; Ruhí et al. 2013). Rather than a sucessional trajectory, dragonfly community dynamics in the created lagoons was markedly stochastic. Several lines of evidence point out in this direction. Firstly, temporal trajectories at each site, as indicated by the NMDS, did not show any convergence across sampling sites. Secondly, stochasticity was the prevalent pattern in our trajectory analysis (Collins et al. 2000). Stochastic initial differences in composition can persist in time (Chase 2007) but habitat differences across lagoons could also be responsible of lack of convergence.

Stochastic variation is related to stable communities (Collins et al. 2000; Bêche & Resh 2007) and this stability can be observed when species abundances change in a way that increases in one species is compensated for by decreases in other species (Ernest et al. 2008; Magurran & Henderson 2010). This idea of density compensation is related to neutral theory (Hubbell 2001) in which stochastic processes in birth, death, colonisation and extinction rates govern community assembly instead of deterministic (niche related) factors (Chase 2007). In aquatic ecosystems, the importance of stochastic factors in regulating diversity has been highlighted when factors such as drought, flow or productivity are not constraining (Bêche & Resh 2007; Chase 2007; Hassal et al. 2012).

Nevertheless, stability is not synonymous of temporal persistence (Scarsbrook 2002). Although communities can show stability in species richness, this does not mean that the identity of these species remains constant (Zamora et al. 2007; Hassal et al. 2012; McGill et al. 2015). Our results showed a slightly large temporal beta diversity from year to year, regardless of assembly age. This result has been documented for Odonata and other insect orders (Hassall et al. 2012), mainly Coleoptera (Fairchild et al. 2000; Zamora et al. 2007), in habitats with seasonal fluctuation in water level (Florencio et al. 2009). Moreover, species replacement explained a higher percentage of the beta diversity partitioned variance. This has been previously found in communities of aquatic macroinvertebrates (Angeler 2013; Florencio et al. 2014) although using different indices.

Temporal beta diversity in aquatic ecosystems can be due to multiple factors, such as temporal extent of the study (Korhonen et al. 2010). For instance, at intermediate timescales (from week to years), beta diversity can be shaped by processes such as local colonisation and extinction driven by both temporal variation in environment and patterns of dispersal across sites (Solimini et al. 2003; Korhonen et al. 2010; Ruhí et al. 2013). High values of temporal beta diversity can denote either highly mobile assemblages or degraded habitats subject to rapid environmental changes or strong disturbances (Romanuk & Kolasa 2001). Curiously, in the present work new assemblies (created lagoons) were slighty more persistent than the older assemblies (lake Banyoles). We lack information about dispersal and sources of disturbance in the lagoons or the lake to account for these differences.

Spatial beta diversity values were also high and dominated by species replacement among sites. However, our results were not strictly comparable to previous estimates of beta diversity components in macroinvertebrate and dragonfly communities (D’Amico et al. 2004; Florencio et al. 2011, 2014) due to different methodology. Recent meta-analyses have shown that spatial beta diversity is jointly driven by species traits, geographical gradients, and ecosystem properties (Soininen et al. 2007a; Korhonen et al. 2010). The higher spatial beta diversity in the lake Banyoles, compared to the created lagoons, could be related to a higher environmental heterogeneity. Firstly, the created lagoons were managed in a similar way and, thus, we hypothesized that this habitat was more homogeneous than the lake. Secondly, higher distance existed between sampling sites of the lake and this could also be a source of heterogeneity (Harabiš et al. 2013; Reece & McIntyre 2009). Other unmeasursed factors, such as water properties or disturbances, could also be influencing the spatial beta diversity. Finally, dispersal could be also influential because assemblages of the lake included more Zygoptera than Anisoptera species and Zygoptera are known to have limited dispersal abilities (Osborn & Samways 1996; Conrad et al. 1999; Angelibert & Giani 2003; Juen & De Marco 2011).

Implications for conservation

Lake Banyoles and its satellite ponds were important for regional dragonfly diversity because they hosted 57% of the Odonata species known for Catalonia, including ibero-atlantic and ibero-magrebian endemics as well as species of conservation concern (Martín & Maynou 2015). Nevertheless, habitat creation increased the conservation value of the lake Banyoles, as indicated by the increasing values of DBI of the new lagoons over time. According to previous works, DBI increases could be related to changes in habitat condition that allowed the presence of species with specific requeriments and/or species of conservation concern (Dolný & Harabiš, 2012; Simaika & Samways, 2012; Hart et al. 2014; Rosset et al. 2013). As far as we know, this is the first time in which DBI has been used in a newly created habitat.

Probably, in this case, the increase in DBI was due to addition of new habitat, not present in the lake.

This apparent success, however, should be interpreted with caution. Unfortunately, larvae/exuviae data were not included in the study and it is well known that adults do not always select habitats where larvae can survive (Osborn & Samways 1996; Shuling et al. 2004; Hardersen 2008). From a metacommunity dynamic viewpoint, sites where species are not completing their life cycle can be considered as sinks sensu Pulliam (1988). Population consequences can be minimal if source habitats are abundant or the ability of the species to detect the suitable habitat is good (Pulliam & Danelson 1991). Otherwise, these “attractive sinks“(Delibes et al. 2001) can become ecological traps (Dwernychuk & Boag 1972; Donovan & Thompson 2001). This concept has been previously applied to artificial wetlands (Tilton 1995) and should be considered in conservation policies (Battin 2004). Wether the created lagoons were ecological traps cannot be decide with the data at hand. Nevertheless, in dragonflies, secondary habitats can have a positive role by holding high diversity (Harabiš & Dolný 2012.; Harabiš et al. 2013) and acting as refuges for many species when primary (Steytler & Samways 1995) or natural habitats (Lotzing 2002) are not available becoming thus crucial for surviving in changing landscape (De Block et al. 2005). In many cases, the role of created habitat as a refuge or as a ecological trap will depend on the way is managed (Harabiš & Dolný 2012; Levy 2015). Even if successful, habitat creation should never be used as a justification for the destruction of primary biotopes (Chovanec 1994).

According to these results, we conclude that created habitats offer the opportunity to test ecological theory regarding community assembly and dynamics. In newly created lagoons near the lake Banyoles, a diverse assembly of dragonfly communities was quickly established, without any apparent successional trajectory. Instead, changes in species composition were stochastic and mirrored those also

found in the lake dragonfly assemblies. Species richness fluctuated only slightly over time, but temporal beta diversity was remarkable. Species replacement was the most important mechanism to explain beta diversity. Created lagoons enhanced the importance of the lake Banyoles for dragonflies and could be a valuable habitat for dragonfly diversity over time. High temporal turnover in this system suggests that habitat creation can be a useful conservation tool when species richness, rather than species identity, is the main objective.

CAPÍTULO 7. DISCUSIÓN GENERAL

El objeto del presente capítulo es relacionar los aspectos que caracterizan las comunidades de Odonata en estado adulto y larvario (Tabla 7.1). De acuerdo con las bases conceptuales expuestas en la Introducción General, se discutirá qué papel tienen los factores locales y regionales en la formación de los ensamblajes, se relacionarán los patrones obtenidos con la diversidad espacial y se analizará el grado de dinamismo de las comunidades (Tabla 7.1). Finalmente, se dan ciertas recomendaciones que se desprenden de los resultados de esta tesis para la conservación de las comunidades de libélulas en hábitats mediterráneos.

Tabla 7.1. Cuadro resumen de los principales resultados que se han obtenido para las características de las comunidades de libélulas estudiadas.

Características de la estruc-tura de las comunidades que se han estudiado	Tipo de comunidad estudiada	Resultados
Factores influyentes en ensamblaje comunidades	Larvas	Factores locales influyen en estructura de ensamblajes (Capítulo 5)
	Adultos	Factores regionales influyen en riqueza de especies (Capítulo 3).
Patrón de la metacomunidad	Larvas	Cuasi-anidado o azaroso y no estable en el tiempo. Anisoptera y Zygoptera difieren en su patrón pero sí se mantiene estable en el tiempo (Capítulo 4).
Diversidad beta espacial	Larvas	Alta. A escala regional las comunidades tienen un grado de disimilitud en su composición de un 80%. Esta tendencia se mantiene tras 22 años (Capítulo 3).
	Adultos	Alta. Durante siete años, las comunidades conservaron la similitud en su composición en un 50% anual (Capítulo 6)
Diversidad beta temporal	Larvas	Alta. Tras 22 años, las comunidades de Odonata presentaron menos de un 30% de similitud en su composición (Capítulo 5).
	Adultos	Alta. Durante siete años, las comunidades de Odonata presentaron una similitud cercana al 50% anual (Capítulo 6).

En los sistemas dulceacuículas, el hidroperíodo es el factor local que más frecuentemente se ha destacado como la determinante de la riqueza de especies (Welborn et al. 1996). Sin embargo, el hidroperíodo no fue un factor determinante en la riqueza de especies de las comunidades de adultos de Odonata. En Menorca, donde los hábitats dulceacuículas estudiados presentan regímenes hídricos diferentes, esto ha quedado patente en adultos (Capítulo 3) y en larvas (Capítulo 5). De hecho, en el estado larvario, la diferenciación de los ensamblajes vino determinada por el tipo de hábitat, relacionado con la distancia al mar en 1988 o con la temperatura del agua en 2010 (Capítulo 5). Según estos resultados, se pudieron distinguir entre especies con preferencia de aguas lóticas y especies distribuidas por los hábitats lénticos, especialmente charcas temporales, tal y como se caracterizan las especies en atlas de zonas mediterráneas ibéricas (Baixeras et al. 2006; Lockwood & Oliver 2007; Sánchez et al. 2009). En Menorca, la escasa influencia del hidroperiodo podría deberse a que las especies presentes son un subconjunto del acervo de libélulas mediterráneas formado por especies generalistas con gran capacidad de adaptación a hábitats de marcada estacionalidad (Ahijado Guzmán 2013). No obstante, en el humedal de Banyoles (Capítulo 6), con un acervo regional más amplio y diverso de especies, las comunidades de adultos observadas en las lagunas de nueva creación (semipermanentes) fueron más ricas y diversas que las del lago (permanente).

En un paisaje donde la mayoría de hábitats son temporales, los principales factores relacionados con la riqueza de especies fueron factores regionales: el área y la conectividad (Capítulo 3). En esta tesis, este hecho sólo ha podido contrastarse para las comunidades de libélulas adultas pero cobra sentido si uno tiene en mente que los adultos son la fase dispersante del ciclo vital en Odonata. La importancia del área, relacionada con la heterogeneidad y selección del hábitat ha sido resaltada por otros autores (Gaines 2006; Oertli et al. 2002; Kadoya et al. 2004). No obstante, es frecuente que la riqueza de las comunidades de libélulas esté relacionada con variables locales como la cobertura de macrófitos acuáticos o algunas variables físicoquímicas del agua (Kadoya et al. 2004; Carchini et al. 2005; Sato & Riddiford 2007; pero véase Schlinder et al. 2003; Carchini et al. 2007). Esto es especialmente cierto en trabajos en los que no siempre se han incluído hábitats temporales, con lo cual la preponderancia de factores locales podría deberse a un sesgo hacia el estudio de hábitats estables. Por otra parte, la conectividad del hábitat facilita que las especies que no disponen de estrategias específicas para combatir la sequía puedan desplazarse en busca de nuevos parches que colonizar (Crumrine et al. 2008). De hecho, de las especies registradas en el presente trabajo, hay pocas especies que efectivamente tengan mecanismos específicos para combatir la sequía tal y como han reportado otros autores (Carchini et al. 2007; McCauley et al. 2008). Además, la conectividad es un factor clave en el ensamblaje de nuevas comunidades (Moore 1991). En el humedal de Banyoles el hecho de que las lagunas de nueva creación estén bien conectadas con otros hábitats acuáticos además de con el lago podría explicar que los nuevos ensamblajes se hayan constituido con tan poco tiempo y que alberguen especies no registradas en el lago (Capítulo 6).

Cuando se han analizado los patrones de las metacomunidades en larvas se ha observado que pueden mostrar un cuasi-anidamiento o una estructura azarosa (Capítulo 4). En otros trabajos en los que se ha utilizado una metodología similar se han detectado, además de estos patrones, aquellos relacionados con una visión clementsiana (Bried et al. 2015) o de anidamiento (De Marco et al. 2015) tal y como sucede en otros organismos dulceacuícolas (Dallas & Draque 2014; Henriques-Silva et al. 2013). Sin embargo, en dichos trabajos no se incluyeron diferentes tipos de hábitats y estuvieron centrados en adultos. La estructura de cuasi-anidamiento se ha explicado en base a factores abióticos como hidroperíodo o proporción de sombra (McCauley et al. 2008; De Marco et al. 2015) y el patrón azaroso se ha relacionado sólo con las especies no residentes (Bried et al. 2015). En este caso, todas las especies fueron residentes al tratarse de comunidades de larvas. Como Anisoptera y Zygoptera presentaron diferentes tipos de patrones se piensa que en los zigópteros, la cuasi-estructura estaría relacionada con una capacidad de dispersión limitada junto con un mayor grado de especialización del hábitat (Angelibert & Giani 2003; Siepielski & McPeek 2013) en comparación con los Anisoptera, cuya capacidad de dispersión y perfil más generalista se relacionaría con una estructura azarosa. Según los resultados obtenidos en el Capítulo 4, la estructura de la metacomunidad se puede ver afectada por la proporción de anisópteros y zigópteros que la forman. De hecho, si con el tiempo esta proporción cambia, también lo hace el patrón observado (Capítulo 4). En los trabajos en los que se ha analizado la estabilidad temporal de los patrones en otros grupos, el cambio de patrón se ha relacionado con una disminución de la importancia de los factores abióticos (McCreadie & Bedwell 2013), por cambios en las limitaciones de dispersión (Fernandes et al. 2014) o con diferentes clasificaciones de las especies estudiadas, como por ejemplo nativas frente exóticas (Erős et al. 2014).

Las comunidades de Odonata presentaron una diversidad beta espacial alta en estado larvario (Capítulo 5) y adulto (Capítulo 6). En estado adulto se observó que las comunidades que geográficamente estaban más próximas eran más similares (Capítulo 6). Esto podría deberse al llamado decaimiento de la similitud con la distancia (Nekola & White 1999) o porque en distancias menores la dispersión puede verse facilitada (Conrad et al. 1999; Rouquette & Thompson 2007b). En las comunidades de larvas, no se ha detectado una diversidad beta espacial diferente para Anisoptera y Zygoptera (Capítulo 5) así que si existen diferencias entre subórdenes en la capacidad de dispersión de las especies, en esta metacomunidad no se detectaron. Estos resultados están en consonancia con los obtenidos por Juen & De Marco (2011) para comunidades de adultos. Sin embargo presentan discrepancias con respecto a lo que se deduce de los diferentes patrones de la metacomunidad observados para las larvas (Capítulo 4) y sugieren que, al menos en el caso de

Zygoptera, se tenga que analizar con profundidad qué tipo de gradiente subyace al patrón asociado, dejando de lado el papel que tiene su capacidad de dispersión.

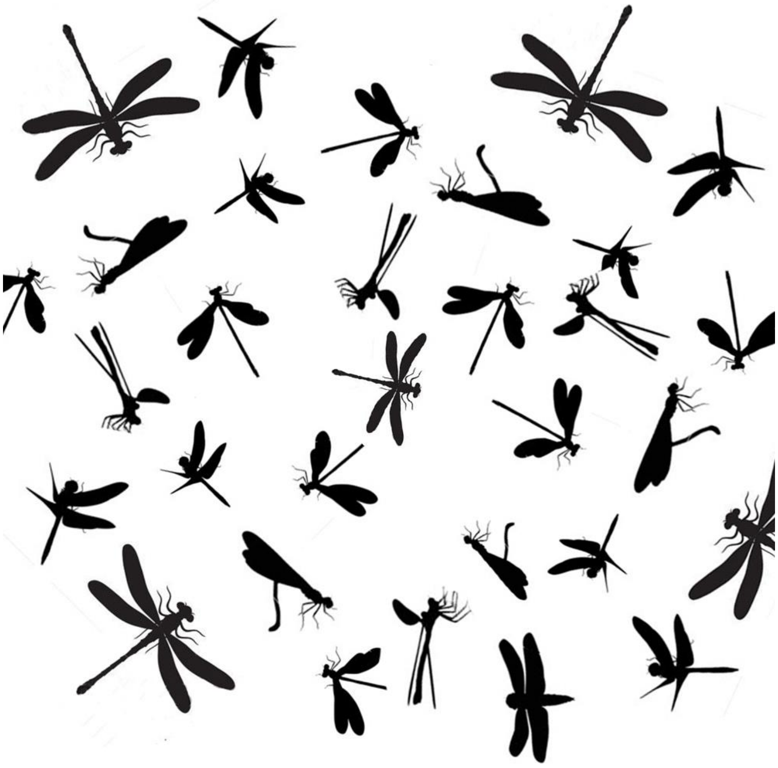
Las comunidades de Odonata fueron dinámicas en estado larvario (Capítulo 5) y en estado adulto (Capítulo 6). En el caso de las larvas se comprobó que esa dinámica estaba correlacionada negativamente con el número de especies y no con el grado de cambio ambiental registrado en la localidad estudiada. La relación negativa entre el número de especies y su diversidad beta temporal ha sido descrita como una medida de estabilidad: cuantas más especies formen la comunidad menor es la probabilidad de cambio (Shurin 2007). En cuanto a la ausencia de relación entre los cambios ambientales y el cambio en la composición de comunidades, se puede pensar en que quizás las variables relacionadas con la estructura del hábitat o de sus alrededores fuesen más importantes que los factores abióticos medidos puesto que en el Capítulo 5, la diversidad temporal medida abarca un período de 22 años, tiempo suficiente para que estos cambios se hubiesen dado y que las comunidades de Odonata se viesen afectadas (Flenner & Sahlén 2008). Sin embargo, excepto por el caso de algunos torrentes los cambios en los alrededores de las localidades estudiadas han sido inapreciables (*www.obsam.cat*). De hecho, en las comunidades de adultos asociadas a charcas temporales esta variable no pareció ser relevante (Capítulo 3) y es en este estadio donde se han observado diferentes respuestas a este tipo de cambios (Kadoya et al. 2008b).

A pesar del alto dinamismo que han mostrado las comunidades de Odonata, la riqueza de especies se ha mantenido más o menos constante en las estaciones de muestreo, independientemente del período de tiempo considerado (Capítulos 5 y 6). Este fenómeno es conocido como suma cero (Hubbell 2001) y sugiere que los mecanismos que regulan la composición de los ensamblajes están relacionados con la cantidad de recursos disponibles en un hábitat. De esta manera, la coexistencia entre especies está regulada de manera global mediante la abundancia total de individuos que explotarán esos recursos y no depende del crecimiento poblacional que individualmente tenga cada especie. La existencia de este tipo de dinámica ha sido descrita para larvas de las especies del género *Enallagma* (Siepielski et al. 2010; Siepielski & McPeek 2013).Otro dato importante fue que la diversidad beta temporal observada fue similar en comunidades ya establecidas y en comunidades recientemente ensambladas (Capítulo 6). Este hecho implica: (1) que en los hábitats de nueva creación prevaleció una dinámica estocástica y no una sucesional como previamente se había documentado (Moore 1991; Chovanec 1994; consúltese sin embargo Steytler & Samways 1995; Chovanec & Raab 1997) y (2) que este tipo de dinámica difícilmente se puede relacionar con factores ambientales (Collins et al. 2000).

Los resultados expuestos en la presente tesis doctoral sugieren que la conservación de las comunidades de Odonata en sistemas mediterráneos requiere de la existencia de hábitats con diferente hidroperíodo que estén conectados. Este planteamiento coincide con el planteado por Picazo et al. (2012) para los coleópteros y Florencio et al. (2014) para el conjunto de los macroinvertebrados y resalta dos ideas muy importantes: (1) el número de especies que albergue un determinado hábitat no puede ser criterio suficiente para designar su protección (Báldi 2008; Tjørve 2010) y (2) para una conservación adecuada de los sistemas y de su fauna asociada debe tenerse en cuenta cuál es su grado de variabilidad (Angélibert et al. 2004; Hassall et al. 2012; Angeler 2013), hecho que en las comunidades de Odonata ha quedado patente y que no debería ser obviado.

Nótese que la presente tesis doctoral tuvo algunas limitaciones. En las comunidades de larvas estudiadas en Menorca (Capítulo 4 y 5) no se dispuso de una información detallada de cambios en las inmediaciones de las estaciones de muestreo ni del grado de conectividad que presentaba cada estación. El patrón observado de la metacomunidad sólo se estudió para el estado larvario, con lo que sería interesante repetir el análisis para los adultos. En el humedal de Banyoles no se tuvo suficiente información sobre la existencia de larvas en las lagunas de nueva creación. En ningún análisis realizado se ha incluído la información relativa a los posibles factores bióticos que podrían influir en las comunidades de Odonata, tales como la presencia de peces o de especies exóticas puesto que además de la dificultad que entraña poder establecer de una manera fiable cuál es su papel en los diferentes ensamblajes, esta información no era bien conocida para la totalidad de los sitios estudiados De la misma manera, la capacidad de dispersión se ha valorado de manera indirecta, sin hacer distinciones entre ratios de sexo o edad de los individuos. No obstante, y a pesar de sus limitaciones, el presente trabajo proporciona información novedosa sobre cómo se estructuran las comunidades de libélulas en ambientes mediterráneos y ofrece la posibilidad de enlazar facetas muy diferentes asociadas al estudio del grupo.

CONCLUSIONES



1. En los sistemas dulceacuícolas temporales de Menorca los factores regionales que influyen en la dipersión de las especies, concretamente el área y la conectividad entre las charcas temporales, tienen un importante papel en el ensamblaje de las comunidades de Odonata adultos.
2. Las comunidades de Odonata, tanto de adultos como en estado larvario, presentan una diversidad beta espacial alta. La diversidad beta espacial es similar en Anisoptera y Zygoptera, lo cual sugiere que las diferencias de capacidad dispersiva entre subórdenes no son demasiado relevantes a las escalas espaciales estudiadas.
3. La estructura de las metacomunidades de libélulas en estado larvario es o bien al azar o cuasi-anidada. Esta estructura difiere entre subórdenes y es consistente con la limitación de dispersión atribuida a los Zygoptera en comparación con los Anisoptera.
4. La estructura de las metacomunidades de Odonata no es estable en el tiempo y ha variado en un periodo de 22 años. Este cambio podría estar causado por la modificación de la proporción desigual de Anisoptera y Zygoptera en ese periodo de tiempo.
5. Las comunidades de Odonata son muy dinámicas. El recambio anual de especies en comunidades de adultos es notable, como indican similaridades inferiores al 50%. En el estadio larvario, el recambio de especies tras 22 años fue muy alto, con similaridades inferiores al 30%.

6. A pesar del alto dinamismo que presentan las comunidades de Odonata, se observa gran estabilidad en la riqueza de especies a lo largo del tiempo, tanto en comunidades de adultos como de larvas. Esta estabilidad es compatible con la existencia de procesos que conducen a una suma cero.

7. Los patrones de diversidad beta espacial y el gran dinamismo de las comunidades de libélulas sugieren que para conservar la diversidad de estos organismos hay que garantizar la existencia de un paisaje formado por sistemas dulceacuícolas heterogéneos que además tengan un alto grado de conectividad.

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