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PATRONES EMERGENTES EN REDES DE POLINIZACIÓN EN COMUNIDADES COSTERAS DE BALEARES Y CANARIAS

ROCÍO CASTRO URGAL

Tesis Doctoral UIB 2016 Patrones emergentes en redes de polinización en comunidades costeras de Baleares y Canarias Rocío Castro Urgal

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Illes Balears

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Programa de Doctorado en Biología de las Plantas

PATRONES EMERGENTES EN REDES DE POLINIZACIÓN EN COMUNIDADES COSTERAS DE BALEARES Y CANARIAS

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DECLARO:

Que la Tesis Doctoral que lleva por título

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presentada por Rocío Castro Urgal para la obtención del título de doctora por la Universidad de las Islas Baleares, ha sido realizada bajo mi supervisión.

Y para que quede constancia de ello, firmo el presente documento en Palma de Mallorca, a 3 de Octubre de 2016.

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Resumen

Las técnicas de análisis de redes complejas permiten a los ecólogos estudiar la multitud de interacciones que se dan en los ecosistemas. La descripción de redes de interacción cada vez más realistas y completas nos proporcionan información sobre las características de las comunidades pero también sobre cada uno de sus componentes. Usando la perspectiva global que ofrecen estas redes de interacción planta-polinizador, esta tesis aporta información relevante que puede ser utilizada en el ámbito de la conservación y la restauración de ecosistemas insulares.

Para avanzar hacia una descripción más funcional de la estructura de las redes ecológicas, se necesitan pesos de interacción lo más precisos posible. A pesar de la gran cantidad de estudios que evalúan la estructura de las redes mutualistas, se sabe todavía relativamente poco acerca de cómo las diferentes formas de medir el peso de las interacciones pueden influir en los parámetros de red que se utilizan para describir este tipo de estructuras. En el primer capítulo de esta tesis, se evalúa cómo el uso de cinco pesos de interacción diferentes, los cuales incluyen progresivamente información más detallada de las interacciones planta-polinizador, influyen considerablemente en los descriptores de la estructura de red utilizados. En las dos comunidades estudiadas, el tipo de peso de interacción utilizado altera significativamente la estructura de la red. Por tanto, considerar cuidadosamente el peso de interacción más apropiado para cada estudio de redes ecológicas puede minimizar potenciales sesgos y/o errores de interpretación.

Gran parte de la investigación ecológica se ha focalizado en tratar de entender por qué las especies son generalistas o especialistas en sus interacciones y cómo las redes de interacciones evolucionan en un entorno determinado. Sin embargo, existe poca información sobre si las especies con las que interactúan los generalistas y especialistas (sus “parejas”) difieren en determinados rasgos. En el segundo capítulo, se evalúan las diferencias de los rasgos de las “parejas” (concretamente, sus abundancias y riqueza funcional) y la variación temporal de estas relaciones entre las especies que han sido previamente categorizadas de acuerdo con dos índices de especialización: el número de “parejas”, en inglés llamado *linkage level* (*L*), y el índice de especialización complementaria *d’*. Las especies especialistas y selectivas, consideradas más vulnerables frente a posibles perturbaciones, disminuyen el riesgo de extinción mediante la interacción con especies abundantes y/o “parejas” funcionalmente diferentes,

respectivamente. Por otro lado, las especies de visitantes florales generalistas son las únicas que muestran cambios a lo largo de la estación en los rasgos de sus “parejas”, impulsados por cambios en la composición de especies de la comunidad.

Las islas son de particular importancia para la conservación de la diversidad global. Sus pequeños tamaños de población y el alto nivel de endemismos las hacen particularmente susceptibles a cambios antropogénicos. Dos diferencias biológicas importantes entre islas oceánicas y continentales son la menor riqueza de especies y el mayor grado de disarmonía taxonómica de las primeras con respecto a las segundas. Aunque existen algunas evidencias de redes de interacción planta-animal menos complejas en islas oceánicas, sólo unos pocos estudios comparan las comunidades insulares entre ellas o con comunidades continentales. En el tercer capítulo se analiza la composición de especies y las propiedades estructurales de redes cuantitativas de visitantes florales en dos comunidades de cada tipo de islas: Islas Canarias (origen oceánico) e Islas Baleares (origen continental). Un mayor número de especies oportunistas sumado a la presencia de especies supergeneralistas en la isla oceánica dieron lugar a valores significativamente más altos de conectancia y anidamiento (ambos cuantitativos) en comparación con la isla continental. Dado que estos dos parámetros parecen estar asociados con la estabilidad de la red, las comunidades insulares oceánicas de polinización parecen ser menos vulnerables a las perturbaciones que las comunidades de islas continentales.

La pérdida del hábitat y los cambios en la calidad del mismo, constituyen las principales amenazas para la supervivencia tanto de las plantas como de sus visitantes florales. El impacto que dichas perturbaciones tenga sobre las interacciones entre especies puede provocar cambios en toda la estructura de la red de visitantes florales. En el cuarto capítulo de esta tesis, se evalúa el efecto de la pérdida de hábitat (más de un 50% de la cubierta vegetal) sobre los patrones de interacción entre las plantas y los insectos que visitan sus flores en una comunidad dunar situada en la isla de Mallorca. Tras la perturbación, se produce una disminución considerable tanto del número de especies y abundancia de visitantes florales como de interacciones en la red. Los escarabajos, las moscas y las hormigas fueron los visitantes florales más afectados, mientras que las abejas y las avispas fueron los menos afectados, probablemente debido a su mayor capacidad de vuelo. Se observa también menor anidamiento, mayor nivel de selectividad y mayor nivel de modularidad de la comunidad tras la pérdida de hábitat. Dichos resultados en conjunto indican que la red de visitantes florales estudiada será menos robusta y con menor grado de resiliencia ante futuras perturbaciones.

En conclusión, gracias a las técnicas de análisis de redes complejas utilizadas en esta tesis entendemos que utilizar un peso de interacción adecuado a la hora de construir las redes de interacción nos aporta información más realista y completa sobre las comunidades de estudio. Conocemos con más detalle el dinamismo y la capacidad de la especies de asegurar su supervivencia en las distintas comunidades utilizando diferentes estrategias. Comprobamos también la mayor vulnerabilidad de una comunidad después de la destrucción de gran parte de su hábitat. Los resultados de esta tesis pueden contribuir a proteger, en la medida de lo posible, los ecosistemas naturales frente a la gran cantidad de perturbaciones provocadas por las actividades humanas.

Abstract

Complex networks analysis allows ecologists to study the multitude of interactions that occur in ecosystems. The description of more realistic and complete interaction networks provides information not only about the characteristics of the communities but also of each one of its components. Using the global perspective offered by these plant-pollinator networks, this thesis provides relevant information that can be used in the field of conservation and island ecosystem restoration.

To move towards a more functional description of the structure of ecological networks, we need interaction weights to be as accurate as possible. Despite the considerable work carried out to assess the structure of mutualistic networks, little is known about how different ways of measuring the interaction weights can influence network parameters used to describe such structures. In the first chapter of this thesis we evaluated how the use of five different link weights, including progressively more detailed information on the plant-pollinator interactions, influences widely used descriptors of network structure. In the two communities studied, the type of interaction weight used significantly alters the network structure. Thus, carefully considering the most appropriate interaction weight for each ecological network study can minimize potential biases and/or misinterpretation of network structures.

Much ecological research has focused on trying to understand why species are generalized or specialized in their interactions and how networks develop in a certain environment. However, less information is available on whether generalized and specialized species differ in particular traits of their interacting partners. In the second chapter, differences in partner' traits (specifically, their abundances and functional richness) among species, previously categorized according to two indices of specialization, are studied, as well as the temporal variation of these relationships. The indices of specialization used are: the number of partners, also called linkage level (*L*), and complementary specialization *d´*. Specialized and selective species, considered the most vulnerable to perturbations, reduce the risk of extinction by interacting with abundant species and/or functionally different "partners", respectively. On the other hand, generalized flower-visitor species are the only ones showing seasonal shifts in their partners' traits, driven by changes in community species composition.

Islands are of particular importance for the conservation of global biodiversity. Their small population sizes and the high level of endemism make them particularly susceptible to anthropogenic change. Two important biological differences between oceanic and continental islands are that the former usually have lower species richness and a higher degree of taxonomic disharmony than the latter. Although there is some evidence of less complex interaction networks on oceanic islands, only a few studies have compared island communities with each other or with mainland communities. In the chapter three, species composition and structural properties of quantitative flower-visitor networks in two communities of each type of island are analyzed: Canary Islands (oceanic origin) and Balearic Islands (continental origin). A greater number of opportunistic species and the presence of supergeneralist species on the oceanic island led to significantly higher values of quantitative connectance and nestedness compared to those on the continental island. Given that these two parameters appear to be associated with network stability, pollination communities on oceanic islands appear to be less vulnerable to perturbations than those of continental islands.

Habitat loss or habitat modification represents the main threats to the survival of both plants and their flower visitors. The impact of such disturbances on those species interactions can lead to changes in the entire flower-visitor network structure. In the fourth chapter, the effect of habitat loss (more than 50% of land cover) on interaction patterns between plants and their flower visitors in a dune community, on Mallorca Island, is evaluated. A significant decrease in both species richness and abundance of floral visitors as well as in the number of network interactions was observed after the disturbance. Beetles, flies and ants were the functional groups most affected, whereas bees and wasps were the least affected, probably because of their strong flight capacity. Moreover, lower nestedness but higher selectivity and modularity of the community were detected after habitat loss. Overall, these results indicate that the flower-visitor network studied will be more vulnerable and less resilient to future perturbations.

In conclusion, thanks to the complex networks analysis used in this thesis we comprehend that using an appropriate interaction weight when building interaction networks gives us more realistic and complete information about the communities of study. We also know, with more detail, the dynamism and species survival capacity in different communities using diverse strategies. Moreover, we observed the increased vulnerability of a community after the destruction of much of its habitat. The results of this thesis may contribute to protecting, as far as possible, natural ecosystems in the face of the huge kind of disturbances caused by human activities.

Resum

Les tècniques d'anàlisi de xarxes complexes permeten als ecòlegs estudiar la multitud d'interaccions que tenen lloc en els ecosistemes. La descripció de xarxes d'interacció cada vegada més realistes i completes ens proporciona informació sobre les comunitats i cada un dels seus components. Aprofitant la perspectiva global que ofereixen les xarxes d'interacció planta-pol·linitzador, aquesta tesi aporta informació rellevant que pot fer-se servir en l'àmbit de la conservació i restauració d'ecosistemes insulars.

Per avançar cap a una descripció més funcional de l'estructura de les xarxes ecològiques es requereix mesurar el pes de cada interacció de la manera més precisa possible. Malgrat l'existència d'un gran nombre d'estudis que avaluen l'estructura de xarxes mutualistes, és poc conegut com influeixen les distintes formes de mesurar el pes de les interacciones sobre els paràmetres de xarxa que s'utilitzen per descriure aquest tipus d'estructures. En el primer capítol d'aquesta tesi s'avalua com l'ús de cinc pesos d'interacció diferents, que inclouen progressivament informació més detallada de les interaccions planta-pol·linitzador, influeixen considerablement en els descriptors de l'estructura de la xarxa usats. En les dues comunitats estudiades, el tipus de pes d'interacció usat altera significativament l'estructura de la xarxa. Considerar el pes d'interacció més apropiat per a cada estudi de xarxes ecològiques pot minimitzar potencials biaixos i/o errors d'interpretació.

Gran part de la investigació ecològica s'ha focalitzat en mirar d'entendre per què les espècies són generalistes o especialistes en les seves interaccions i com les xarxes d'interaccions evolucionen en un entorn determinat. Per contra, existeix poca informació sobre si les espècies amb les que interactuen els generalistes i especialistes (les seves "parelles") difereixen en determinats trets. En el segon capítol s'avaluen les diferències de les característiques de les "parelles" (concretament, abundància i riquesa funcional) i la variació temporal d'aquestes relacions entre espècies prèviament categoritzades d'acord a dos índexs d'especialització: el nombre de "parelles", en anglès anomenat linkage level, i un índex d'especialització complementària (*d'*). Les espècies especialistes i selectives, considerades més vulnerables enfront a possibles pertorbacions, disminueixen el seu risc d'extinció mitjançant la interacció amb espècies abundants i/o "parelles" funcionalment diferents, respectivament. D'altra banda, les espècies de visitants florals generalistes són les úniques que mostren canvis al llarg de l'estació en els trets de les seves "parelles", impulsats per canvis en la composició d'espècies de la comunitat.

Les illes són de gran importància per a la conservació de la diversitat global. El seus petits tamanys poblacionals i l'alt nivell d'endemismes les fan particularment susceptibles als canvis antropogènics. Dues diferències biològiques importants entre illes oceàniques i continentals són la menor riquesa d'espècies i el major grau de disharmonia taxonòmica de les primeres respecte les segones. Malgrat existeixen algunes evidències de xarxes d'interacció planta-animal menys complexes en illes oceàniques, només uns pocs estudis comparen comunitats insulars entre elles o amb comunitats continentals. En el tercer capítol, s'analitza la composició d'espècies i les propietats estructurals de xarxes quantitatives de visitants florals de dues comunitats de cada tipus d'illes: Illes Canàries (origen oceànic) i Illes Balears (origen continental). El major nombre d'espècies oportunistes i la presència d'espècies super-generalistes en l'illa oceànica va donar lloc a valors significativament més alts de connectància i anidament (ambdós quantitatius) en comparació amb l'illa continental. Com aquests dos paràmetres semblen estar associats amb l'estabilitat de les xarxes, les comunitats insulars oceàniques de pol·linització podrien ser menys vulnerables a les pertorbacions que les comunitats d'illes continentals.

La pèrdua de l'hàbitat i els canvis en la qualitat d'aquest, constitueixen una de les principals amenaces per a la supervivència tant de les plantes com dels seus visitants florals. L'impacte que aquestes pertorbacions poden causar sobre les interaccions entre espècies pot provocar canvis en tota l'estructura de la xarxa de visitants florals. En el quart capítol s'avalua l'efecte de la pèrdua d'hàbitat (més d'un 50% de la coberta vegetal) sobre els patrons d'interaccions entre les plantes i els insectes que visiten les seves flors en una comunitat de dunes de l'illa de Mallorca. Després de la pertorbació es produeix una disminució considerable tant del nombre d'espècies i abundància dels visitants florals com d'interaccions a la xarxa. Els escarabats, les mosques i les formigues foren els visitants florals més afectats, mentres que abelles i vespes foren els menys afectats probablement per la seva major capacitat de vol. S'observa també menor anidament, major nivell de selectivitat i modularitat a la comunitat després de la pèrdua d'hàbitat. En conjunt, aquest resultats indiquen que la xarxa de visitants florals estudiada serà menys robusta i tindrà menor resiliència enfront a futures pertorbacions.

En conclusió, gràcies a les tècniques d'anàlisi de xarxes complexes emprades en aquesta tesi hem pogut comprendre que usar un pes d'interacció adient a l'hora de construir les xarxes ecològiques ens aporta informació més realista i completa sobre les comunitats d'estudi. D'aquesta manera podem conèixer amb més detall el dinamisme i la capacitat de les espècies per assegurar la seva supervivència en diferents comunitats mitjançant diverses estratègies. Hem constatat també la major vulnerabilitat d’una comunitat després de la destrucció de gran part del seu hàbitat. Per tant, els resultats d’aquesta tesi poden contribuir a protegir, en la mesura del possible, els ecosistemes naturals enfront a la gran quantitat de pertorbacions causades per l’activitat humana.

Introducción general

Introducción general

Importancia de las interacciones planta-polinizador

Se estima que el 87.5 % de las especies de plantas con flor dependen de los animales para su polinización (Ollerton *et al.* 2011). A su vez, los polinizadores se benefician y dependen de la interacción con las plantas, ya que se alimentan del néctar y/o el polen de sus flores. Las interacciones entre las plantas y sus polinizadores son una de las relaciones mutualistas más importantes en los ecosistemas. Tanto es así que la polinización también se considera un servicio ecosistémico fundamental (Costanza *et al.* 1997; Hein 2009) y de vital importancia para el ser humano, ya que el 35 % de la producción mundial de los cultivos depende de los polinizadores (Klein *et al.* 2007). Desafortunadamente, este servicio ecosistémico tan importante para nuestra supervivencia está en peligro debido a diversos factores causantes del cambio global como son: la fragmentación de hábitats, los cambios en los usos del suelo, la introducción de especies exóticas o el aumento de la contaminación (Traveset & Richardson 2006; Hegland *et al.* 2009; Potts *et al.* 2010; Burkle *et al.* 2013; González-Varo *et al.* 2013; Spiesman & Inouye 2013). Todos estos factores también están provocando una disminución de las abejas a nivel global (Tylianakis 2013; Vanbergen *et al.* 2013).

En las últimas décadas, los estudios sobre las interacciones mutualistas planta-animal han pasado de enfoques tradicionales centrados en pares o grupos pequeños de especies a enfoques comunitarios que abarcan complejas redes de relaciones entre múltiples especies. Estos estudios a nivel comunitario han demostrado que la especialización recíproca entre especies es más bien rara y que la mayoría de las especies interactúan con diversos mutualistas, que pueden incluso pertenecer a diferentes clases u órdenes (Waser *et al.* 1996). Este tipo de investigaciones ha ofrecido una nueva perspectiva en el campo de la ecología, ya que con ellas se consigue una visión de la estructura de toda la comunidad, de la fuerza y dependencia de unas especies respecto a las otras y de la dinámica y mecanismos causantes, considerando las especies presentes en su conjunto y no como entidades aisladas. Estos trabajos son realmente importantes para entender y avanzar en el conocimiento de la ecología. Así, a la hora de estudiar la biodiversidad de un ecosistema es importante no solo determinar la riqueza de especies presentes, sino también las interacciones existentes entre ellas. Conocer las características de una comunidad, tanto a nivel global como sus particularidades, permite diseñar y aplicar mejores medidas destinadas a la protección de hábitats y especies, considerando también la conservación de la red de interacciones (Kaiser-Bunbury *et al.* 2010a; Tylianakis *et al.* 2010; Devoto *et al.* 2012; Valiente-Banuet *et al.* 2015).

Evolución de los estudios de redes planta-polinizador

Las técnicas de análisis de redes complejas, desarrolladas en el campo de las matemáticas por Erdös & Renyi (1959), resultan de gran utilidad en una gran cantidad de disciplinas de investigación, desde la neurobiología hasta Internet (Borgatti & Everett 1997; Strogatz 2001). Durante los años 70 los ecólogos empezaron a utilizar este tipo de aproximaciones para estudiar la multitud de interacciones que se dan en los ecosistemas (Paine 1966; May 1973; Cohen 1977; Pimm 1979). En las últimas décadas, el desarrollo de métodos computacionales más potentes, los avances de nuevas técnicas de análisis en otros campos de investigación como ciencias sociales, física, informática o matemáticas (Strogatz 2001; Albert & Barabasi 2002; Newman 2003; Watts 2004) y el incremento de diseños experimentales con observaciones a largo plazo, han permitido la descripción de redes de interacción cada vez más informativas y completas, que permiten conocer tanto las características de las comunidades como las de cada uno de sus componentes.

Los primeros estudios sobre redes mutualistas solo consideraban la presencia o ausencia de interacciones entre las especies, construyendo redes cualitativas o binarias, representadas por matrices de 1 y 0. En este tipo de redes todas las interacciones entre las plantas y sus visitantes florales se consideraban igualmente "importantes" (Jordano 1987; Memmott & Waser 2002; Bascompte *et al.* 2003). Gracias a esta primera "generación" de redes se logró la identificación de algunos patrones generales como la distribución de grado (*degree distribution*) que sigue una ley de potencia o potencia truncada (Waser *et al.* 1996; Jordano *et al.* 2003), el anidamiento (*nestedness*) (Bascompte *et al.* 2003) o la modularidad (*modularity*) (Olesen *et al.* 2007). Estas propiedades de las redes de interacción son muy importantes porque están muy relacionadas con los mecanismos que permiten el funcionamiento de los ecosistemas que describen (Gómez *et al.* 2011).

Sin embargo, los ecólogos no tardaron en reconocer que la representatividad de las redes binarias era limitada, ya que no son capaces de describir la gran heterogeneidad que existe en la frecuencia de interacción entre las distintas especies. Por tanto, se hizo necesaria la descripción de redes cuantitativas, representadas por matrices donde el valor de cada celda indica el peso de cada interacción. Para describir las propiedades de estas redes cuantitativas también se desarrollaron nuevas medidas y parámetros, facilitando su interpretación biológica (Bersier *et al.* 2002; Blüthgen *et al.* 2006). Otra característica muy importante de estos parámetros cuantitativos es que están menos afectados por sesgos en el esfuerzo de muestreo y, por tanto, los hace más útiles a la hora de comparar diferentes redes (Banašek-Richter *et al.* 2004; Blüthgen *et al.* 2008; Vizentin-Bugoni *et al.* 2016).

El número de estudios sobre polinización que utiliza redes cuantitativas ha crecido en los últimos años, aunque existe una gran variabilidad en la forma en que los investigadores toman los datos en el campo y construyen las matrices de interacción. Esta variabilidad es debida, principalmente, a la gran heterogeneidad de hábitats muestreados (bosques, sabanas, praderas, etc.) y al objetivo final de cada estudio, pero también se debe a la falta de consenso sobre la variable más adecuada a utilizar como peso de las interacciones. La medida más simple utilizada en las redes de polinización es el número de visitas de los polinizadores a cada especie de planta (Elberling & Olesen 1999; Olesen *et al.* 2002; Bartomeus *et al.* 2008; Ebeling *et al.* 2008; Weiner *et al.* 2011). Otros estudios, sin embargo, consideran que es mejor utilizar el número de flores visitadas por polinizador, ya que se considera un buen predictor del efecto total sobre el rendimiento reproductivo per cápita de las plantas visitadas (Vázquez *et al.* 2005). Sin embargo, la abundancia de recursos disponibles en la comunidad (*e.g.* flores), también puede ser importante para determinar las frecuencias de interacción. Los índices de especialización complementaria, tanto a nivel de especies (d') como a nivel comunitario (H_2') (Blüthgen *et al.* 2006), representan un intento de dar importancia a dicha disponibilidad de recursos. Sin embargo, la abundancia de flores en estos casos suele estimarse indirectamente basándose en las frecuencias totales de visitas, que no son necesariamente buenos estimadores de la disponibilidad real de recursos. Hay estudios en los que sí se integra la abundancia de flores en la cuantificación de las interacciones (Kaiser-Bunbury *et al.* 2009, 2011), donde el peso de cada interacción es el resultado del número total de visitas/flor estandarizado por el tiempo de censo y por la abundancia floral de cada especie vegetal.

La gran variabilidad existente en la toma y análisis de datos hace que la comparación entre estudios sea difícil, ya que la topología de las redes descritas puede verse afectada por los diferentes sesgos metodológicos (Gibson *et al.* 2011; Rivera-Hutinel *et al.* 2012; Chacoff *et al.* 2012; Fründ *et al.* 2016). El peso de interacción puede influir en las propiedades de las redes mutualistas, pudiendo dar lugar a diferentes interpretaciones de cómo se ven afectadas las comunidades ecológicas. Para evitar sesgos y errores de interpretación y conseguir avanzar hacia una descripción más funcional de la estructura de las redes ecológicas, es necesario que estos pesos de interacción sean cuantificados de la manera más precisa y descriptiva posible.

¿Qué sabemos sobre las especies con las que interactúan los más generalistas y los más especialistas de una comunidad?

El análisis de redes facilita la síntesis y la comprensión de la complejidad de interacciones que se encuentran en las comunidades naturales y, por lo tanto, es una herramienta poderosa para revelar información sobre el grado de especialización de las especies que interactúan entre sí en una comunidad (Joppa *et al.* 2009; Junker *et al.* 2013).

El nivel de especialización de las interacciones planta-polinizador ha sido foco de interés en investigación desde hace siglos (Mitchell *et al.* 2009 y sus referencias). A pesar de ello, no existe una definición del todo precisa de especialización en el estudio de la polinización (Olesen 2000; Ollerton *et al.* 2007; Dormann 2011). Lo que parece estar claro es que especialización y generalización son los extremos de un gradiente continuo (Johnson & Steiner 2000) y son conceptos relativos que dependen del contexto: las especies pueden tener diferentes niveles de especialización en diferentes lugares, pudiendo comportarse como especies generalistas en un entorno con pocos polinizadores y especialistas en un entorno rico en polinizadores (Waser *et al.* 1996). La cuantificación del nivel de especialización ecológica depende en gran medida de los datos utilizados, el organismo estudiado y el mecanismo ecológico de interés. Por ejemplo, la especialización en el comportamiento versus la especialización de hábitat (Devictor *et al.* 2010).

En las redes de interacción binarias, la especialización de cada especie se define cualitativamente como el número total de especies con las que interactúa (grado, *species linkage level*, *L*). Las especies que visitan o son visitadas por un amplio número de especies se consideran generalistas (*e.g.* un polinizador que visita una gran variedad de especies de plantas), mientras que las especies que visitan o son visitadas por pocas especies se consideran especialistas (*e.g.* especies de polinizadores que visitan una sola especie de planta). Con el uso de datos cuantitativos en las redes de interacción se planteó un nuevo concepto de especialización definiendo *d'*, un índice de especialización complementaria a nivel de especie (Blüthgen *et al.* 2006). Este índice tiene en cuenta no solo el número de especies con las que se interactúa, sino también su disponibilidad en la comunidad. No es lo mismo interactuar con una especie muy abundante que interactuar con una especie rara en la comunidad. Por tanto, *d'* puede considerarse un índice de selectividad (término que utilizaremos de aquí en adelante). Un polinizador que visita una planta proporcionalmente a su disponibilidad en la comunidad se considera oportunista, mientras que un polinizador que visita plantas raras desproporcionadamente más a menudo que las más comunes se considera selectivo. Del mismo modo, una planta se considera oportunista si recibe la visita de los polinizadores en proporción a su disponibilidad y será selectiva si recibe desproporcionadamente más visitas de los polinizadores raros que de los más comunes.

Varios estudios han explorado los rasgos que contribuyen al nivel de generalización de las especies en las redes. Características como la fenología y la abundancia (Dupont *et al.* 2003; Vázquez & Aizen 2003; Olesen *et al.* 2008; Stefanescu & Traveset 2009; Zhang *et al.* 2011; Junker *et al.* 2013), el color de la flor (Renoult *et al.* 2015) y la morfología de flores e insectos (Chamberlian *et al.* 2014) pueden determinar los niveles de generalización y selectividad de cada especie. Sin embargo, todavía se desconoce si los rasgos de las especies con las que interactúan las especies más generalistas, o las más oportunistas, difieren de los que presentan aquellas especies con las que interactúan las especies más especialistas o selectivas. Los rasgos o mecanismos que regulan las interacciones entre especies pueden ser considerados como la "micro-estructura" de una red (Junker *et al.* 2010; Kaiser-Bunbury *et al.* 2014). Por tanto, a la hora de decidir con qué especies interactuar, la abundancia y/o riqueza funcional de las especies de una comunidad, es decir, el número de grupos funcionales para los visitantes florales o número de familias de plantas, pueden ser factores importantes para determinar dicha micro-estructura y su grado de vulnerabilidad frente a posibles perturbaciones.

Las interacciones entre las plantas y sus visitantes florales varían durante y entre temporadas reflejando los cambios en la composición de la comunidad (Herrera 1988; Olesen *et al.* 2008; Dupont *et al.* 2009; Lázaro *et al.* 2010; Olesen *et al.* 2011; Fang & Huang 2012; Rasmussen *et al.* 2013). Conocer los factores que causan este tipo de dinámica temporal de las especies, y sus consecuencias ecológicas y evolutivas, es crucial para entender mejor la micro-estructura de las comunidades planta-polinizador y elaborar proyectos de conservación más adecuados. Por tanto, otro aspecto a tener en cuenta al estudiar el nivel de generalización de las especies es que la selección de las características de las especies con las que interactúan puede cambiar a lo largo de la temporada, por ejemplo, cambiando la elección de las especies dependiendo del contexto floral.

Características de las redes de visitantes florales en islas

Las islas son ecosistemas ideales para el estudio de determinados procesos ecológicos debido a su baja riqueza de especies, alto nivel de endemicidad y extensión limitada en comparación con áreas continentales. En base a sus rasgos geológicos, podemos clasificar las islas como oceánicas o continentales (fragmentos continentales según Whittaker & Fernández-Palacios 2007). Estas dos clases de islas se diferencian principalmente por su biota residente inicial. Las islas continentales tienen una biota inicial idéntica a la de las zonas continentales de las que proceden (Thornton 2007), mientras que las islas oceánicas, generalmente formadas a partir de actividad volcánica submarina, están inicialmente desprovistas de vida y, por lo tanto, su biota es enteramente el resultado de la dispersión a larga distancia y de la especiación *in situ*.

Las islas, particularmente las oceánicas, presentan floras y faunas disarmónicas, es decir, contienen diferentes proporciones de los taxones que se encuentran en las zonas de origen continental y muchas veces carecen completamente de grupos enteros de taxones (*e.g.* grandes mamíferos terrestres). Para colonizar una isla, una especie debe dispersarse desde la parte continental, establecerse y reproducirse (Carlquist 1974). La disarmonía de las biotas insulares es el resultado de los filtros ecológicos que regulan cada uno de estos procesos. Por ejemplo, los visitantes florales con probóscides largas, especialmente las abejas, están típicamente sub-representadas en comunidades de islas oceánicas (Inoue 1993). Por el contrario, pequeños insectos (moscas, escarabajos, avispas y polillas pequeñas) tienen mayor representación, posiblemente debido a su mayor capacidad de dispersión facilitada por fuertes vientos (Barrett 1996). En general, las redes de polinización en islas oceánicas muestran un empobrecimiento de polinizadores (Gillespie & Roderick 2002; Traveset *et al.* 2016), lo que se traduce en redes de interacción con una baja proporción de especies animales respecto a las vegetales (A:P; Olesen & Jordano 2002; Trøjelsgaard & Olesen 2013). En las islas continentales, la disarmonía de la biota es menos pronunciada, aunque puede aumentar con el tiempo, en función del aislamiento, como consecuencia de la extinción de taxones ancestrales procedentes del continente (Gillespie & Roderick 2002).

Otra característica importante de las comunidades de islas oceánicas es la presencia de especies “supergeneralistas" (*sensu* Olesen *et al.* 2002), es decir, especies con niveles muy altos de generalización (gran número de especies con las que interactúan) en comparación con las demás especies de la comunidad (*e.g.* Kaiser-Bunbury *et al.* 2009; Padrón *et al.* 2009; Traveset *et al.* 2013). Menos información existe respecto al grado de selectividad de las especies (índice de especialización complementaria (*d’*); Blüthgen *et al.* 2006) en estos dos tipos de islas. Se podría esperar que un polinizador, al alcanzar una nueva isla, independientemente de su origen (continental u oceánico) y suponiendo que no hubiera restricciones morfológicas en las interacciones con las flores, se integrará en la red de polinización mediante la interacción con las especies vegetales más abundantes, actuando así como oportunista, es decir, mostrando una baja selectividad. Sin embargo, también cabría esperar que las especies fuesen más oportunistas en las islas oceánicas, debido al fenómeno de relajación ecológica y a la gran diversidad de nichos por explotar al existir una menor competencia inter-específica con respecto a islas continentales o zonas continentales (MacArthur *et al.* 1972; Blondel *et al.* 1988). Esta relajación ecológica se puede observar también a nivel de las interacciones en la comunidad debido a la posibilidad de establecer nuevas y variadas interacciones, como es el caso de las aves en las Islas Galápagos (Traveset *et al.* 2015).

El uso de los análisis de redes en comunidades insulares también ha contribuido a la comprensión de la importancia de mantener y restaurar la integridad de las interacciones entre especies en las islas (Kaiser-Bunbury *et al.* 2010a). En las comunidades insulares, las especies son más vulnerables a las perturbaciones humanas debido a sus pequeños tamaños de población y rangos de distribución (Cox & Elmqvist 2000; Simberloff 2000). A pesar de la importancia del enfoque de redes de interacción, pocos son los proyectos de conservación y restauración que incorporan esta información sobre la estructura de la comunidad y la resiliencia de las comunidades restauradas frente a posibles perturbaciones en sus planes de actuación (Memmott 2009; Kaiser-Bunbury *et al.* 2010a; Menz *et al.* 2011; Devoto *et al.* 2012).

Cambio global y redes de visitantes florales

Como hemos visto anteriormente, las interacciones entre las plantas y sus polinizadores juegan un papel crucial en la conservación de la biodiversidad y el funcionamiento de los ecosistemas. La pérdida de hábitat y los cambios en la calidad del mismo representan las principales amenazas para estas interacciones y, por lo tanto, para la supervivencia tanto de las plantas como de sus polinizadores, pudiendo provocar cambios en la estructura de la red (Tylianakis *et al.* 2007; Hagen *et al.* 2012; Ferreira *et al.* 2013). La disminución de recursos florales y de zonas adecuadas para anidar, provocadas por modificaciones del hábitat, puede reducir la disponibilidad y diversidad de polinizadores, influyendo en los niveles de polinización cruzada y, en última instancia, afectando a la producción de frutos (Aguilar *et al.* 2006; Winfree *et al.* 2011; Hagen *et al.* 2012; Viana *et al.* 2012; Ferreira *et al.* 2013; Vanbergen *et al.* 2014). Del mismo modo, el éxito reproductivo de las plantas también puede verse afectado por cambios en su propia densidad de población, cambiando la conectividad de sus polinizadores en diferentes escalas espaciales, de metros a kilómetros (Vanbergen *et al.* 2014). Dado que la polinización es un valioso servicio ecosistémico (Klein *et al.* 2007), es crucial evaluar la forma en la que los patrones de interacción pueden ser modificados (*e.g.* Kaiser-Bunbury *et al.* 2010b; González *et al.* 2011; Ferreira *et al.* 2013).

Las interacciones especialistas están consideradas las más vulnerables a la reducción del hábitat y, por lo tanto, es común observar un aumento del número de especies generalistas después de una perturbación (Ashworth *et al.* 2004; Aizen *et al.* 2012; Vanbergen *et al.* 2014). También se ha observado en diferentes sistemas una disminución en el anidamiento de la red en hábitats perturbados (Vanbergen *et al.* 2014; Moreira *et al.* 2015; Revilla *et al.* 2015), lo que ha llevado a predecir una menor robustez y resistencia de las redes de visitantes florales a futuras perturbaciones (Bascompte 2009; Fortuna *et al.* 2013) así como una disminución en el número de especies que coexisten (Bastolla *et al.* 2009). La pérdida de especies y sus interacciones en una red perturbada también puede conducir a la formación de compartimentos aislados dentro de la red (Spiesman & Inouye 2013) con un mayor riesgo de desaparecer como consecuencia de perturbaciones futuras en comparación con especies presentes en una red muy conectada. Diferentes modelos muestran que la distribución del número de interacciones pasa a ser muy sesgada cuando se pasa de un hábitat prístino a otro perturbado, y que existe un umbral crítico de destrucción del hábitat en el cuál las redes mutualistas responden con un colapso repentino (Keitt 2009; Kaiser-Bunbury *et al.* 2010b; Viana *et al.* 2012; Fortuna *et al.* 2013).

Las especies altamente conectadas dentro de sus módulos/compartimentos y con otras especies en otros módulos (*hubs*), junto con las especies que enlazan diferentes módulos (los conectores) son consideradas especies clave para el mantenimiento de la estructura de red (Olesen *et al.* 2007). Si una alteración provoca su extinción, la red puede romperse y conducir a una cascada de extinción (Kaiser-Bunbury *et al.* 2010b; Fortuna *et al.* 2013). El papel funcional de cada especie dentro de la red puede cambiar notablemente a lo largo de un gradiente de alteración del hábitat, por lo que, por ejemplo, una especie de planta puede actuar como hub en un lugar pero como conector en otro (Campos-Navarrete *et al.* 2013; Nielsen & Totland 2014).

Principalmente debido a un mayor aislamiento de los parches de hábitat y a la reducción de la complejidad del paisaje causada por la simplificación del medio ambiente (Ferreira *et al.* 2013 y sus referencias), un patrón frecuente observado después de la pérdida y fragmentación del hábitat es un cambio en la diversidad de polinizadores. Sin embargo, se espera que no todas las especies de polinizadores respondan de manera similar a cambios en el hábitat. Se sabe que las abejas solitarias se ven más afectadas por la destrucción del hábitat que las abejas sociales, posiblemente debido a que las primeras son más especialistas (Williams *et al.* 2010; Ferreira *et al.* 2015). Por otra parte, si bien en algunos casos la abundancia de visitantes florales y la riqueza de especies están asociadas con la abundancia de flores (Hegland & Boeke 2006; Hagen & Kraemer 2010), otros estudios consideran que el factor subyacente para el cambio temporal en la diversidad de polinizadores es la diversidad de plantas (Potts *et al.* 2003; Ghazoul 2006; Blüthgen *et al.* 2007; Ebeling *et al.* 2008). Existe poca información sobre cómo los diferentes grupos funcionales de polinizadores que conviven en una comunidad responden a perturbaciones del hábitat (Burkle *et al.* 2013; Aguirre-Gutiérrez *et al.* 2015; Lázaro *et al.* 2016).

Estructura y objetivos de la tesis doctoral

Estructura y objetivos de la tesis doctoral

En esta tesis se exploran diferentes aspectos de las redes de polinización en varias comunidades de los archipiélagos de Baleares y Canarias. Las comunidades insulares son de especial interés por tratarse de sistemas frágiles, de extensión limitada y un alto nivel de endemicidad. A esta fragilidad natural hay que añadirle la gran vulnerabilidad de estas zonas debido a la presión urbanística y al aprovechamiento con fines turísticos. Usando la perspectiva global que ofrecen las redes de interacciones mutualistas, la presente tesis aporta información relevante que puede ser utilizada en el ámbito de la conservación y la restauración de ecosistemas insulares.

Esta memoria de tesis doctoral está estructurada en los siguientes capítulos:

El ***primer capítulo*** es de carácter teórico y el principal objetivo es evaluar cómo la utilización de diferentes medidas del peso de las interacciones en las redes cuantitativas influye en la estructura de la red de visitantes florales. Los pesos utilizados para realizar las comparaciones en este trabajo incluyen, progresivamente, información cada vez más detallada de las interacciones (número de visitas, tiempo total de censo, número de flores observadas, número de flores visitadas y abundancia total de flores de cada especie de planta en la comunidad). Para avanzar hacia una descripción más funcional de la estructura de las redes ecológicas, se necesitan pesos de interacción lo más precisos posible, minimizando potenciales sesgos y/o errores de interpretación.

Una vez seleccionado el tipo de peso de interacción más adecuado para realizar los diferentes análisis, el objetivo del ***segundo capítulo*** es profundizar en el estudio del nivel de generalización/selectividad de las especies presentes en las redes, evaluando su relación con las características de las especies con las que interactúan (sus abundancias y riqueza funcional) y la variación temporal de estas relaciones. Esta información es especialmente interesante para el diseño de planes de conservación de las especies más especialistas y más selectivas de la comunidad, que suelen ser las más vulnerables frente a las perturbaciones.

Usando una perspectiva más amplia, propia de estudios biogeográficos, en el ***tercer capítulo*** se estudian las redes de visitantes florales de dos islas con distinto origen: una oceánica (Lanzarote, Canarias) y una continental (Mallorca, Baleares). El objetivo de este estudio es comparar la composición de especies, el grupo de visitantes florales predominante y la estructura de las redes mutualistas de cuatro comunidades costeras.

Esta información nos permitirá conocer el grado de similitud existente entre las comunidades estudiadas, considerando las diferencias de origen, área, edad y fuentes de colonización de las islas.

Por último, el objetivo del ***cuarto capítulo*** es estudiar los efectos de una gran perturbación urbanística, causante de la pérdida de más del 53% del hábitat de una comunidad, sobre la red de visitantes florales. La pérdida de especies, sus interacciones y, en general, la disminución de la biodiversidad debido a perturbaciones provocadas directamente por la acción del ser humano es una de las problemáticas actuales que puede ser estudiada con conocimientos específicos a nivel de comunidad, como los obtenidos a través del análisis de las redes ecológicas.

Capítulo 1

Efecto de los diferentes pesos de las interacciones sobre la estructura de las redes cuantitativas de visitantes florales

Chapter 1

How different link weights affect the structure of quantitative flower-visitation networks

El contenido de este capítulo ha sido publicado como:

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Resumen

A pesar de la gran cantidad de estudios que evalúan la estructura de las redes mutualistas cualitativas y cuantitativas, poco se sabe acerca de cómo las diferentes formas de medir el peso de las interacciones, es decir la importancia de cada par de interacciones, pueden influir en los parámetros de red que se utilizan para describir este tipo de estructuras. El uso de un adecuado "peso” es especialmente importante si queremos avanzar hacia una perspectiva más funcional en estudios de redes ecológicas. En este trabajo evaluamos cómo el uso de cinco pesos de interacción diferentes, empezando por el más simple (el número de visitas) e incluyendo progresivamente información del tiempo total de censo, número de flores observadas, número de flores visitadas y la abundancia de flores total de cada especie de planta en la comunidad, influyen considerablemente en los descriptores de la estructura de red utilizados. Se analizaron diferentes parámetros a nivel de red: anidamiento cuantitativo (*weighted nestedness*), número efectivo de plantas visitadas por visitantes florales (*flower-visitor generality*), número efectivo de visitantes florales por planta (*plant generality*), índice de especialización complementaria H_2', homogeneidad de las interacciones (*interaction evenness*) y diversidad de las interacciones (*interaction diversity*) y dos parámetros a nivel de especie: el índice de especialización *d’* y la fuerza de las interacciones (*strength*). Se construyeron dos redes de visitantes florales cuantitativas de dos comunidades diferentes muestreadas durante dos años consecutivos, en las que también se midió de forma independiente la abundancia de flores de cada especie vegetal. Los resultados mostraron que el tipo de peso de interacción utilizado puede alterar significativamente la estructura de la red. Se encontró una clara tendencia hacia interacciones más especializadas (disminución de *flower-visitor generality* y aumento de H_2' y *d’*), una mayor heterogeneidad en la frecuencia de las interacciones (menor *interaction evenness* e *interaction diversity*) y un mayor anidamiento cuantitativo cuando el peso de interacción gana en complejidad. Sin embargo, estandarizar sólo por el tiempo total censado tuvo poco efecto en los parámetros de red. Nuestros hallazgos resaltan la importancia de considerar cuidadosamente el peso de interacción más apropiado para cada estudio de redes ecológicas, haciendo hincapié en que las comparaciones entre las redes que utilizan diferentes pesos podrían dar lugar a resultados erróneos y, por lo tanto, a malas interpretaciones ecológicas de las estructuras de red.

How different link weights affect the structure of quantitative flower-visitation networks

Introduction

In the last decades, the focus of research in mutualistic plant-animal interactions has shifted from traditional studies on interactions between pairs of species to community-level studies. This change in perspective was promoted by increasing evidence that reciprocal specialization between species is rather rare and that most species interact with multiple mutualistic partners (Waser *et al.* 1996). The community perspective in ecology was further fueled by developments in complex network analysis techniques profitably used in a multitude of research disciplines (Borgatti & Everett 1997; Strogatz 2001; Montoya *et al.* 2006).

Early studies of mutualistic interactions at the community level only considered the presence or absence of an interaction between species. In these binary networks, all realized links are considered equally 'important' (*e.g.* Jordano 1987; Memmott & Waser 2002; Bascompte *et al.* 2003). This first "generation" of networks allowed the identification of some general patterns, such as the right-skewed distribution of links per species (Waser *et al.* 1996; Jordano *et al.* 2003), nestedness (Bascompte *et al.* 2003), asymmetry of interactions (Vázquez & Aizen 2004; Bascompte *et al.* 2006) and modularity (Olesen *et al.* 2007). These network properties may play important roles for the functioning of the systems they describe (Gómez *et al.* 2011). However, it was soon widely recognized by ecologists that the accuracy of such binary networks was limited as they fail to describe the strong heterogeneity in the frequency of interactions among species observed in the field. Thus, the development of weighted measures that describe the intensity of exchange of benefits between partners in mutualistic interactions (their interaction strength) has become necessary, increasing the reliability of network properties and facilitating their biological interpretation (Bersier *et al.* 2002; Blüthgen *et al.* 2006).

The number of studies using a quantitative network approach has also grown in recent years. In food webs, interaction strength is usually based on the energy flow through the system. In mutualistic networks, by contrast, there is great variability in the way researchers gather field data and construct interaction matrices owing to the huge heterogeneity in habitat types (forest, savannahs, meadows, etc.) and to particular study aims. Such variability makes comparisons across studies difficult. Moreover, Gibson *et al.* (2011) have recently shown that the topology of plant-pollinator networks can be affected by methodological biases. A review of 22 published studies analyzing the structure of weighted plant-pollinator networks shows the heterogeneity across these studies, which differ both in link weight as well as in total census time (Table 1.1).

The simplest and most commonly used link weight in pollination networks is the number of pollinator visits to each plant species. The number of flowers visited by a pollinator is another measure claimed to be a good predictor of the per capita reproductive performance of insect-pollinated plants and used as a proxy of the functional impact of an interaction (Vázquez *et al.* 2005). Still, another measure of link strength takes into account the abundance of available resources (flowers in the case of pollination networks) in the entire community, which may be important in determining which flowers are visited by a given flower-visitor. The recently developed species-level (*d'*) and network-level (H_2') complementary specialization indices (Blüthgen *et al.* 2006) represent an attempt to account for such resource availability. However, floral abundance is usually estimated indirectly based on visitation frequency totals, which are not necessarily good proxies of actual resource availability. One recent study has tested the effect of independently measured flower availability on several network properties such as network specialization, species richness and flower-visitor abundance (Weiner *et al.* 2011), finding that flower abundance is important for the distribution of visitors within a site. However, Lopezaraiza-Mikel *et al.* (2007) found that higher visitation rate is not exclusively explained by flower abundance. The only studies that integrate floral abundance into the link weight measure are those by Kaiser-Bunbury *et al.* (2009) and Kaiser-Bunbury *et al.* (2011). Although it would also be ideal to account for flower-visitor abundance, such information is hardly available, owing to the difficulty of tracking insects.

Our aim here is to examine how link weight may affect properties of mutualistic networks, possibly leading to different interpretations regarding their functional consequences for ecological communities (Gómez *et al.* 2011). By using new empirical data from two different communities during 2 years, we compare five different types of link weights, which include progressively more detailed information, available from studies based on plot observations, on the observed plant-pollinator interactions. The simplest weight we use is the number of insect visits to flowers. Then, we standardize this number by total observation time, getting a visitation rate measure. The third link weight considers the number of flowers observed in each census. In a next step, information on

Table 1.1. List of the 22 published flower-visitation network studies included in the review about the differences between the sampling methods used in each study. The table summarizes: the link weight used in the network analysis, observation time (time spent observing a specific number of flowers of a plant species in each census) and study period (number of field work months per year, number of study years and, when it is know, number of total field work days in brackets).

Reference	Link weight	Observation time	Study period
Mosquin & Martin (1967)	No. of visits	n.a.	3 days
Small (1976)	No. of visits	10 h / plant	3 months
Schemske *et al.* (1978)	No. of visits	n.a.	3 months, 2 years
Motten (1982)	No. of visits / flower/ h	30 min / census	5 years
Primack (1983)	No. of visits	n.a.	2 seasons (18 days)
Primack (1983)	No. of visits	n.a.	3 months, 2 years
Primack (1983)	No. of visits	n.a.	3 months (24 days)
Barrett & Helenurm (1987)	No. of visits	n.a.	5 months, 3 years
Kato *et al.* (1990)	No. of visits	10 min / census	7 months, 4 years (31 days)
Inoue *et al.* (1990)	No. of visits	6 h / day	8 months, 4 years (48 days)
Elberling & Olesen (1999)	No. of visits	10 h / plant	3 months
Memmott (1999)	No. of visits	Transects (no time)	1 month
Olesen *et al.* (2002)	No. of visits	30 min / census	1 month, 2 years
Olesen *et al.* (2002)	No. of visits	30 min / census	1 month
Vázquez & Simberloff (2002, 2003)	(Proportion of visits x total no. visits) / total census	10 min / census	1 season
Ollerton *et al.* (2003)	No. of visits	63 h	2 months
Ebeling *et al.* (2008)	No. of visits	6 min / census	2 years (17 days)
Bosch *et al.* (2009)	No. of visits	4 min / census	4 months (24 days)
Kaiser-Bunbury *et al.* (2009)	Total no. of visits / total no. of flowers / h	30 min / census	6 months (12 days)
Alarcón *et al.* (2008, 2010)	No. of visits	20-40 min per transect	6 weeks, 2 years (12 days)
Weiner *et al.* (2011)	No. of visits	n.a.	4 months
Chacoff *et al.* (2012)	No. of visits	5 min / census	4 months, 4 years

the flower-visitor's behavior is included, specifically the proportion of flowers visited per time unit. Finally, the fifth and most complex link weight additionally includes the independently estimated flower abundance of each flowering species. More than discerning which link weight is best to include in pollination networks, which will depend on the question being addressed, the type of network descriptors chosen and the methodology applied in the fieldwork, our objective in this study is to assess the consistency of network parameters when different link weights are used for the same interactions. If such parameters do differ significantly, it will imply that link weight must be standardized when networks are compared, *e.g.* across habitats, through time or along ecological gradients.

Materials and methods

Study sites and sampling procedure

The study was carried out in two sites on Mallorca (Balearic Islands) in two consecutive years (2009 and 2010): Son Bosc (39º46’28.11’’N; 3º07’45.34’’E) is a diverse dune marshland in the north, whereas Sa Coma de n’Arbona (39º47’59.51’’N; 2º47’07.81’’E) is located on the western-exposed slope of Puig Major, the highest peak of the Serra de Tramuntana mountain range in the northwest of the island, at *ca.* 1200 m above sea level (see further description of the study sites in Supplementary Material 1A). In Son Bosc, sampling took place between April and July whereas in Puig Major (where the flowering season is delayed due to its higher altitude) the study was performed between May and August.

Flower abundance was estimated every two weeks at each site, counting the number of all open flowers of each flowering plant encountered within permanent belt transects. In Son Bosc, 13 and 10 belt transects (50 m x 2 m) in 2009 and 2010 were surveyed, covering a total area of 1300 m^2 and 1000 m^2, respectively. In Puig Major, 9 belt transects (three 20 m × 2 m, four 25 m × 2 m, one 30 m × 2 m and one 40 m × 2 m) were sampled both years, covering a total area of 460 m^2. Flower abundance was calculated for each species as the number of open flowers divided by the total area surveyed. For species with tightly clustered inflorescences (*e.g.* the capitula of Asteraceae) we scored only single inflorescences.

All plants in bloom were censused throughout the flowering season. Once or twice per week we made insect censuses on flowers from haphazardly selected individuals and from 10:00 am to 17:00 pm on calm and sunny days. Insect visits to flowers were recorded from a distance of approximately 1m to minimize interference with insect behavior. We recorded contacts between insects and flowers during three-minute periods at Son Bosc and five-minute periods at Puig Major (longer here due to lower insect activity at high altitudes). During each census we recorded: (a) identity of flowering plant species; (b) number of open flowers of each individual plant observed; (c) identity of each flower visitor (species name if possible or morphotype otherwise); (d) number of individuals of each species visiting flowers and (e) number of flowers visited by each flower visitor. Unidentified insects in the field were collected for further identification by taxonomists. Plant identification followed Beckett (1993) and Western Mediterranean Virtual Herbarium (http://herbarivirtual.uib.es).

Total time spent censusing flower-visitor interactions was 42:18 h (2009) and 49:39 h (2010) in Son Bosc and 13:20 h (2009) and 38:15 h (2010) in Puig Major. Total number of censuses differed across species, sites and years proportional to the duration of a plant species flowering period in the community.

Construction of quantitative flower-visitation networks

For each community, we built five types of matrices each one using a different link weight as follows:

> ***M1: no. of visits***. Number of visits of an insect species to flowers of a plant species was used as link weight.
>
> ***M2: no. of visits/time***. Number of visits was standardized by total observation period spent on each plant species during the entire season.
>
> ***M3: no. of visits per flower/time***. Same as *M2* but number of visits was also standardized by number of open flowers observed in each censused individual. This is a way to quantify insect visits on a floral basis.
>
> ***M4: proportion of flowers visited/time***. Same as *M3* but considering number of flowers visited by each insect species instead of number of visits. Thus, this weighting of interactions considers the proportion of flowers of a given plant species visited by each flower-visitor species in each census (flowers visited/flowers observed).
>
> ***M5: (Proportion of flowers visited/time) × flower abundance***. Same as *M4* but considering also the estimated total number of flowers of each plant species in the community that was available each day of census.

To minimize potential artifacts due to temporally “forbidden links” (*sensu* Jordano *et al.* 2003), we constructed a total of 12 temporal interaction networks (“temporal snapshots”, Kaiser-Bunbury *et al.* 2010b), one per month in Son Bosc and one for every 2 months in Puig Major (as network sizes in the latter community were smaller; Table 1.2). The temporal snapshots reflect network structures more realistically than full-season networks as they include those species that coexist in time. Thus, a total of 60 matrices (12 temporal networks x five link weights) were analyzed.

Network parameters

For each of the 60 matrices we calculated eight of the most widely used quantitative descriptors of the structure of weighted ecological interaction networks. At network level we calculated nestedness (weighted *NODF*), complementary specialization H_2', plant generality (G_p), flower-visitor generality (G_{fv}), interaction evenness (*IE*) and interaction diversity (*ID*). At species level we obtained species specialization *d'* and strength for plants and flower visitors (see Supplementary Material 1B). We used the *bipartite* package version 1.17 (Dormann *et al.* 2009) run in R 2.11.

Statistical analysis

General linear mixed models with link weight as a fixed factor, and month nested within year and year nested within site (Son Bosc and Puig Major) as random factors were used to test whether link weight explained significant variation in network parameters, one at a time, as response variables. If the minimal adequate model based on an AIC model selection procedure included the fixed factor link weight, a posteriori Tukey’s test with the general linear hypothesis function (glht; ‘many-to-one comparison procedure’ [Dunnett 1955]) was performed to identify which matrices differed from each other. The response variables G_p, G_{fv}, mean d_p', mean d_{fv}', mean St_p, mean St_{fv}, mean weighted St_p, and mean weighted St_{fv} were log-transformed for a better fit with a normal distribution of the residuals. These analyses were done using the packages *lme4* (Bates *et al.* 2011) and *multcomp* (Hothorn *et al.* 2008) in R 2.11.

In order to confirm that our results describe patterns that are different from random, we compared them with an appropriate null model (Dormann *et al.* 2009) (see Supplementary Material 1C: Figs. SM 1.1 - SM 1.2).

Table 1.2. Number of flower-visitor species, flowering plant species and their interactions (individual visits) for each of the 12 temporal networks of each site.

Temporal Networks	Flower-visitor species	Plant species	Total interactions
Son Bosc April 2009	30	40	756
Son Bosc May 2009	66	50	904
Son Bosc June 2009	60	22	539
Son Bosc July 2009	31	18	477
Son Bosc April 2010	42	33	814
Son Bosc May 2010	74	48	1233
Son Bosc June 2010	70	40	871
Son Bosc July 2010	41	21	277
Puig Major May-June 2009	35	17	181
Puig Major July-August 2009	31	11	221
Puig Major May-June 2010	41	21	121
Puig Major July-August 2010	48	19	376

Results

The number of individual visits observed in one ‘observation unit’ (3 or 5 min census) varied much across plant species, ranging from 0 to 36. In Son Bosc, we observed a total of 164 flower-visitor species visiting 80 plant species and recorded a total of 5871 interactions (*i.e.* individual visits) during the 2 years, whereas in Puig Major we found 93 flower-visitor species visiting 34 plant species, recording a total of 899 interactions during the same 2 years. Table 1.2 shows this information for each of the 12 temporal networks.

Effect of link weight type on network properties

M1 vs. *M2*: Standardizing visitation frequency by total observation time resulted in an increase of H_2' (Fig. 1.1B; $z = 3.31$, $p < 0.01$), mean d_p' (Fig. 1.2C; $z = 3.83$, $p < 0.01$) and mean d_{fv}' (Fig. 2D; z = 6.49, p < 0.001), but no significant change was detected in other parameters (Figs. 1.1 - 1.2).

M2 vs. *M3*: When accounting for number of flowers of each individual plant observed in each census, four parameters decreased: *IE* (Fig. 1.1E; $z = -3.03$, $p < 0.05$), ID_{fv} (Fig. 1.1F; $z = -2.87$, $p < 0.05$), ID_p (Fig. 1.1F; $z = -5.63$, $p < 0.001$) and mean weighted St_p (Fig.

1.2E; $z = -4.87$, $p < 0.001$), while two parameters increased: weighted *NODF* (Fig. 1.1A; $z = 2.83$, $p < 0.05$) and mean d_{fv}' (Fig. 1.2D; $z = 4.95$, $p < 0.001$).

M3 vs. *M4*: When using number of visited flowers instead of number of visits as link weight (standardizing by time and flowers observed), parameters did not change significantly, except for mean weighted St_{fv}, which decreased (Fig. 1.2F; $z = -3.91$, $p < 0.001$).

M4 vs. *M5*: The inclusion of total flower abundance in link weight significantly modified three network-level parameters: G_{fv} (Fig. 1.1C; $z = -7.24$, $p < 0.001$), *IE* (Fig. 1.1E; $z = -7.01$, $p < 0.001$) and ID_p (Fig. 1.1F; $z = -3.61$, $p < 0.01$) decreased; and two species-level parameters: mean weighted d_p' (Fig. 1.2A; $z = 4.63$, $p < 0.001$) and mean weighted St_p (Fig. 1.2E; $z = 9.80$, $p < 0.001$) increased.

When comparing the simplest (*M1*) with the most complex link weight (*M5*), we found significant changes in all examined parameters but two (G_p and mean weighted d_{fv}'). A clear trend toward a higher weighted *NODF*, H_2', mean d_p' and mean d_{fv}' was found. By contrast, G_{fv}, *IE*, ID_{fv}, ID_p and mean weighted St_{fv} tended to decrease (Figs. 1.1 - 1.2).

Discussion

Our findings show that the weight given to each interaction in quantitative flower-visitation networks affects most network properties. This indicates that using one or another indiscriminately is not a trivial decision, as the ecological interpretation of network structure may notably differ.

Standardizing the number of visits simply by census time (*M2*) could be important for those networks where sampling effort in time differed across plants during the whole flowering season, as it is in our case, as the number of visits to a plant could be mainly driven by the time spent observing it. However, we found that accounting for census time had only weak effects on network properties, probably due to the strong positive correlation between values in *M1* and *M2* ($r_s = 0.693$, $p < 0.01$), *i.e.* usually, more abundant insects show higher visitation rates. Similar results were obtained by Vázquez & Simberloff (2003).

When censusing flower visitors on plants, especially in those with many flowers, we usually observe only a limited area of the entire individual. We might expect that areas with more flowers might have a higher chance to receive more visits than others in which

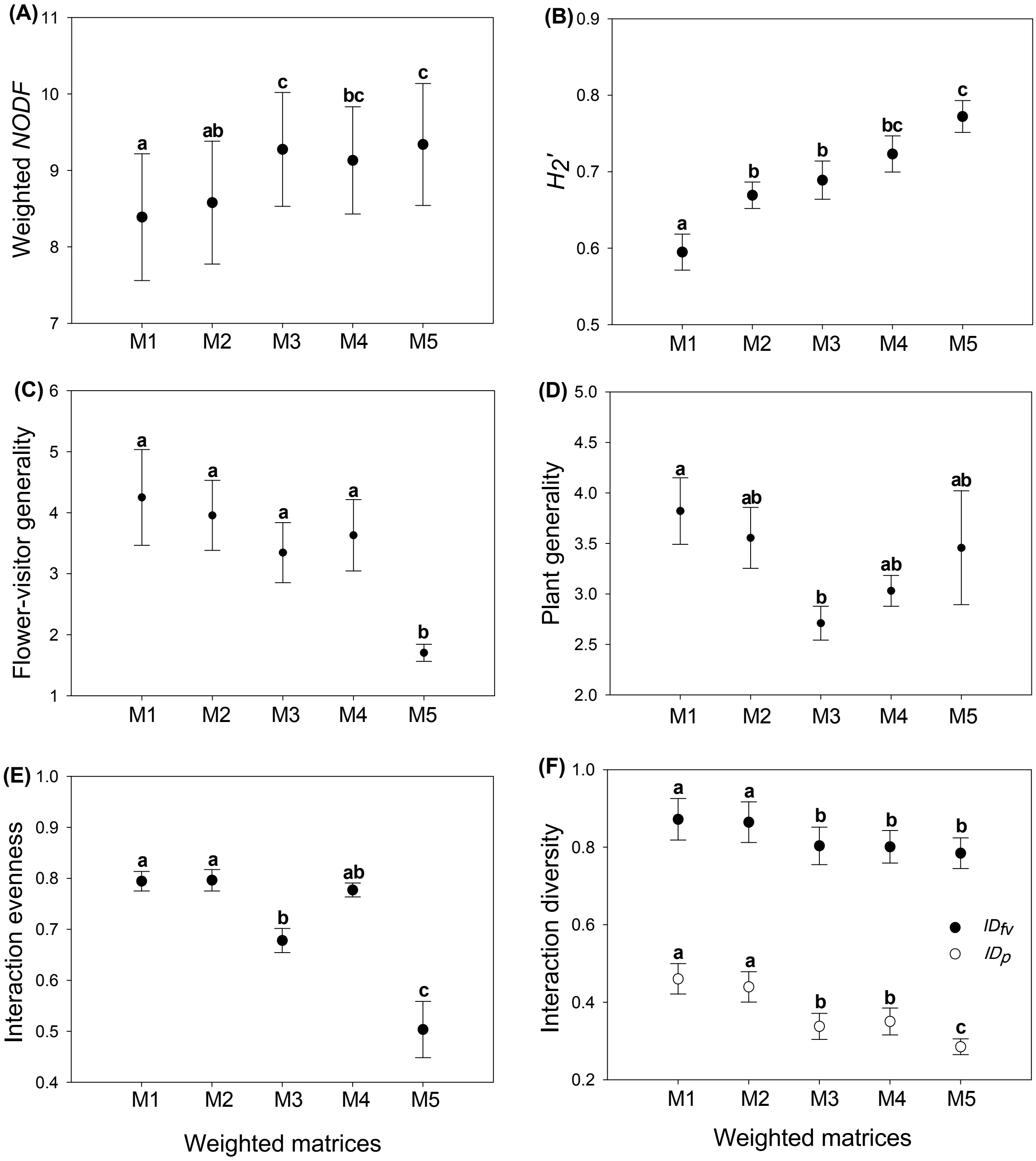

Figure 1.1. Mean (± SE) of the network-level parameters (A) weighted *NODF*, (B) H_2', (C) flower-visitor generality (G_{fv}), (D) plant generality (G_p), (E) interaction evenness and (F) interaction diversity (ID_{fv} and ID_p) of the 12 temporal networks (4 one-month networks for each of two subsequent years in Son Bosc, and 2 two-month networks for the same 2 years in Puig Major) for weighted matrices: *M1* (no. of visits), *M2* (no. of visits/time), *M3* (no. of visits per flower/time), *M4* (proportion of flowers visited/time) and *M5* (proportion of flowers visited/time x flower abundance). For each parameter, values with the same letter are not significantly different from each other.

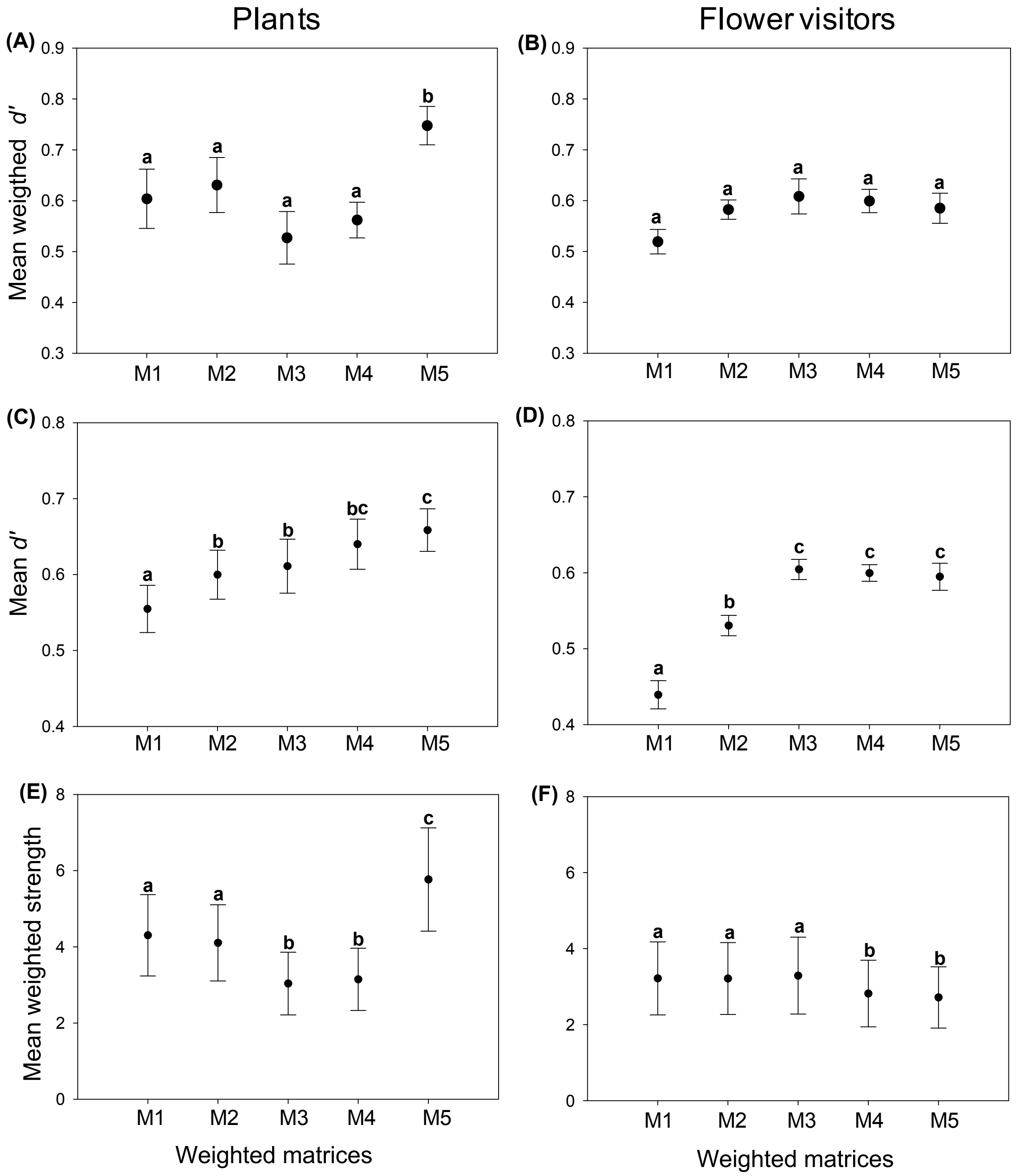

Figure 1.2. Mean (± SE) of the species-level parameters (A) mean weighted d_p', (B) mean weighted d_{fv}', (C) mean d_p', (D) mean d_{fv}', (E) mean weighted St_p and (F) mean weighted St_{fv} of the 12 temporal networks (4 one-month networks for each of two subsequent years in Son Bosc and 2 two-month networks for the same 2 years in Puig Major) for weighted matrices: *M1* (no. of visits), *M2* (no. of visits/time), *M3* (no. of visits per flower/time), *M4* (proportion of flowers visited/time) and *M5* (proportion of flowers visited/time x flower abundance). For each parameter, values with the same letter are not significantly different from each other.

we observed only a few flowers. However, the correlation between visitation rate (no. visits/min) and number of visits per flower per minute was weak ($r_s = 0.262$, $p < 0.01$), and this is probably why we find significant differences in parameters between *M2* and *M3*. Flower visitors appear to become more specialized (higher *d'* values) in *M3*, which indicates that at least some insects tend to visit plants even if these have less flowers. Interestingly, community interactions also become less diverse and more heterogeneous. Moreover, weighted strength of plants decreased in *M3*, which implies that the importance of any particular plant for flower-visitor community is lower. Finally, nested pattern of interactions became somewhat greater, suggesting that the community is more structured and organized (less abundant and specialized interactions tend to be proper subsets of more abundant and generalized ones) when accounting for number of flowers observed.

The link weight included in *M4* is related to the number of flowers visited by each insect species. In a single foraging bout, the same visitor can visit one or many flowers, which can have important implications for plant reproductive success (*e.g.* Vázquez *et al.* 2005; Sánchez-Lafuente *et al.* 2012); from the visitor's viewpoint, the amount of energy gained also depends on the number of flowers visited per plant and unit time. Quite surprisingly, however, network descriptors in *M4* were quite similar to those found in *M3*. When testing the relationship between link weights used in *M3* and *M4*, we again found a strong positive and significant correlation ($r_s = 0.895$, $p < 0.01$); the more visits (bouts) a plant receives the higher will be the number of flowers visited on it. However, for each interaction, this relationship will depend upon the number of flowers visited in a single bout.

Finally, when accounting for flower abundance of each plant species in link weight, we are including information on its relative importance in the entire community. A particular flower visitor with a given flower visitation rate (*e.g.* 20 flowers/min) can be considered to be more specialized if it visits less-abundant flowers. This link weight (*M5*) showed changes compared to *M4*. In particular, an overall higher heterogeneity of interactions at network level was detected; from the plants' perspective, there was a lower interaction diversity with their flower visitors and plant species appeared to be more specialized; from the animals' perspective, they appeared to visit a lower effective mean number of plants per species and the importance of plants for any particular flower-visitor in the community was also greater.

The only species-level parameter that was consistent regardless of link weight was mean strength (results not shown). Although plants' and flower-visitors' dependencies changed with weight given to an interaction, there was probably a compensatory effect, some species becoming more dependent on others whereas others becoming less dependent.

The differences between effects of link weight on plant and flower-visitor species parameters might be attributed to non-independent measurements of flower-visitor abundance in contrast to independent measurement of flower abundance. So far, however, most flower-visitation networks have been sampled from the plants' perspective, mainly due to methodological difficulties of tracking flower visitors. Only recently researchers have begun to include the pollinators' perspective on plant-pollinator interactions at the community level, for example by exploring the structure of pollen-transport networks (Gibson *et al.* 2006; Bosch *et al.* 2009; Alarcón 2010).

The parameters obtained using different link weights in our temporal network replicates showed that they do not only change in absolute values (or mean values for species level parameters) but also in rank order for the different weighted networks. The level of rank concordance of link weights between temporal networks (Kendall's *W* test) shows that most network parameters exhibit large differences in link weight rank (see Supplementary Material 1C: Figs. SM 1.3 - SM 1.4 and Table SM 1.1). In other words, the rank of a particular link weight varies among the different temporal networks. However, there are some exceptions, like plant interaction diversity which shows high rank concordance between temporal networks regardless the link weight used (Kendall's $W = 0.839$, $p < 0.001$).

Recommendations for comparing weighted flower-visitation networks

A review of 22 published studies revealed a great variability in the way researchers have gathered data and constructed matrices of flower-visitation networks. On the one hand, there are large differences in census durations, ranging from 4 to 30 min, as well as in total observation time per plant species, from a few days to several years (Table 1.1). Our results show that this heterogeneity in total census time per plant is not crucial when describing the structure of quantitative flower-visitation networks. On the other hand, there are also differences in link weight used in such studies: Most consider the number of visits, though in some cases they account for time, flowers visited or total floral abundance. In this case, our findings lead us to recommend that if our goal is to compare topologies across networks, we should use the same link weight in all of them to reduce the risk of drawing erroneous conclusions.

The important question of which weight is most appropriate for a particular ecological network study is not trivial and ultimately depends upon the research objective, the sampling method used in field work and the indices calculated to describe network structure. However, it is clear that if we aim to move toward a more functionally relevant description of the structure of ecological networks, we need interaction weights that are as accurate as possible to avoid biases and misinterpretations and that are standardized across the entire network. A structure as much related to function as possible can help us, for instance, to better predict the communitywide impacts of species invasions or the consequences of the loss of species or interactions in the community.

Supplementary Material 1A

Characteristics of studies sites

The vegetation at Son Bosc is dominated by *Daucus carota* (Umbelliferae), *Helichrysum stoechas* (Asteraceae), *Lotus corniculatus* (Leguminosae) and *Lotus cytisoides* (Leguminosae). The most abundant flower visitors are *Meligethes* sp. (Coleoptera: Nitidulidae), *Spermophagus* sp. (Coleoptera: Chrysomelidae), *Dilophus antipedalis* (Diptera: Bibionidae) and *Apis mellifera* (Hymenoptera: Apidae). Annual mean temperature is 16° C and annual mean rainfall is 410 mm, occurring mostly from September to December (Agencia Estatal de Meteorología, AEMET).

At Puig Major, the plant community is characterized by small and spiny cushion plants, including many endemics (18 species, 30% of all flowering plants). The vegetation is dominated by *Teucrium marum* (Lamiaceae), *Hypericum balearicum* (Hypericaceae), *Rosmarinus officinalis* (Lamiaceae) and *Euphorbia characias* (Euphorbiaceae). The most abundant insects visiting flowers are *Attalus* sp. (Coleoptera: Malachiidae), *Mordellistena* sp. (Coleoptera: Mordellidae), *Plagiolepis pygmaea* (Hymenoptera: Formicidae) and *Oedemera flavipes* (Coleoptera: Oedemeridae). Annual mean temperature is 9° C and annual mean rainfall is 1240 mm, occurring mostly from October to March (Guijarro 1986).

Heterogeneity in flower-visitation network studies

A review of 22 previous studies was performed to show the high variability in the way that researches have gathered field data to construct quantitative plant-pollinator networks. We included all studies with weighted links available through the Web Interaction Database and also incorporated some more recent studies. This compilation is not intended to be an exhaustive search of all plant-pollinator network studies performed with quantitative interaction data, but simply to show the variability in the way researchers have constructed such networks (Table 1.1).

Supplementary Material 1B

Description of the network-level parameters calculated

Nestedness (**weighted *NODF***; Almeida-Neto & Ulrich 2011): networks are nested if those species with fewer interactions are preferentially associated with a subset of species that interact with the most connected ones. The difference between presence-absence nestedness (*NODF*) and *WNODF* expresses how much of the nestedness in interaction composition looks like a gradient of abundances. A high value of nestedness indicates that the community is highly structured and organized.

Complementary specialization H_2' (Blüthgen *et al.* 2006) characterizes the degree of complementary specialization in bipartite networks and it is derived from Shannon entropy. H_2' is related with weighted *d'* described in detail below, across all species. It ranges between 0 (no specialization, high niche overlap) and 1 (complete specialization, high niche differentiation).

Plant generality G_p (Bersier *et al.* 2002) is the effective mean number of flower visitors per plant derived from Shannon diversity of links. It is a measure of the weighted ratio of flower visitors to plant species. It is equivalent to the parameter named "vulnerability" in antagonistic prey-predator networks.

Flower-visitor generality G_{fv} (Bersier *et al.* 2002) is the effective mean number of plants visited per flower visitor derived from Shannon diversity of links. It is a measure of the weighted ratio of plants visited by each flower-visitor species.

Interaction evenness *IE* (Tylianakis *et al.* 2007) is a measure of the uniformity of interactions between species in a network based on Shannon's evenness. An uneven network has a high skewness in the distribution of interaction weights. It ranges from 0 (completely uneven) to 1 (completely uniform).

Interaction diversity ID is the Shannon diversity of interactions of a species averaged across all animal species (ID_{fv}) or plant species (ID_p). It provides a measure of the complexity of associations in the community (*e.g.* Albrecht *et al.* 2007).

Description of the species-level parameters calculated

Species specialization d_p' for plants and d_{fv}' for flower visitors (Blüthgen *et al.* 2006) measures the level of specialization of each species accounting for the available resources provided by the interaction partners (generally calculated as total number of realized interactions with other species of a given species in a bipartite network, *i.e.* its marginal total in the matrix). It ranges between 0 (no specialization) and 1 (complete specialization). This specialization index increases with the deviation from random selection of the available interaction partners based on their abundance. Thus, a flower-visitor species, for example, that visits flowering plant species proportionally to their availability in the community is considered generalized, while a species that visits rare plants disproportionately more is considered specialized.

Strength St_p for plants and St_{fv} for flower visitors (Bascompte *et al.* 2006) is the sum of dependencies of each plant or flower-visitor species, respectively. The dependence of a plant on a flower visitor, for example, is the proportion of interactions between these two species out of the total interactions of a particular plant species. Therefore, the strength of a flower-visitor species is the sum of dependences of all plants interacting with this flower visitor. It is a measure of the importance of this flower visitor from the perspective of the plant set and vice versa.

We calculated both the mean and the weighted mean of the specialization *d'* index and strength values for plants and flower visitors for each of the 60 temporal matrices. For flower visitors, the mean was weighted by their total number of visits to flowers, whereas for plants it was weighted by their total flower abundance in the community. The weighted means of *d'* and strength, thus, are measurements that have been standardized by the different abundances of each animal and flowering species giving more value to those results we get from species we have seen a greater number of times and by playing down singleton values that may not be reflecting the true *d'* or strength.

Supplementary Material 1C

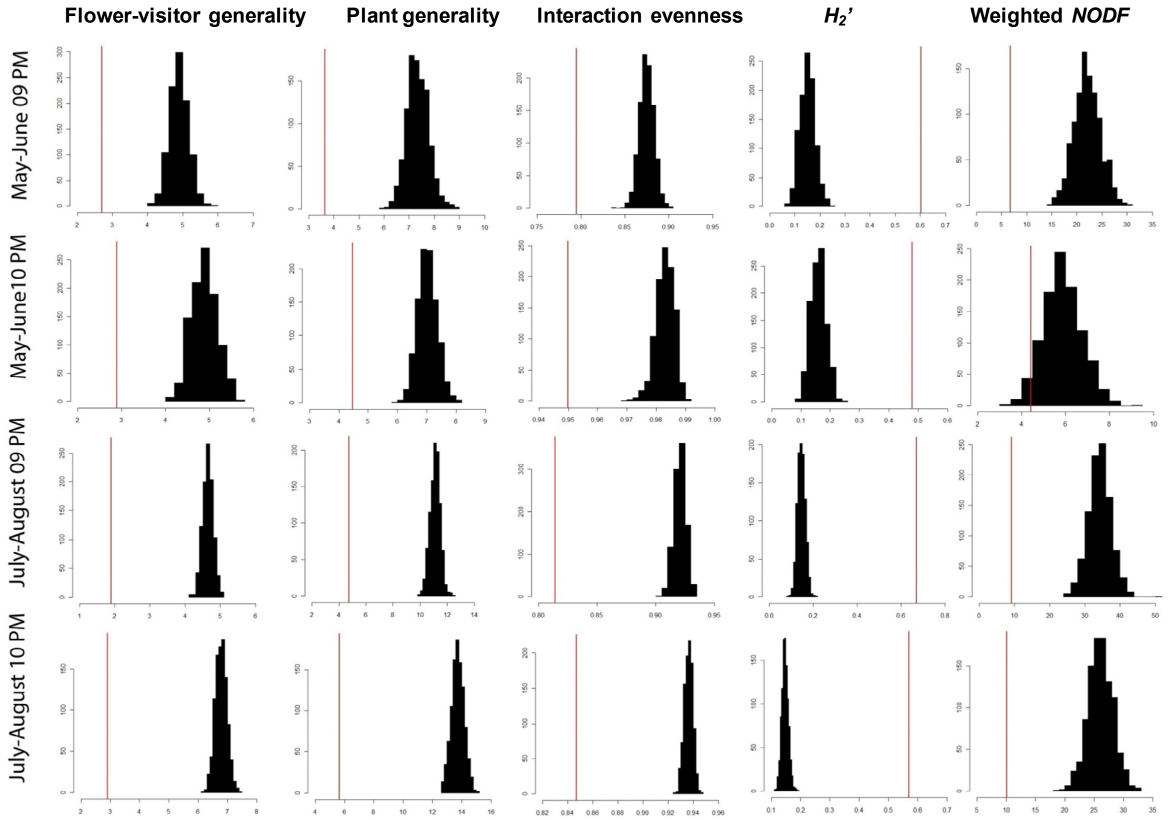

Figure SM 1.1. Network-parameter values of Puig Major *M1* (link weight: number of visits) for the analysis of each temporal network. Red vertical lines indicate observed values whereas histograms represent the distribution of the 1000 null model values calculated using the *Patefield* algorithm (method *r2d*) implemented in the *bipartite* package of R.

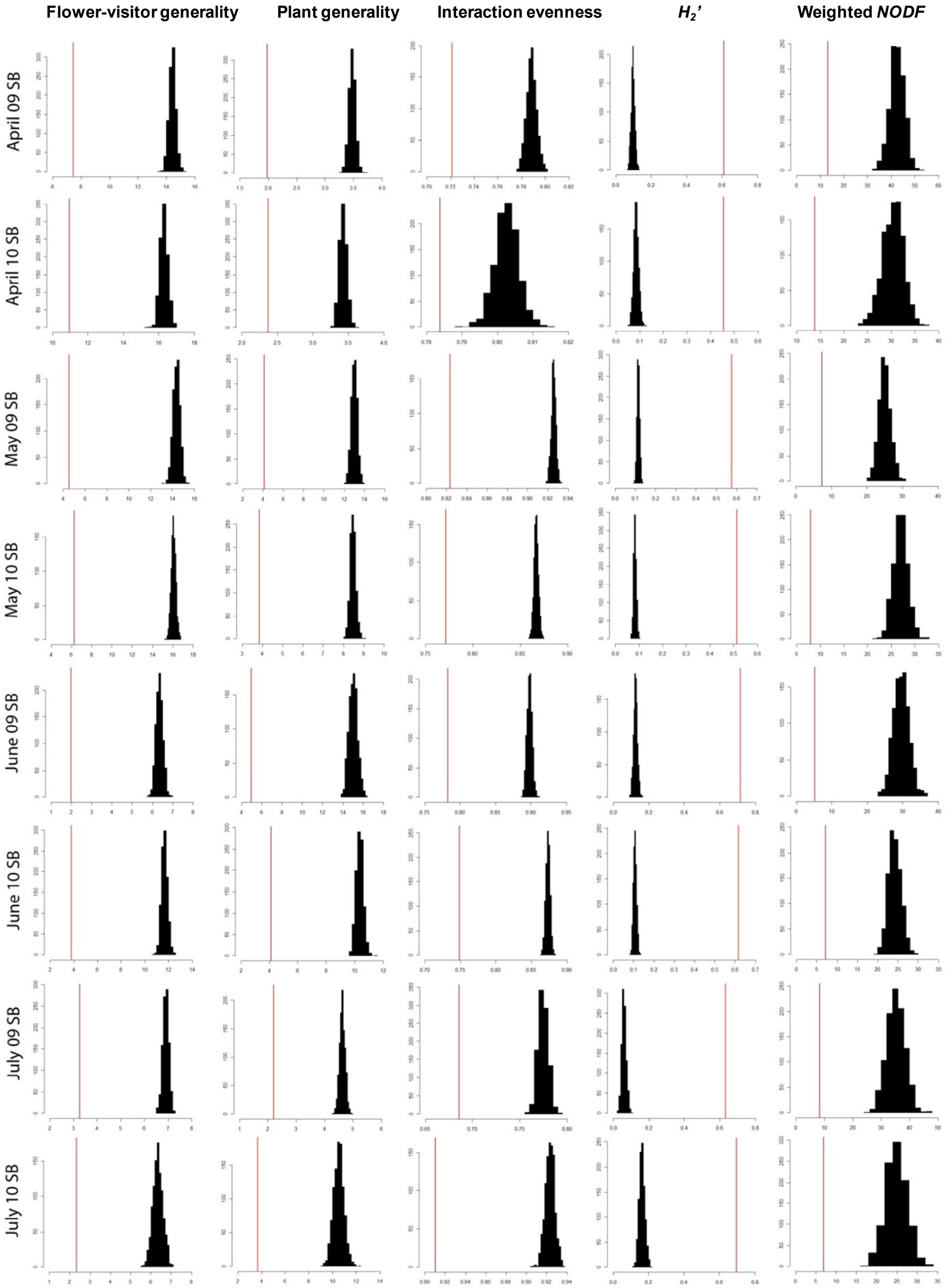

Figure SM 1.2. Network-parameter values of Son Bosc *M1* (link weight: number of visits) for the analysis of each temporal network. Red vertical lines indicate the observed value whereas histograms represent the distribution of 1000 null model values calculated using the *Patefield* algorithm (method *r2d*) implemented in the *bipartite* package of R.

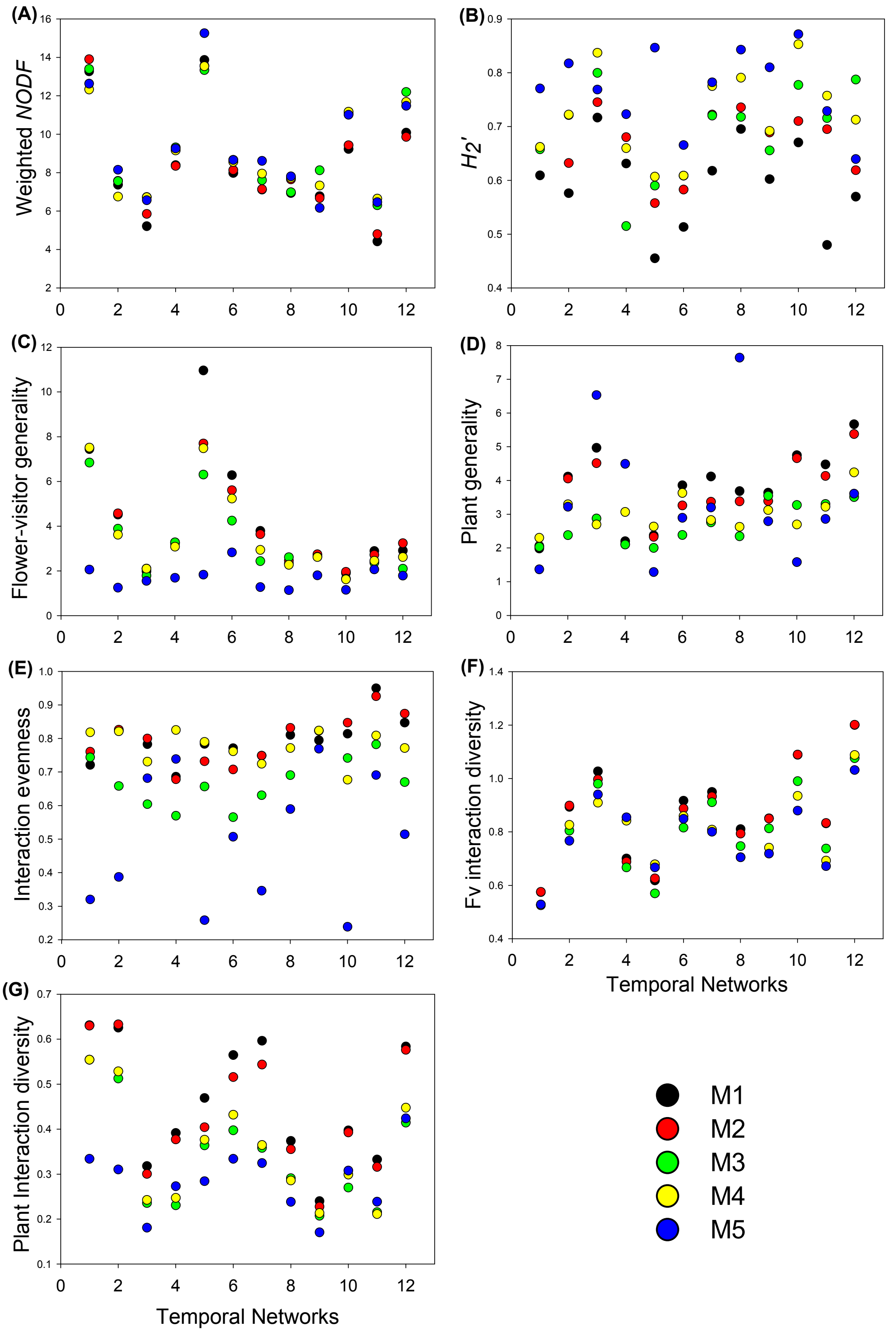

Figure SM 1.3. Network-level parameters calculated for each of the 12 temporal networks (1-8 from Son Bosc and 9-12 from Puig Major, see text for details) with five different link weights. Each color represents a different type of weighted matrix. Note that parameter values vary depending on link weight and that changes in rank order occur when comparing different temporal networks.

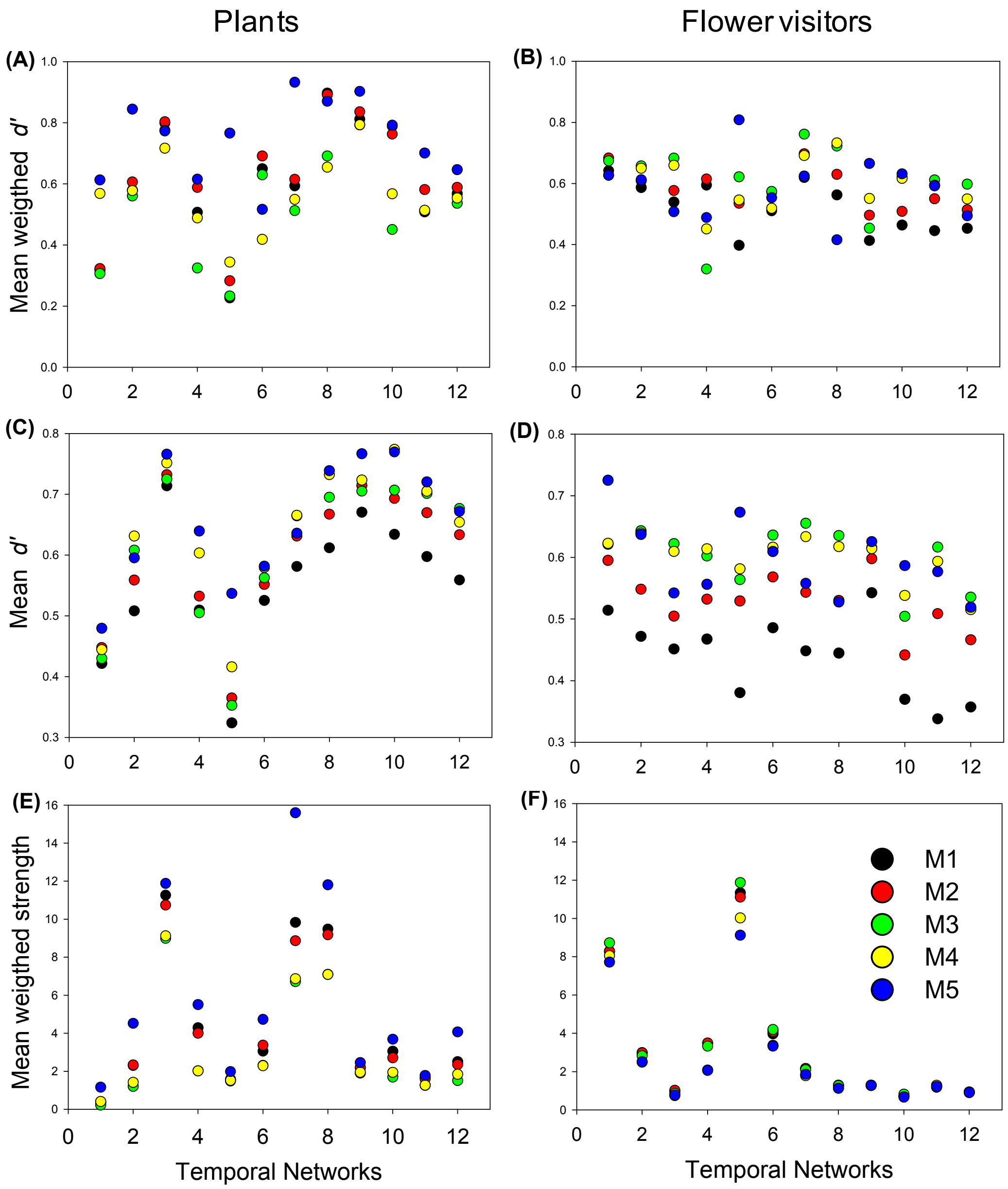

Figure SM 1.4. Species-level parameters calculated for each of the 12 temporal networks (1-8 from Son Bosc and 9-12 from Puig Major, see text for details) with five different link weights. Each color represents a different type of weighted matrix. Note that parameter values vary depending on link weight and that changes in rank order occur when comparing different temporal networks.

Table SM 1.1. Kendall's *W* and level of significance of each network parameters of this study. Kendall's *W* test calculates the degree of concordance between ranks of each link weight (*M1*, *M2*, *M3*, *M4* and *M5*) in our 12 temporal networks (see text for details). Kendall's *W* varies between 0 (any concordance in rank parameter across temporal networks) and 1 (total concordance in rank parameter across temporal networks). Network parameters are ordered from the most to the least concordant across the 12 temporal networks.

Network parameters	**Kendall's *W***	***p* - value**
Plant mean weighted strenght	0.883	<0.001
Plant interaction diversity	0.839	<0.001
Fv mean *d'*	0.790	<0.001
H_2'	0.767	<0.001
Plant mean *d'*	0.738	<0.001
Fv generality	0.704	<0.001
Interaction evenness	0.584	<0.001
Plant weighted mean *d'*	0.532	<0.001
Fv interaction diversity	0.471	<0.001
Fv mean weighted strenght	0.374	0.001
Plant generality	0.347	0.002
Fv weighted mean *d'*	0.335	0.003
Weighted *NODF*	0.282	<0.001

Capítulo 2

Características de las especies con las que interactúan las especies generalistas y especialistas en redes de visitantes florales

Chapter 2

Contrasting partners' traits of generalized and specialized species in flower-visitation networks

El contenido de este capítulo ha sido publicado como:

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DOI: http://dx.doi.org/10.1371/journal.pone.0150824

Resumen

Gran parte de la investigación ecológica se ha focalizado en tratar de entender por qué las especies son generalistas o especialistas en sus interacciones y cómo las redes de interacciones evolucionan en un entorno determinado. Ahora se sabe que rasgos como la fenología y la abundancia de las especies son determinantes de su nivel de generalización (es decir, el número de especies con las que interactúan). Sin embargo, hay menos información disponible sobre si las especies con las que interactúan los generalistas y especialistas (sus "parejas") difieren en determinados rasgos. Dichas "parejas" pueden variar, por ejemplo, en su abundancia y/o en la diversidad de grupos funcionales a los que pertenecen. Por otra parte, las especies pueden exhibir cambios a través del tiempo (por ejemplo, durante la época de floración) eligiendo "parejas" con diferentes rasgos, aunque poco sabemos sobre cómo ocurren realmente estos cambios. Evaluar el proceso de cómo se establecen dichas interacciones a nivel de red en ambos tipos de especies (generalistas y especialistas) es importante para una mejor comprensión de cómo los diferentes tipos de perturbaciones pueden afectar la dinámica de la comunidad. Utilizando datos de cuatro redes cuantitativas de visitantes florales y medidas independientes de la disponibilidad de flores obtenidas durante la observación de las interacciones, evaluamos las diferencias de los rasgos de las "parejas" entre las especies que han sido previamente categorizadas de acuerdo con dos índices de especialización: (1) el número de "parejas", en inglés llamado *linkage level* (*L*), que es cualitativo y (2) el índice de especialización complementaria *d'*, aquí llamado nivel de selectividad, que es cuantitativo. Se encontró que: (1) las especies con *L* bajos (especialistas) interactúan principalmente con especies comunes en la comunidad mientras que las especies generalistas interactúan con especies que presentan una gran heterogeneidad de abundancias y de riqueza funcional, (2) ambas especies selectivas y oportunistas (con alta y baja *d'*, respectivamente) interactúan con una riqueza funcional de "parejas" igualmente alta (número de grupos funcionales o familias) y (3) las especies de visitantes florales generalistas son las únicas que muestran cambios a lo largo de la temporada en los rasgos de sus "parejas", impulsados por los cambios en la composición de especies de la comunidad. El riesgo de extinción frente a perturbaciones generalmente se espera que sea más alto para las especies especialistas (con pocas "parejas") y para especies selectivas (que visitan especies poco abundantes o escasas). Sin embargo, nuestros resultados muestran que, mediante la interacción con especies abundantes y/o "parejas" funcionalmente diferentes, respectivamente, estas especies se pueden mantener en la comunidad y ser menos vulnerables a las perturbaciones.

Contrasting partners' traits of generalized and specialized species in flower-visitation networks

Introduction

Specialization in plant-pollinator interactions has been the focus of much research interest ever since Darwin (Mitchell *et al.* 2009). Despite this, a non-ambiguous definition of specialization in pollination is still non-existent (Olesen 2000; Ollerton *et al.* 2007; Dormann 2011). What seems clear is that specialization and generalization are context-dependent concepts: species may have different levels of specialization in varying locations, being generalized species in a poor pollinator environment but specialized in a rich pollinator environment. Moreover, they are the extremes of a gradient continuum (Waser *et al.* 1996). The quantification of ecological specialization is also highly dependent on the data used, the organism studied, and the ecological mechanism of interest (*e.g.* behavior specialization vs. specialization for habitat) (Devictor *et al.* 2010).

The study of plant-pollinator interactions has moved, in the last decades, from focusing on species pairs to the entire community, especially due to the development of complex network analysis techniques used in a multitude of research disciplines (Borgatti & Everett 1997; Strogatz 2001; Montoya *et al.* 2006). This new approach has promoted a better understanding of complex interactions between mutualistic partners and has allowed gathering evidence that moderate generalization is more the rule rather than the exception (Waser *et al.* 1996). The first studies on pollination (and other mutualistic) interactions implementing this network approach were based on presence/absence interactions between species, giving each interaction the same weight (Jordano 1987; Memmott & Waser 2002; Olesen & Jordano 2002; Bascompte *et al.* 2003). In such studies, specialization is defined qualitatively as the species' total number of interactions (*i.e.* species linkage level, *L*), so species linking to a high number of partners are considered generalized (*e.g.* one pollinator visiting a wide array of plant species) whereas species with low number of partners are specialized (*e.g.* one pollinator species visiting only one plant species). However, a plant pollinated by ten species of moths, for example, could be considered less generalized and therefore more vulnerable to disturbance than another plant pollinated by five species belonging to different pollinator functional groups. It was soon widely recognized by ecologists that this qualitative measure of generalization was limited as it fails to describe the strong heterogeneity in the frequency and availability of interaction partners and it is deeply dependent on network size.

The subsequent use of quantitative data to describe interaction strength between partners led to the emergence of a new concept of specialization (Blüthgen *et al.* 2006), the species-level complementary specialization index (*d'*), based on Shannon diversity. This index takes into account not only the number of partners but also their availability in the community. Thus, it can be considered as an index of selectiveness (term used hereafter). A pollinator that visits a plant species proportionally to its availability in the community is considered opportunistic whereas one that visits rare plants disproportionately more than common ones is considered as selective. Likewise, an opportunistic plant is visited by pollinators proportionally to their availability whereas a selective plant is visited disproportionately more by rare than by common pollinators.

Several studies have explored the traits that contribute to the generalization level in flower-visitation networks. Traits such as phenology and abundance (Dupont *et al.* 2003; Vázquez & Aizen 2003; Olesen *et al.* 2008; Stefanescu & Traveset 2009; Zhang *et al.* 2011; Junker *et al.* 2013; Fort *et al.* 2016), flower color (Renoult *et al.* 2015) or flower and insect morphology (Chamberlain *et al.* 2014) have been shown to influence the number of different interactions a species can have. However, much less is known on whether the partners' traits differ between generalized and specialized species and between selective and opportunistic species. The traits or mechanisms regulating interactions between species can actually be considered the "microstructure" of a network (Junker *et al.* 2010; Kaiser-Bunbury *et al.* 2014). The traits of species to which other species link to, for instance their abundance or their functional richness (here defined as the number of functional groups for flower visitors or the number of families for plants) are probably important determining such microstructure and their degree of vulnerability to disturbances.

In the present study, we are interested in investigating whether the partners' traits of generalized and opportunistic species differ from those of specialized and selective species. Specifically, we aim at testing the following hypotheses: (1) to avoid risk of extinction, specialized species interact mainly with the most abundant species in the community. By contrast, (2) generalized species interact with species showing a greater heterogeneity of abundances (lower evenness of partners' abundances). Moreover, (3) specialized and selective species should interact with a rich assemblage of partners because, in case of partners' decline (*e.g.* an insect group or an entire plant family), they can interact with partners from other functional groups. (4) Generalized and opportunistic species show a high heterogeneity of partners' functional richness which makes them more resistant against the extinction of a particular functional group. The four hypotheses are depicted in Figure 2.1.

The first hypothesis is related to network properties describing the overall patterns of interactions, such as nestedness and interaction asymmetry (Bascompte *et al.* 2003; Vázquez & Aizen 2004; Bascompte *et al.* 2006).

The temporal dynamics of species interactions needs also to be considered to better understand the microstructure of plant-pollinator communities. Partners' traits may change along time (*e.g.* season) as interactions between plants and their flower visitors vary within and across seasons reflecting changes in community composition (Herrera 1988; Olesen *et al.* 2008; Dupont *et al.* 2009; Olesen *et al.* 2011; Fang & Huang 2012). Therefore, we might further expect specialized and selective species to be more constant in their partners' traits through time than generalized and opportunistic species, which might be more variable following changes in species composition and abundances.

In order to test these hypotheses, we used data from four different communities for which we built quantitative flower-visitation networks, gathering independent measures of flower availability.

Materials and methods

Ethics statement

Servei de Protecció d'Espècies, Espais de Natura Balear (Conselleria d'Agricultura, Medi Ambient i Territori) and Cabildo of Lanzarote provided permission to work at the study sites.

Study sites and sampling procedure

Flower visitation networks were constructed from observations carried out in four coastal communities, two on Mallorca, Balearic Islands (Son Bosc and Cala Mesquida, SB and CM hereafter) and two on Lanzarote, Canary Islands (Caletón Blanco and Las Conchas, CB and LC hereafter) (see further description of the communities in Castro-Urgal & Traveset 2014). The study was conducted in April-July 2010 on Mallorca and in January-April 2011 on Lanzarote, which covered the entire flowering spring season for both islands. Sampling started early in the year on Lanzarote because of the tight association between rainfall and plant flowering on this dry island.

Flower density was estimated every two weeks at each community by counting all open flowers of each plant observed along each of the ten (50 x 2 m^2) permanent belt transects established in SB and in each of the 30 (0.5 x 0.5 m^2) random plots located in the other three communities. Random plots instead of transects were used in these sites to capture the high heterogeneity of each area. Flower density was calculated for each species as the number of open flowers divided by the total area surveyed. For species with tightly clustered inflorescences (*e.g.* the capitula of Asteraceae), each inflorescence was scored as an individual flower. Flower-visitor abundance was estimated as the total number of individuals observed visiting flowers. Although the ideal would be to have also independent measures of flower-visitor abundance, this is usually not possible owing to the difficulties of tracking different types of insects.

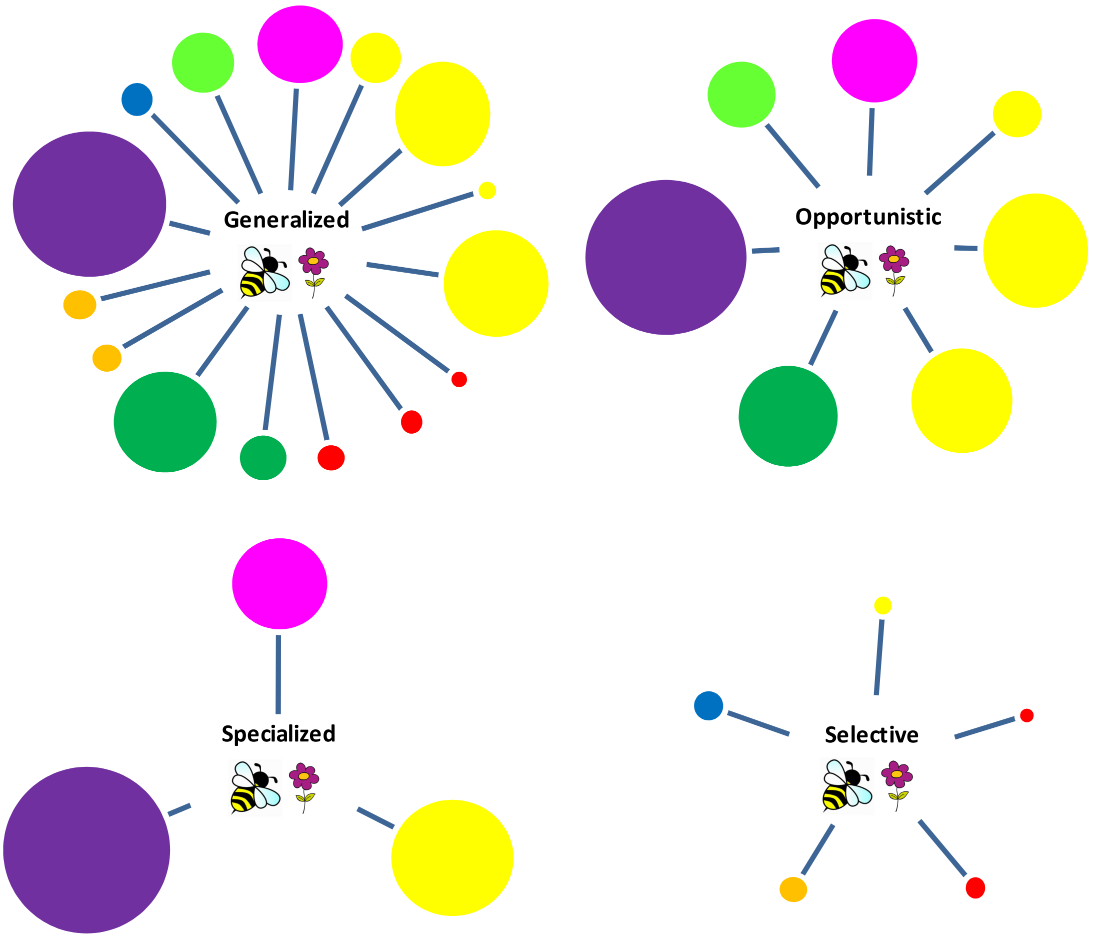

Figure 2.1. Representation of our hypotheses of species partners' traits depending on the degree of specificity. Each circle represents a partner (plant or flower-visitor), whereas its size represents the abundance in the community. The variety of colors represents the functional richness of species with which it interact (families in the case of plants and functional groups in the case of flower-visitors). Drawings: http://www.zazzle.es and http://meluxx23.blogspot.com.es

On each census day at each community, all plants in bloom were observed the same amount of time to prevent the bias of finding more interactions in more abundant plant species. Censuses were performed once or twice a week at each site. We made randomized focal censuses, *i.e.* observing individuals of each flowering plant species at a time, between 10:00 and 17:00 h on sunny and low-wind days. Interactions were recorded from a distance of approximately 1 m from the focal plant species to minimize interference with insect behavior during sampling. We recorded contacts between insects and flowers during 3-min periods at SB, 6-min periods at CM and 7.5-min periods in both sites on Lanzarote. Longer censuses were carried out in the last three locations because of the lower number of simultaneous species in bloom than at SB. During each census we recorded: (a) identity of the flowering plant species; (b) number of open flowers of each individual plant observed; (c) identity of each flower visitor (species name if possible or morphotype otherwise); (d) number of individuals of each species visiting flowers and (e) number of flowers visited by each individual flower visitor. Insects that could not be identified in the field were collected for further identification by taxonomists.

Total time spent censusing flower-visitor interactions was 49:39 h at SB, 84:45 h at CM, 56:38 h at CB and 80:53 h at LC. Differences in total observation times among sites were a result of differences in the duration of the flowering period of their constituent plant species.

Construction of quantitative flower-visitation networks

Quantitative interaction networks were constructed using flower visitation rate (FVR) as interaction weight, a measure of the intensity of mutual interaction strength between partners. The FVR of species was calculated as the number of flowers contacted by each flower-visitor species during a census, standardized by number of flowers observed, total census time per plant species and specific flower abundance (Castro-Urgal *et al.* 2012).

Additionally, in order to analyze the differences in partners' traits and the temporal dynamics of the most generalized, specialized, selective and opportunistic species in each community along the season, we built 16 temporal interaction networks ("temporal snapshots", Kaiser-Bunbury *et al.* 2010b), one per month in each community. Temporal snapshots reflect network structures more realistically than full-season networks as they include only those species that coexist in time.

Specialization indexes

Both *L* and *d'* were calculated for all species in the four season networks, *i.e.* with data from the entire season (367 flower-visitors and 150 plant species), using the *bipartite* package version 1.17 (Dormann *et al.* 2009) run in R 2.11. In order to work with more reliable specialization indices, we excluded from the dataset those plant species that had been censused less than 30 min in total as well as those flower-visitors observed less than five times. With this information, for each community we chose the 10 most generalized (highest *L*) and the 10 most specialized (lowest *L*) species (five plant and five flower-visitor species) which were present at least in two temporal networks. Likewise, we chose the 10 most opportunistic (lowest *d'*) and the 10 most selective (highest *d'*) species in each community. In some cases, the same species was in two categories, *e.g.* when it was both among the most generalized and among the most opportunistic. In total, we selected 117 species for which we obtained their partner profile (see Tables SM 2.1 - SM 2.4).

Species and partners' traits

We evaluated the evenness of partners' abundances by calculating Pielou's measure of species evenness, *i.e.* $J' = H'/\ln(S)$ (Pielou 1966). This evenness index varies between 0 and 1. The lower the variation among partner's abundances, the higher J' is. For species with only one interacting partner we consider $J' = 1$.

Moreover, we estimated the abundance of a species in a community context, and categorized species as following:

> **Highly abundant (5)**: We look at the number of flowers that the most abundant species have on each community each month. Then, we see if another species has an abundance above 80% (because we have five categories). If so, we assign the same category rank.
>
> **Abundant (4)**: In the next step we do the same as before but having excluded the highly abundant species. We look at the number of flowers that the most abundant species have and see if another species has an abundance above 75% (because we have now four categories). If so, we assign the same rank category.

Common (3): Again, with the remaining dataset (*i.e.* excluding the species in the two previous categories) we look at the more abundant species and see if another species is above 66% (three categories left). If so we assign the same rank category.

Low abundant (2): We do the same as for the other four previous categorizations, but in this case we look for species above 50% in their abundance. If so, we assign the same rank category. The rest of them (below 50%) are considered **Scarce (1)**.

We further categorized each species into families (in the case of plants) and into functional groups (in the case of insects). In the latter case, we considered a total of 10 functional groups depending on insect size and foraging behavior: large bees (> 1cm), small bees (< 1cm), flies, hoverflies, beetles, wasps, butterflies, true bugs, ants and others (grasshoppers and acari).

Statistical analysis

To test for differences in plants and flower-visitors partners' traits (functional richness, rank abundance and evenness of abundances), we conducted general linear mixed models (GLMMs) with trait as dependent variable (one at a time), specialization index as fixed factor, and month nested within community as random factor. Separate models were built for the two types of specialization indexes, those considering linkage level (generalized/specialized) and those considering selectiveness level (opportunistic/ selective).

Secondly, we tested if partner's traits changed throughout the season depending on the degree of specialization and the degree of selectiveness or if species were constant in their partner's traits. We conducted GLMMs for each specialization index separately (generalized, selective, opportunistic and selective) with trait as dependent variable (one at a time), using month as fixed factor and month nested within community as random factor.

The Tukey's test (with the glht; 'many-to-one comparison procedure' [Dunnett 1955]) was used to test for differences across groups when significant differences in a given factor were detected. For the analyses that included linkage level as fixed factor, flower-visitors' functional richness was log transformed for a better fit with residual normal distribution. All analyses were performed using packages *lme4* (Bates *et al.* 2011) and *multcomp* (Hothorn *et al.* 2008) in R 2.11.

Results

Differences in partners' traits

As expected, generalized species showed lower evenness of partners' abundance (plants: Fig. 2.2A; $z = 7.523$, $p < 0.001$ and flower-visitors: Fig. 2.2B; $z = 4.768$, $p < 0.001$) and greater partners' functional richness (plants: Fig. 2.2E; $z = -12.9$, $p < 0.001$ and flower-visitors: Fig. 2.2F; $z = -10.55$, $p < 0.001$) than specialized species. However, rank abundance of partners did not differ between them (Figs. 2.2C - 2.2D). These findings suggest that generalized species interact with many different species showing great variability in abundance among them whereas specialized species interact only with few but common species (very high evenness of abundances and the highest rank, near 3; *i.e.* with common species).

By contrast, opportunistic and selective species differed in their partner's rank abundance (plants: Fig. 2.2C; $z = 4.781$, $p < 0.001$ and flower-visitors: Fig. 2.2D; $z = 4.563$, $p < 0.001$). Moreover, the evenness of abundances was lower between the partners of opportunistic plant species than those of selective plant species (Fig. 2.2A; $z = 2.061$, $p < 0.05$). However, both showed a similar partner's functional richness (Figs. 2.2E - 2.2F), indicating that they interact with a similar diversity of partners. These results show that opportunistic species interact mainly with diverse but abundant species whereas selective species interact with diverse but scarce species.

Seasonal patterns of species partners' traits

The evenness in flower abundance and family richness of partners used by generalized flower-visitor species varied significantly across the season. However, the rank abundance of their partners did not vary across the season. By contrast, specialized species were more constant through time. Generalized insect species visited flowers with the greatest variability in abundance during the third month of the season (significant differences where found only between the first and the third month: Fig. 2.3A; $z = -2.994$, $p < 0.05$). However, it was the second month when they interacted with the largest number of partner's families, though significant differences where found only between the second and the last month (Fig. 2.3B; $z = -2.738$, $p < 0.05$). The highest number of plant families in each community in three of the four communities was found also during the second month of the season (Table 2.1); however, the month showing highest evenness on flower abundances varied among the four communities (Table 2.1). Neither opportunistic nor selective flower-visitor species varied significantly in any of the three partners' traits, *i.e.* they consistently interacted with partners with the same traits across the season.

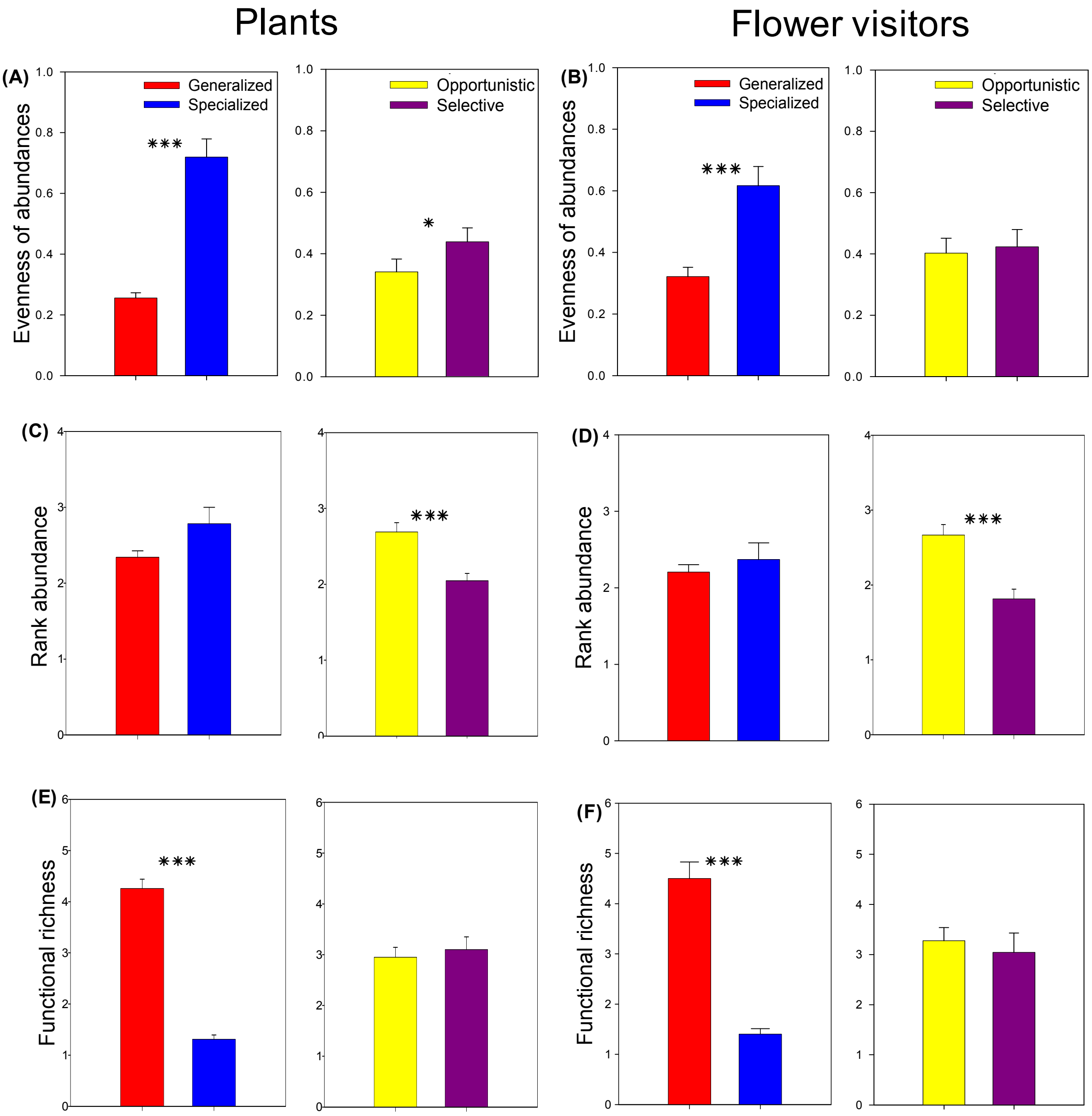

Figure 2.2. Mean (± SE) of partners' traits of generalized (red), specialized (blue), opportunistic (yellow) and selective (purple) species. (A-B) Evenness of partner's abundance, (C-D) partner's rank abundance (5 = highly abundant and 1 = scarce), (E-F) partner's functional richness. For each parameter, significant differences between categories are indicated by * (p < 0.5) and *** (p < 0.001).

Regarding plants, no significant temporal differences were found between either generalized and specialized or opportunistic and selective species in their partner traits.

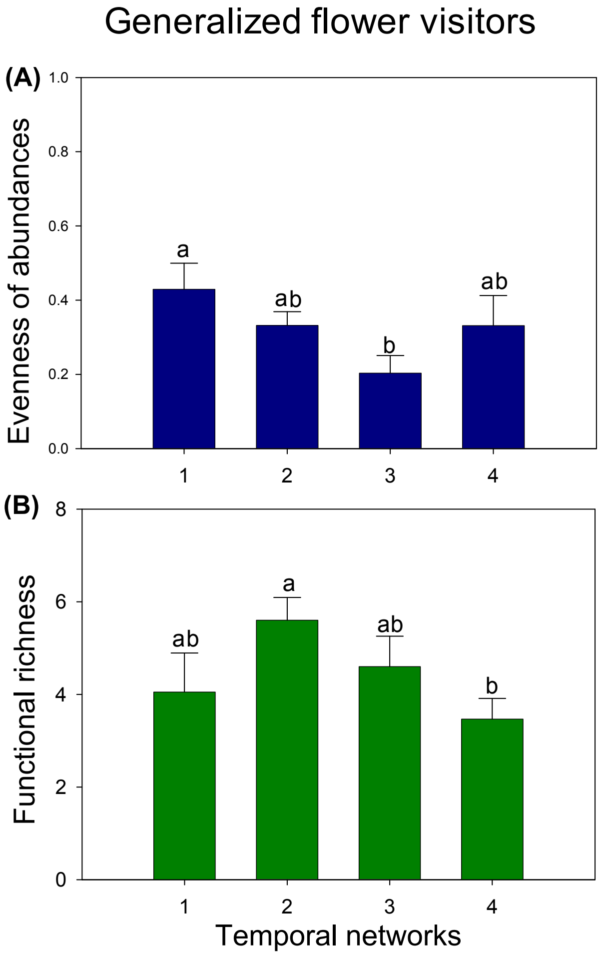

Figure 2.3. Changes across the season (temporal networks) in partners' traits of generalized flower-visitor species. Each temporal network represents one month of the season. Mean (± SE) of (A) evenness of partners' abundances and (B) partners' functional richness. For each parameter, values with the same letter are not significantly different from each other.

Discussion

Our findings support the prediction that the partners of generalized species have the highest functional richness and are highly heterogeneous in abundance, *i.e.* generalized species visit (in the case of animals) or are visited (in the case of plants) by a wide range of different partners being abundant or scarce and belonging to different pollinator functional groups and plant families. Also as expected, specialized species tended to visit or be visited mostly by common species belonging to the same plant family or pollinator

Table 2.1. Descriptive measures of each study area per month.

Study area	Month	Total interactions	Plants			Flower visitors		
			No. species	Family richness	Heterogeneity of abundances	No. species	Functional group richness	Heterogeneity of abundances
Caletón Blanco	1 (January)	158	10	8	0.4375	24	8	0.4187
	2 (February)	153	14	10	**0.4636**	24	8	**0.4298**
	3 (March)	**431**	14	**11**	0.4220	23	7	0.1808
	4 (April)	257	**15**	10	0.3645	**28**	**9**	0.4046
Las Conchas	1 (January)	**628**	15	11	0.4224	35	8	0.5153
	2 (February)	411	19	**13**	**0.4258**	30	**9**	0.2940
	3 (March)	428	**21**	11	0.2928	32	8	0.4919
	4 (April)	459	19	10	0.1077	**36**	**9**	**0.5184**
Cala Mesquida	1 (April)	148	17	7	0.2598	26	7	0.2822
	2 (May)	786	**31**	**13**	0.3139	57	**10**	0.3780
	3 (June)	**829**	28	10	0.2485	**78**	**10**	**0.4063**
	4 (July)	279	9	3	**0.3340**	35	8	0.3951
Son Bosc	1 (April)	814	33	20	**0.4132**	42	9	0.2195
	2 (May)	**1233**	**48**	**24**	0.3110	**74**	9	0.3480
	3 (June)	871	40	20	0.0474	70	**10**	0.4087
	4 (July)	277	21	13	0.0015	41	8	**0.5110**

The highest value of each measurement within each study area is indicated in **bold**.

functional group, thus avoiding or decreasing the extinction risk of losing mutualistic interactions due to the different drivers of global change (Kiers *et al.* 2010). This finding also supports previous results from studies that have shown that reciprocal specialization between species is rather rare and that interactions among mutualistic partners are highly asymmetric, a pattern that contributes to increase community nestedness (Vázquez & Aizen 2004; Bascompte *et al.* 2006). This pattern has shown to decrease interspecific competition in those communities with highest niche overlap, nested or fully connected networks (Bastolla *et al.* 2009; Valdovinos *et al.* 2013).

We also found support for the prediction that both opportunistic and selective species have a high functional richness of partners. This result is particularly interesting as it shows that selective species, considered so far to be most vulnerable to disturbances, might be maintained in the community by interacting with such a wide array of partners. Interacting with scarce but functionally rich partners might actually be a ‘strategy’ of selective species to avoid competition for abundant resources and ensure their maintenance in the community. Curiously, opportunistic species showed less functional richness of partners than generalized species, what illustrates the difference between the two types of specialization indices. Generalized species visit or are visited by species regardless of their abundance, but the partners of opportunistic species are always abundant species. Some of the plant families or pollinator functional groups in the study communities do not have abundant species. This is the case of plant families such as Aizoaceae, Malvaceae and Papaveraceae or of pollinator functional groups such as true bugs and butterflies. Moreover, selective species showed higher functional richness of partner's than specialized species. This is because selective species mainly visit or are visited by scarce partners and most plant families and pollinator functional groups are actually very scarce species in our communities whereas, as mentioned above, specialized species interact mainly with common species of a lower number of plant families or insect functional groups.

Some studies have shown a high variability in species and interaction turnover within the same season and across seasons (Herrera 1988; Olesen *et al.* 2008; Dupont *et al.* 2009; Fang & Huang 2012) but rather little is known about the mechanisms of such changes. Interaction turnover may occur because species change preferences responding to the abundance of their partners, or because a new species suddenly appears in the community, *i.e.* interaction turnover may be due to temporal dynamics in the selection of partner's traits. The temporal fluctuation in species and interactions could be cushioned if one lost species is replaced by another with the same or similar traits (Fang & Huang 2012). Our results actually show that this is the case for almost all species chosen for our study. Despite new flower-visitor species appear and disappear and abundances change, all selected plants (generalized, specialized, opportunistic and selective) were very constant in their partner's traits across the season. Similarly, specialized, selective and opportunistic flower-visitor species did not change their partners' use across time. By contrast, the generalized flower-visitor species exhibited shifts through time in their partners' traits depending on the species composition in the community across the season. The diet breadth of generalized pollinators is known to be a flexible trait, resulting in part from adaptation of foraging choices to resource availability (Fontaine *et al.* 2008; Valdovinos *et al.* 2013).

Although our findings are based on a single season, we believe they are well informative on the microstructure of pairwise interactions, as we analyze flowering species and flower-visitor species that coexist in time (*i.e.* "forbidden links" due to phenological mismatching between partners are reduced to minimum). We also reduced biases due to sampling effort by censusing (each census day) the same amount of time both rare and abundant species and by using an interaction weight that accounts for both the number of observed flowers in each census as well as the flower abundance of each plant species observed (Castro-Urgal *et al.* 2012). Using the total number of individuals observed visiting flowers to estimate flower-visitor abundance is arguably limited but the best estimate we can obtain. Even so, the results for flower-visitors were similar to those obtained for plants, for which we did have independent estimates of abundance, supporting the general trends we found. Nevertheless, to generalize on our findings, further exploration of other communities and with data from more seasons might be required. Moreover, other relevant partners' traits, such as the type of reward offered by the flowers (Petanidou *et al.* 2006), floral display and floral and insect size and form (Stang *et al.* 2006, 2007), color (Whitney *et al.* 2009) or scents (Junker *et al.* 2010) should be considered if we are to unravel the different mechanisms influencing the microstructure of a pollination network.

The concept of specialization in plant-pollinator systems is inevitably connected to the notion of extinction cascades in natural ecosystems, *i.e.* the idea that if the pollinator of a specialized plant becomes extinct, then the plant is bound to follow and vice versa. However, we have shown that the most specialized species interact with abundant species in the community, what gives robustness to the pollination networks in the face of disturbances and species loss. By linking to common species, specialized species contribute to increase nestedness, which is important to network robustness and stability to species extinctions (Bascompte *et al.* 2003; Memmott *et al.* 2004; Fortuna & Bascompte 2006; Saavedra & Stouffer 2013). Likewise, selective species visit or are visited by partners belonging to different families or functional groups and this may provide them with a higher resistance to cope with partners' extinction.

These considerations are therefore important in the context of global change. Based on our results, we predict that the great majority of both plants and flower-visitors will find new interaction partners with similar traits to those that could vanish, *i.e.* we predict that the probability of species re-wiring is high and extinction cascades may not occur as rapidly as previously thought in these types of communities (Petanidou *et al.* 2008; Burkle & Alarcón 2011). However, studies that incorporate measures of pollinator services are badly needed to determine how this rewiring could affect plant fitness and pollinator-mediated selection.

Supplementary Material

Table SM 2.1. Information on plant species chosen of each network. Here we indicate: zone, family, plant species, species code (sp.code), linkage level (*L*), level of selectiveness (*d'*) and the grade of specificity (generalized, specialized, opportunistic or selective species). For this study were chosen five of the most generalized (highest *L*), five of the most specialized (lowest *L*), five of the most opportunistic (lowest *d'*) and five of the most selective (highest *d'*) plant species in each community, present at least in two temporal networks.

Table SM 2.2. Information on flower-visitor species chosen of each network. Here we indicate: zone, functional group (FG), flower-visitor species, species code (sp.code), linkage level (*L*), level of selectiveness (*d'*) and the grade of specificity (generalized, specialized, opportunistic or selective species). For this study were chosen five of the most generalized (highest *L*), five of the most specialized (lowest *L*), five of the most opportunistic (lowest *d'*) and five of the most selective (highest *d'*) flower-visitor species in each community, present at least in two temporal networks.

Table SM 2.3. Detailed information of plant dataset. Here we indicate for each grade of specificity (generalized [A], specialized [B], opportunistic [C] or selective species [D]): zone, species code (sp.code), month, linkage level (*L*), level of selectiveness (*d'*), functional richness, rank abundance and evenness of abundances.

Table SM 2.4. Detailed information of flower-visitor dataset. Here we indicate for each grade of specificity (generalized [A], specialized [B], opportunistic [C] or selective species [D]): zone, species code (sp.code), month, linkage level (*L*), level of selectiveness (*d'*), functional richness, rank abundance and evenness of abundances.

Table SM 2.1

Zone	Family	Plant species	sp.code	*L*	*d'*	Specificity
Caletón Blanco	Asteraceae	*Launaea arborescens*	lau.arb	22	0.29	Generalized and opportunistic
	Asteraceae	*Pulicaria canariensis*	pul.can	-	0.25	Opportunistic
	Caryophyllaceae	*Policarpaea nivea*	pol.niv	11	0.40	Generalized and selective
	Chenopodiaceae	*Atriplex* sp.	atr.sp	3	0.43	Specialized and selective
	Chenopodiaceae	*Traganum moquinii*	tra.moq	2	0.24	Specialized and opportunistic
	Cruciferae	*Cakile maritima*	cak.mar	15	0.52	Generalized and selective
	Euphorbiaceae	*Euphorbia balsamifera*	eup.bal	24	-	Generalized
	Leguminosae	*Ononis tournefortii*	ono.tou	-	0.74	Selective
	Orobanchaceae	*Cistanche phelipaea*	cis.phe	-	0.54	Selective
	Polygonaceae	*Poligonum maritimum*	pol.mar	3	-	Specialized
	Solanaceae	*Nicotiana glauca*	nic.gla	2	0.12	Specialized and opportunistic
	Resedaceae	*Reseda crystallina*	ama.peq	4	0.22	Specialized and opportunistic
	Zygophyllaceae	*Zygophyllum fontanesii*	zyg.fon	11	-	Generalized
Las Conchas	Aizoaceae	*Mesembryanthemum crystalinum*	mes.cry	2	0.95	Specialized and selective
	Asteraceae	*Senecio leucanthemifolius*	ama.pin	16	-	Generalized
	Asteraceae	*Launaea arborescens*	lau.arb	24	0.28	Generalized and opportunistic
	Chenopodiaceae	*Atriplex* sp.	atr.sp	2	-	Specialized
	Cruciferae	*Cakile maritima*	cak.mar	19	-	Generalized
	Cruciferae	*Matthiola bolleana*	mat.bol	-	0.65	Selective
	Frankeniaceae	*Frankenia capitata*	fra.cap	-	0.30	Opportunistic
	Geraniaceae	*Erodium hesperium*	ero.hes	2	0.30	Specialized and opportunistic
	Leguminosae	*Ononis tournefortii*	ono.tou	3	-	Specialized
	Leguminosae	*Lotus glinoides*	lot.gli	1	0.83	Specialized and selective
	Leguminosae	*Ononis hesperia*	ono.hes	-	0.25	Opportunistic
	Polygonaceae	*Poligonum nivea*	pol.niv	16	0.62	Generalized and selective
	Umbelliferae	*Astydamia latifolia*	ast.lat	30	0.64	Generalized and selective
	Zygophyllaceae	*Zygophyllum fontanesii*	zyg.fon	-	0.31	Opportunistic
Cala Mesquida	Asteraceae	*Aetheoriza bulbosa*	aet.bul	3	-	Specialized
	Asteraceae	*Asteriscus aquaticus*	ast.aqu	-	0.41	Opportunistic
	Asteraceae	*Bellis annua*	bel.ann	-	0.79	Selective
	Asteraceae	*Galactites tomentosa*	gal.tom	14	0.42	Generalized and opportunistic
	Asteraceae	*Helichrysum stoechas*	hel.sto	-	0.67	Selective
	Asteraceae	*Launaea cervicornis*	lau.cer	19	0.79	Generalized and selective
	Asteraceae	*Reichardia tingitana*	rei.tin	-	0.42	Opportunistic
	Asteraceae	*Scolimus hispanicus*	sco.his	16	-	Generalized
	Caryophyllaceae	*Polycarpon polycarpoides*	pol.pol	2	0.79	Specialized and selective
	Cistaceae	*Cistus monspeliensis*	cis.mon	20	0.43	Generalized and opportunistic
	Euphorbiaceae	*Euphorbia paralias*	eup.par	42	0.78	Generalized and selective
	Leguminosae	*Astragalus balearicus*	ast.bal	2	-	Specialized
	Leguminosae	*Ononis natrix*	ono.nat	2	-	Specialized
	Liliaceae	*Asphodelus aestivus*	asp.aes	-	0.34	Opportunistic
	Poaceae	*Lagurus ovatus*	lag.ova	3	-	Specialized
Son Bosc	Asteraceae	*Centaurea aspera*	cen.asp	-	0.28	Opportunistic
	Cistaceae	*Cistus salvifolius*	cis.sal	19	-	Generalized
	Cistaceae	*Fumana* sp.	fum.sp	2	-	Specialized
	Convolvulaceae	*Convolvulus arvensis*	con.arv	20	-	Generalized
	Cruciferae	*Cakile maritima*	cak.mar	1	0.98	Specialized and selective
	Cruciferae	*Eruca vesicaria*	eru.ves	2	-	Specialized
	Dipsacaceae	*Scabiosa marititma*	sca.mar	-	0.32	Opportunistic
	Euphorbiaceae	*Euphorbia terracina*	eup.ter	24	-	Generalized
	Gentianaceae	*Blackstonia perfoliata*	bla.per	3	0.84	Specialized and selective
	Labiatae	*Sideritis romana*	sid.rom	-	0.79	Selective
	Labiatae	*Teucrium dunense*	med.lit	-	0.76	Selective
	Leguminosae	*Lotus corniculatus*	lot.cor	-	0.33	Opportunistic
	Liliaceae	*Asphodelus fistulosus*	asp.fis	-	0.17	Opportunistic
	Myoporaceae	*Myoporum tenuiflorum*	all.ros	-	0.15	Opportunistic
	Rosaceae	*Potentilla reptans*	pot.rep	22	-	Generalized
	Scrophulariaceae	*Bellardia trixago*	bel.tri	3	-	Specialized
	Umbelliferae	*Daucus carota*	dau.car	28	0.89	Generalized and selective

Table SM 2.2

Zone	FG	Flower-vistor species	sp.code	*L*	*d'*	Specificity
Caletón Blanco	Beetle	*Aulacoderus canariensis*	aul.can	1	0.54	Specialized and selective
	Fly	*Chetogena acuminata*	che.acu	5	0.32	Specialized and opportunistic
	Fly	*Sarcophaga* sp1	sar.sp1	5	0.16	Specialized and opportunistic
	Fly	*Tethinidae* sp.	tet.sp	13	0.25	Generalized and opportunistic
	Formicidae	*Camponotus feae*	cam.fea	2	0.64	Specialized and selective
	Formicidae	*Plagiolepis maura*	pla.mau	8	0.33	Generalized and opportunistic
	Formicidae	*Temnothorax productus*	tem.pro	6	0.47	Generalized and selective
	Other	*Vanesa cardui*	van.car	4	0.32	Specialized and opportunistic
	Small bee	*Lasioglossum* sp.	las.sp	10	-	Generalized
	Small bee	*Osmia lanzarotensis*	osm.lan	-	0.68	Selective
	Wasp	*Leptochilus fortunatus*	lep.for	7	0.48	Generalized and selective
Las Conchas	Beetle	*Attalus* sp.	att.sp	11	0.36	Generalized and opportunistic
	Beetle	*Dasytes lanzarotesis*	das.lan	-	0.29	Opportunistic
	Beetle	*Meligethes variicollis*	mel.var	-	0.70	Selective
	Fly	*Bombylius aaroni*	bom.aar	12	-	Generalized
	Fly	*Lucilia sericata*	luc.ser	2	0.46	Specialized and selective
	Fly	*Sarcophaga* sp3	sar.sp3	12	0.27	Generalized and opportunistic
	Fly	*Tethinidae* sp.	tet.sp	14	-	Generalized
	Hoverfly	*Eupecodes corollae*	eup.cor	-	0.30	Opportunistic
	Large bee	*Anthophora alluaudi*	ant.all	12	0.28	Generalized and opportunistic
	Small bee	*Hylaeus hohmanni*	hyl.hoh	1	-	Specialized
	Small bee	*Lasioglossum* sp.	las.sp	-	0.54	Selective
	Small bee	*Nomioides deceptor*	nom.dec	2	0.97	Specialized and selective
	Small bee	*Osmia lanzarotensis*	osm.lan	5	0.71	Specialized and selective
	Wasp	*Dasytes lanzarotesis*	das.lan	4	-	Specialized
Cala Mesquida	Beetle	*Acmaodera convolvulii*	acm.con	-	0.80	Selective
	Beetle	*Bruchidius* sp1	bru.sp	15	0.17	Generalized and opportunistic
	Beetle	*Psilotrix* sp.	psi.sp	16	-	Generalized
	Fly	*Chloropidae* sp.	chl.sp	-	0.23	Opportunistic
	Fly	*Oscinomorpha* sp.	osc.sp	15	-	Generalized
	Fly	*Sarcophaga filia*	sar.fil	1	-	Specialized
	Fly	*Sarcophaga uncicurva*	sar.unc	-	0.64	Selective
	Fly	*Hecamede albicans*	hec.alb	2	-	Specialized
	Fly	*Paragus tibialis*	par.tib	-	0.81	Opportunistic
	Fly	*Trachysiphonella* sp.	tra.sp	-	0.20	Opportunistic
	Large bee	*Apis mellifera*	api.mel	13	-	Generalized
	Large bee	*Chalicodoma sicula*	cha.sic	-	0.80	Selective
	Other	*Lepydargyrus ancorifer*	lep.anc	1	0.63	Specialized and selective
	Formicidae	*Plagiolepis pygmaea*	pla.pyg	12	0.24	Generalized and opportunistic
	Small bee	*Hoplitis leucomelana*	hop.leu	1	0.81	Specialized and selective
	Small bee	*Ceratina parvula*	cer.par	2	-	Specialized
Son Bosc	Beetle	*Byrrhidae* sp.	byr.sp	3	-	Specialized
	Beetle	*Chlorophorus trifasciatus*	chl.tri	-	0.19	Opportunistic
	Beetle	*Isomira* sp.	iso.sp	4	-	Specialized
	Beetle	*Meligethes* sp.	mel.sp	32	0.78	Generalized and selective
	Beetle	*Oedemera simplex*	oed.sim	-	0.22	Opportunistic
	Beetle	*Oxythryrea funesta*	oxy.fun	2	-	Specialized
	Beetle	*Psilotrix* sp.	psi.sp	21	-	Generalized
	Beetle	*Spermophagus* sp.	spe.sp	28	-	Generalized
	Fly	*Stevenia deceptoria*	ste.dec	-	0.26	Opportunistic
	Fly	*Stomorhina lunata*	sto.lun	-	0.13	Opportunistic
	HoverFly	*Eristalinus aeneus*	eri.aen	4	0.05	Specialized and opportunistic
	HoverFly	*Paragus tibialis*	par.tib	-	0.79	Selective
	HoverFly	*Sphaenophoria* sp.	sph.sp	21	-	Generalized
	Large bee	*Apis mellifera*	api.mel	-	0.84	Selective
	Large bee	*Rhodhantidium septemdentatum*	rho.sep	15	-	Generalized
	Small bee	*Andrena micrandrena*	and.mic	4	0.96	Specialized and selective
	Small bee	*Lasioglossum griseolum*	las.gri	-	0.92	Selective

Table SM 2.3 (A)

Specificity: Generalized

Zone	sp.code	Month	*L*	Functional richness	Rank abundance	Evenness of abundances
Caletón Blanco	cak.mar	1 (January)	5	5	2.80	0.183
	cak.mar	2 (February)	4	3	2.75	0.184
	cak.mar	3 (March)	3	3	3.00	0.026
	cak.mar	4 (April)	7	5	2.71	0.263
	eup.bal	1 (January)	10	4	1.70	0.453
	eup.bal	2 (February)	9	4	2.22	0.309
	eup.bal	3 (March)	11	4	2.27	0.143
	eup.bal	4 (April)	9	5	2.22	0.275
	lau.arb	1 (January)	7	4	2.71	0.257
	lau.arb	2 (February)	10	6	1.70	0.282
	lau.arb	3 (March)	5	5	2.40	0.088
	lau.arb	4 (April)	7	6	2.86	0.248
	pol.niv	1 (January)	5	2	2.60	0.175
	pol.niv	2 (February)	8	4	2.13	0.263
	pol.niv	3 (March)	3	2	3.67	0.090
	pol.niv	4 (April)	4	3	3.25	0.171
	zyg.fon	1 (January)	6	5	2.33	0.184
	zyg.fon	2 (February)	4	3	2.75	0.176
	zyg.fon	3 (March)	4	2	2.75	0.040
	zyg.fon	4 (April)	1	1	5.00	1.000
Las Conchas	ama.pin	1 (January)	4	2	2.75	0.192
	ama.pin	2 (February)	6	4	2.50	0.242
	ama.pin	3 (March)	7	5	2.29	0.265
	ama.pin	4 (April)	5	3	2.80	0.318
	ast.lat	1 (January)	15	4	1.73	0.371
	ast.lat	2 (February)	12	6	1.67	0.262
	ast.lat	3 (March)	9	5	1.33	0.299
	ast.lat	4 (April)	13	6	1.54	0.391
	cak.mar	1 (January)	10	6	1.80	0.115
	cak.mar	2 (February)	8	4	2.50	0.247
	cak.mar	3 (March)	10	4	2.30	0.307
	cak.mar	4 (April)	5	4	3.20	0.318
	lau.arb	1 (January)	11	5	2.27	0.191
	lau.arb	2 (February)	8	5	2.38	0.247
	lau.arb	3 (March)	7	3	2.71	0.282
	lau.arb	4 (April)	12	5	2.33	0.289
	pol.niv	1 (January)	7	2	1.71	0.242
	pol.niv	2 (February)	7	3	2.00	0.230
	pol.niv	3 (March)	6	3	1.83	0.189
	pol.niv	4 (April)	3	2	1.67	0.184
Cala Mesquida	cis.mon	1 (April)	2	2	2.00	0.217
	cis.mon	2 (May)	19	6	1.53	0.519
	eup.par	2 (May)	17	6	1.71	0.453
	eup.par	3 (June)	32	8	1.66	0.433
	eup.par	4 (July)	15	5	2.27	0.425
	gal.tom	1 (April)	4	3	3.50	0.224
	gal.tom	2 (May)	9	5	2.22	0.113
	gal.tom	3 (June)	6	3	1.67	0.344
	lau.cer	2 (May)	5	3	2.60	0.072
	lau.cer	3 (June)	13	6	2.31	0.330
	lau.cer	4 (July)	3	3	2.33	0.181
	sco.his	3 (June)	12	4	1.25	0.455
	sco.his	4 (July)	6	3	1.67	0.271
Son Bosc	cis.sal	1 (April)	8	3	1.88	0.079
	cis.sal	2 (May)	15	6	2.60	0.254
	con.arv	2 (May)	4	3	4.75	0.182
	con.arv	3 (June)	13	6	2.08	0.225
	con.arv	4 (July)	7	4	2.43	0.334
	dau.car	2 (May)	14	6	1.93	0.221
	dau.car	3 (June)	19	7	1.74	0.269
	dau.car	4 (July)	12	6	2.00	0.333
	eup.ter	1 (April)	9	4	2.44	0.139
	eup.ter	2 (May)	8	4	2.25	0.160
	eup.ter	3 (June)	7	6	2.29	0.144
	pot.rep	2 (May)	11	6	2.45	0.251
	pot.rep	3 (June)	15	6	1.93	0.265

Table SM 2.3 (B)

Specificity: Specialized						
Zone	sp.code	Month	*L*	Functional richness	Rank abundance	Evenness of abundances
Caletón Blanco	ama.peq	2 (February)	1	1	5.00	1.000
	ama.peq	3 (March)	1	1	5.00	1.000
	ama.peq	4 (April)	4	3	3.25	0.199
	atr.sp	3 (March)	1	1	5.00	1.000
	atr.sp	4 (April)	2	2	2.00	0.198
	nic.gla	2 (February)	1	1	5.00	1.000
	nic.gla	3 (March)	2	2	4.50	0.079
	pol.mar	1 (January)	1	1	1.00	1.000
	pol.mar	2 (February)	2	2	4.50	0.139
	pol.mar	3 (March)	2	1	3.50	0.009
	pol.mar	4 (April)	1	1	5.00	1.000
	tra.moq	1 (January)	1	1	3.00	1.000
	tra.moq	2 (February)	1	1	4.00	1.000
Las Conchas	atr.sp	1 (January)	1	1	4.00	1.000
	atr.sp	2 (February)	1	1	1.00	1.000
	ero.hes	1 (January)	1	1	1.00	1.000
	ero.hes	2 (February)	1	1	4.00	1.000
	lot.gli	2 (February)	1	1	2.00	1.000
	lot.gli	3 (March)	1	1	2.00	1.000
	lot.gli	4 (April)	1	1	1.00	1.000
	mes.cry	3 (March)	1	1	1.00	1.000
	mes.cry	4 (April)	2	2	2.50	0.142
	ono.tou	3 (March)	2	2	2.50	0.156
	ono.tou	4 (April)	2	2	2.00	0.156
Cala Mesquida	aet.bul	1 (April)	3	2	3.67	0.167
	aet.bul	2 (May)	1	1	4.00	1.000
	ast.bal	1 (April)	2	1	3.50	0.219
	ast.bal	2 (May)	1	1	2.00	1.000
	lag.ova	1 (April)	1	1	5.00	1.000
	lag.ova	2 (May)	3	2	2.67	0.168
	ono.nat	2 (May)	1	1	2.00	1.000
	ono.nat	3 (June)	2	2	1.00	0.273
	pol.pol	1 (April)	1	1	3.00	1.000
	pol.pol	2 (May)	2	2	1.50	0.241
Son Bosc	bel.tri	1 (April)	2	1	4.50	0.062
	bel.tri	2 (May)	1	1	1.00	1.000
	bla.per	2 (May)	1	1	1.00	1.000
	bla.per	3 (June)	3	3	1.67	0.156
	bla.per	4 (July)	1	1	1.00	1.000
	cak.mar	3 (June)	1	1	1.00	1.000
	cak.mar	4 (July)	1	1	2.00	1.000
	eru.ves	1 (April)	1	1	4.00	1.000
	eru.ves	4 (July)	1	1	4.00	1.000
	fum.sp	3 (June)	1	1	2.00	1.000
	fum.sp	4 (July)	1	1	1.00	1.000

Table SM 2.3 (C)

Specificity: Opportunistic						
Zone	**sp.code**	**Month**	***d'***	**Functional richness**	**Rank abundance**	**Evenness of abundances**
Caletón Blanco	ama.peq	2 (February)	0.28	1	5.00	1.000
	ama.peq	3 (March)	0.07	1	5.00	1.000
	ama.peq	4 (April)	0.27	3	3.25	0.199
	lau.arb	1 (January)	0.46	4	2.71	0.257
	lau.arb	2 (February)	0.57	6	1.70	0.282
	lau.arb	3 (March)	0.22	5	2.40	0.088
	lau.arb	4 (April)	0.25	6	2.86	0.248
	nic.gla	2 (February)	0.35	1	5.00	1.000
	nic.gla	3 (March)	0.05	2	4.50	0.079
	pul.can	2 (February)	0.38	3	3.00	0.146
	pul.can	3 (March)	0.10	3	3.33	0.082
	pul.can	4 (April)	0.46	4	2.17	0.180
	tra.moq	1 (January)	0.17	1	3.00	1.000
	tra.moq	2 (February)	0.47	1	4.00	1.000
Las Conchas	ero.hes	1 (January)	0.52	1	1.00	1.000
	ero.hes	2 (February)	0.31	1	4.00	1.000
	fra.cap	2 (February)	0.30	1	4.00	1.000
	fra.cap	3 (March)	0.45	2	1.33	0.200
	fra.cap	4 (April)	0.31	3	2.00	0.320
	lau.arb	1 (January)	0.35	5	2.27	0.191
	lau.arb	2 (February)	0.30	5	2.38	0.247
	lau.arb	3 (March)	0.48	3	2.71	0.282
	lau.arb	4 (April)	0.44	5	2.33	0.289
	ono.hes	1 (January)	0.58	2	4.00	0.047
	ono.hes	2 (February)	0.25	4	2.80	0.198
	ono.hes	3 (March)	0.26	3	2.50	0.205
	zyg.fon	1 (January)	0.36	3	2.75	0.062
	zyg.fon	2 (February)	0.61	2	1.50	0.141
	zyg.fon	3 (March)	0.47	1	1.00	1.000
Cala Mesquida	asp.aes	1 (April)	0.47	2	2.50	0.098
	asp.aes	2 (May)	0.29	2	2.00	0.203
	asp.aes	3 (June)	0.99	1	1.00	1.000
	ast.aqu	2 (May)	0.42	3	3.00	0.038
	ast.aqu	3 (June)	0.47	6	3.00	0.240
	ast.aqu	4 (July)	0.68	2	2.50	0.041
	cis.mon	1 (April)	0.83	2	2.00	0.217
	cis.mon	2 (May)	0.67	6	1.53	0.519
	gal.tom	1 (April)	0.73	3	3.50	0.224
	gal.tom	2 (May)	0.45	5	2.22	0.113
	gal.tom	3 (June)	0.72	3	1.67	0.344
	rei.tin	1 (April)	0.72	2	2.67	0.080
	rei.tin	2 (May)	0.39	4	2.40	0.239
	rei.tin	3 (June)	0.53	3	2.33	0.221
	rei.tin	4 (July)	0.77	2	1.50	0.181
Son Bosc	asp.fis	1 (April)	0.61	3	3.00	0.073
	asp.fis	2 (May)	0.59	3	3.60	0.171
	asp.fis	3 (June)	0.32	3	3.00	0.166
	asp.fis	4 (July)	0.69	1	4.00	1.000
	cen.asp	2 (May)	0.48	5	2.70	0.214
	cen.asp	3 (June)	0.20	3	2.50	0.179
	cen.asp	4 (July)	0.58	2	2.25	0.240
	lot.cor	1 (April)	0.94	3	2.25	0.019
	lot.cor	2 (May)	0.42	3	1.33	0.237
	lot.cor	3 (June)	0.45	2	2.25	0.207
	lot.cor	4 (July)	0.85	3	2.50	0.234
	myo.ten	2 (May)	0.23	1	2.50	0.158
	myo.ten	3 (June)	0.14	5	3.50	0.213
	sca.mar	2 (May)	0.37	3	3.17	0.181
	sca.mar	3 (June)	0.15	5	1.75	0.390
	sca.mar	4 (July)	0.94	4	2.75	0.285

Table SM 2.3 (D)

Specificity: Selective						
Zone	**sp.code**	**Month**	***d'***	**Functional richness**	**Rank abundance**	**Evenness of abundances**
Caletón Blanco	atr.sp	3 (March)	0.12	1	5.00	1.000
	atr.sp	4 (April)	0.95	2	2.00	0.198
	cak.mar	1 (January)	0.79	5	2.80	0.183
	cak.mar	2 (February)	0.58	3	2.75	0.184
	cak.mar	3 (March)	0.34	3	3.00	0.026
	cak.mar	4 (April)	0.78	5	2.71	0.263
	cis.phe	1 (January)	0.74	2	2.50	0.197
	cis.phe	2 (February)	0.40	3	2.00	0.271
	cis.phe	3 (March)	0.32	4	3.00	0.091
	cis.phe	4 (April)	0.54	3	2.25	0.250
	ono.tou	3 (March)	1.00	1	1.00	1.000
	ono.tou	4 (April)	0.82	2	2.67	0.200
	pol.niv	1 (January)	0.45	2	2.60	0.175
	pol.niv	2 (February)	0.69	4	2.13	0.263
	pol.niv	3 (March)	0.19	2	3.67	0.090
	pol.niv	4 (April)	0.47	4	3.25	0.171
Las Conchas	ast.lat	1 (January)	0.76	4	1.73	0.371
	ast.lat	2 (February)	0.78	6	1.67	0.262
	ast.lat	3 (March)	0.72	5	1.33	0.299
	ast.lat	4 (April)	0.67	6	1.54	0.391
	lot.gli	2 (February)	0.53	1	2.00	1.000
	lot.gli	3 (March)	0.85	1	2.00	1.000
	lot.gli	4 (April)	0.95	1	1.00	1.000
	mat.bol	1 (January)	0.26	1	3.00	1.000
	mat.bol	2 (February)	0.85	1	1.00	1.000
	mat.bol	3 (March)	0.90	4	2.00	0.242
	mat.bol	4 (April)	0.54	2	2.50	0.082
	mes.cry	3 (March)	1.00	1	1.00	1.000
	mes.cry	4 (April)	0.95	2	2.50	0.142
	pol.niv	1 (January)	0.58	2	1.71	0.242
	pol.niv	2 (February)	0.75	3	2.00	0.230
	pol.niv	3 (March)	0.80	3	1.83	0.189
	pol.niv	4 (April)	0.93	2	1.67	0.184
Cala Mesquida	bel.ann	1 (April)	0.83	2	2.00	0.499
	bel.ann	2 (May)	0.63	1	1.00	1.000
	bel.ann	3 (June)	0.43	2	1.50	0.203
	eup.par	2 (May)	0.74	6	1.71	0.453
	eup.par	3 (June)	0.78	8	1.66	0.433
	eup.par	4 (July)	0.79	5	2.27	0.425
	hel.sto	2 (May)	0.47	3	2.08	0.386
	hel.sto	3 (June)	0.78	6	1.81	0.356
	lau.cer	2 (May)	0.90	3	2.60	0.072
	lau.cer	3 (June)	0.73	6	2.31	0.330
	lau.cer	4 (July)	0.60	3	2.33	0.181
	pol.pol	1 (April)	0.59	1	3.00	1.000
	pol.pol	2 (May)	0.92	2	1.50	0.241
Son Bosc	bla.per	2 (May)	1.00	1	1.00	1.000
	bla.per	3 (June)	0.81	3	1.67	0.156
	bla.per	4 (July)	1.00	1	1.00	1.000
	cak.mar	3 (June)	0.93	1	1.00	1.000
	cak.mar	4 (July)	0.98	1	2.00	1.000
	dau.car	2 (May)	0.88	6	1.93	0.221
	dau.car	3 (June)	0.95	7	1.74	0.269
	dau.car	4 (July)	0.87	6	2.00	0.333
	sid.rom	2 (May)	1.00	2	1.00	1.000
	sid.rom	3 (June)	0.83	2	2.00	0.039
	sid.rom	4 (July)	0.90	3	2.17	0.369
	teu.dun	3 (June)	0.83	7	1.82	0.348
	teu.dun	4 (July)	0.56	4	1.86	0.417

Table SM 2.4 (A)

Specificity: Generalized

Zone	sp.code	Month	*L*	Functional richness	Rank abundance	Evenness of abundances
Caletón Blanco	las.sp	1 (January)	3	3	3.00	0.314
	las.sp	2 (February)	7	5	2.57	0.362
	las.sp	3 (March)	3	3	3.67	0.213
	las.sp	4 (April)	6	5	1.67	0.243
	lep.for	2 (February)	2	2	3.00	0.177
	lep.for	3 (March)	1	1	3.00	1.000
	lep.for	4 (April)	4	3	1.50	0.290
	pla.mau	1 (January)	2	2	2.50	0.098
	pla.mau	2 (February)	4	4	2.00	0.332
	pla.mau	3 (March)	6	5	2.50	0.283
	pla.mau	4 (April)	4	4	2.50	0.180
	tem.pro	1 (January)	4	4	3.00	0.351
	tem.pro	2 (February)	4	4	2.25	0.352
	tem.pro	3 (March)	2	2	3.00	0.164
	tet.sp	1 (January)	6	5	2.50	0.437
	tet.sp	2 (February)	11	8	2.36	0.427
	tet.sp	3 (March)	13	10	2.85	0.420
	tet.sp	4 (April)	8	6	2.63	0.315
Las Conchas	ant.all	1 (January)	8	5	2.50	0.168
	ant.all	2 (February)	8	6	3.75	0.262
	ant.all	3 (March)	11	6	2.91	0.202
	ant.all	4 (April)	6	5	2.17	0.197
	att.sp	1 (January)	1	1	3.00	1.000
	att.sp	2 (February)	4	3	3.25	0.158
	att.sp	3 (March)	9	4	2.22	0.264
	att.sp	4 (April)	9	4	1.56	0.173
	bom.aar	1 (January)	2	2	2.50	0.180
	bom.aar	2 (February)	5	4	3.00	0.193
	bom.aar	3 (March)	8	4	2.63	0.210
	bom.aar	4 (April)	9	5	1.22	0.354
	sar.sp3	1 (January)	6	5	3.33	0.177
	sar.sp3	2 (February)	5	5	4.00	0.213
	sar.sp3	3 (March)	5	4	2.80	0.140
	sar.sp3	4 (April)	7	5	2.00	0.193
	tet.sp	1 (January)	7	5	2.71	0.195
	tet.sp	2 (February)	8	7	3.63	0.262
	tet.sp	3 (March)	6	4	3.17	0.136
	tet.sp	4 (April)	3	1	1.00	0.340
Cala Mesquida	api.mel	1 (April)	3	2	3.67	0.207
	api.mel	2 (May)	8	6	2.13	0.330
	api.mel	3 (June)	8	6	2.50	0.189
	api.mel	4 (July)	1	1	3.00	1.000
	bru.sp	1 (April)	1	1	1.00	1.000
	bru.sp	2 (May)	7	4	1.86	0.289
	bru.sp	3 (June)	6	3	2.33	0.140
	bru.sp	4 (July)	3	2	3.33	0.043
	osc.sp	1 (April)	3	1	1.67	0.237
	osc.sp	2 (May)	8	5	1.50	0.339
	osc.sp	3 (June)	11	5	1.55	0.119
	pla.pyg	1 (April)	3	2	2.00	0.247
	pla.pyg	2 (May)	6	5	1.83	0.220
	pla.pyg	3 (June)	6	4	2.17	0.142
	psi.sp	1 (April)	5	2	1.40	0.590
	psi.sp	2 (May)	12	4	1.42	0.303
	psi.sp	3 (June)	8	2	2.25	0.166
Son Bosc	mel.sp	1 (April)	22	15	1.59	0.343
	mel.sp	2 (May)	16	10	1.06	-
	mel.sp	3 (June)	2	2	3.00	0.005
	mel.sp	4 (July)	5	3	1.00	-
	psi.sp	1 (April)	15	11	1.27	0.852
	psi.sp	2 (May)	12	6	1.33	0.253
	psi.sp	3 (June)	2	1	1.00	0.088
	rho.sep	1 (April)	3	3	1.00	0.346
	rho.sep	2 (May)	7	7	1.14	0.871
	rho.sep	3 (June)	8	6	1.50	0.173
	rho.sep	4 (July)	1	1	1.00	1.000
	spe.sp	1 (April)	10	7	1.50	0.413
	spe.sp	2 (May)	22	11	1.32	0.449
	spe.sp	3 (June)	10	7	1.40	0.002
	spe.sp	4 (July)	6	5	2.17	1.000
	sph.sp	1 (April)	1	1	1.00	1.000
	sph.sp	2 (May)	7	6	1.29	0.514
	sph.sp	3 (June)	16	13	1.31	0.006
	sph.sp	4 (July)	2	2	3.00	0.313

Table SM 2.4 (B)

Specificity: Specialized

Zone	sp.code	Month	*L*	Functional richness	Rank abundance	Evenness of abundances
Caletón Blanco	aul.can	1 (January)	1	1	1.00	1.000
	aul.can	2 (February)	1	1	2.00	1.000
	aul.can	3 (March)	1	1	2.00	1.000
	aul.can	4 (April)	1	1	1.00	1.000
	che.acu	1 (January)	2	2	2.00	0.163
	che.acu	2 (February)	5	4	3.20	0.342
	che.acu	3 (March)	2	1	2.00	0.203
	che.acu	4 (April)	1	1	1.00	1.000
	sar.sp1	1 (January)	4	4	2.50	0.364
	sar.sp1	4 (April)	3	3	2.75	0.150
	van.car	1 (January)	1	1	1.00	1.000
	van.car	2 (February)	2	1	2.50	0.043
Las Conchas	das.lan	3 (March)	2	2	3.00	0.116
	das.lan	4 (April)	2	1	1.00	0.144
	hyl.hoh	1 (January)	1	1	5.00	1.000
	hyl.hoh	2 (February)	1	1	5.00	1.000
	hyl.hoh	3 (March)	1	1	5.00	1.000
	luc.ser	1 (January)	2	2	3.50	0.028
	luc.ser	2 (February)	1	1	5.00	1.000
	luc.ser	3 (March)	1	1	5.00	1.000
	luc.ser	4 (April)	1	1	5.00	1.000
	nom.dec	2 (February)	1	1	3.00	1.000
	nom.dec	3 (March)	1	1	1.00	1.000
	nom.dec	4 (April)	1	1	1.00	1.000
	osm.lan	2 (February)	3	1	2.33	0.054
	osm.lan	3 (March)	5	2	2.60	0.229
	osm.lan	4 (April)	2	1	1.50	0.158
Cala Mesquida	cer.par	3 (June)	2	1	1.00	0.160
	cer.par	4 (July)	2	1	1.50	0.230
	hec.alb	2 (May)	2	1	4.00	0.145
	hec.alb	3 (June)	2	1	4.00	0.076
	hop.leu	2 (May)	1	1	1.00	1.000
	hop.leu	3 (June)	1	1	1.00	1.000
	lep.anc	2 (May)	1	1	1.00	1.000
	lep.anc	3 (June)	1	1	1.00	1.000
	sar.fil	3 (June)	1	1	5.00	1.000
	sar.fil	4 (July)	1	1	5.00	1.000
Son Bosc	and.mic	2 (May)	2	2	1.00	0.586
	and.mic	3 (June)	2	2	2.00	0.004
	byr.sp	1 (April)	2	1	1.00	0.204
	byr.sp	2 (May)	3	1	1.00	-
	eri.aen	3 (June)	2	2	3.00	0.004
	eri.aen	4 (July)	2	2	3.00	1.000
	iso.sp	1 (April)	2	2	1.00	0.288
	iso.sp	2 (May)	2	2	1.00	0.554
	oxy.fun	2 (May)	2	2	1.00	0.704
	oxy.fun	3 (June)	1	1	1.00	1.000

Table SM 2.4 (C)

Specificity: Opportunistic

Zone	sp.code	Month	*d'*	Functional richness	Rank abundance	Evenness of abundances
Caletón Blanco	che.acu	1 (January)	0.57	2	2.00	0.163
	che.acu	2 (February)	0.33	4	3.20	0.342
	che.acu	3 (March)	0.41	1	2.50	0.203
	che.acu	4 (April)	0.59	1	1.00	1.000
	pla.mau	1 (January)	0.44	2	2.50	0.098
	pla.mau	2 (February)	0.39	4	2.00	0.332
	pla.mau	3 (March)	0.31	5	2.50	0.283
	pla.mau	4 (April)	0.62	4	2.50	0.180
	sar.sp1	1 (January)	0.41	4	2.50	0.364
	sar.sp1	4 (April)	0.22	3	3.33	0.150
	tet.sp	1 (January)	0.58	5	2.50	0.437
	tet.sp	2 (February)	0.48	8	2.36	0.427
	tet.sp	3 (March)	0.24	10	2.85	0.420
	tet.sp	4 (April)	0.40	6	2.63	0.315
	van.car	1 (January)	0.55	1	3.00	1.000
	van.car	2 (February)	0.40	1	2.50	0.043
Las Conchas	ana.pro	1 (January)	0.15	1	5.00	1.000
	ana.pro	2 (February)	0.14	1	5.00	1.000
	ant.all	1 (January)	0.69	5	2.50	0.168
	ant.all	2 (February)	0.47	6	3.75	0.262
	ant.all	3 (March)	0.44	6	2.91	0.202
	ant.all	4 (April)	0.36	5	2.17	0.197
	att.sp	1 (January)	0.33	1	3.00	1.000
	att.sp	3 (March)	0.45	4	2.22	0.264
	att.sp	4 (April)	0.46	4	1.56	0.173
	das.lan	3 (March)	0.22	2	3.00	0.001
	das.lan	4 (April)	0.53	1	1.00	0.153
	eup.cor	2 (February)	0.36	3	3.67	0.079
	eup.cor	4 (April)	0.34	1	5.00	1.000
	sar.sp3	1 (January)	0.33	5	3.33	0.177
	sar.sp3	2 (February)	0.46	5	4.00	0.213
	sar.sp3	3 (March)	0.81	4	2.80	0.140
	sar.sp3	4 (April)	0.39	5	2.00	0.193
Cala Mesquida	bru.sp	1 (April)	0.81	1	1.00	1.000
	bru.sp	2 (May)	0.28	4	1.86	0.289
	bru.sp	3 (June)	0.09	3	2.33	0.140
	bru.sp	4 (July)	0.16	2	3.33	0.043
	chl.sp	2 (May)	0.55	1	1.00	1.000
	chl.sp	4 (July)	0.12	1	5.00	1.000
	par.tib	2 (May)	0.80	4	3.00	0.209
	par.tib	3 (June)	0.80	5	2.56	0.227
	pla.pyg	1 (April)	0.73	2	2.00	0.247
	pla.pyg	2 (May)	0.48	5	1.83	0.220
	pla.pyg	3 (June)	0.22	4	2.17	0.142
	tra.sp	2 (May)	0.52	2	2.00	0.151
	tra.sp	3 (June)	0.21	3	3.33	0.096
	tra.sp	4 (July)	0.12	1	5.00	1.000
Son Bosc	chl.tri	2 (May)	0.36	2	2.50	0.058
	chl.tri	3 (June)	0.14	5	2.60	0.031
	eri.aen	3 (June)	0.11	2	3.00	0.004
	eri.aen	4 (July)	0.06	2	3.00	1.000
	oed.sim	2 (May)	0.62	3	1.33	0.819
	oed.sim	3 (June)	0.24	4	2.25	0.002
	ste.dec	1 (April)	0.67	2	1.33	-
	ste.dec	2 (May)	0.26	5	1.83	0.277
	ste.dec	3 (June)	0.34	1	5.00	1.000
	sto.lun	2 (May)	0.72	1	1.00	1.000
	sto.lun	3 (June)	0.11	5	1.67	0.011

Table SM 2.4 (D)

Specificity: Selective

Zone	sp.code	Month	*d'*	Functional richness	Rank abundance	Evenness of abundances
Caletón Blanco	aul.can	1 (January)	0.59	1	1.00	1.000
	aul.can	3 (March)	0.50	1	2.00	1.000
	aul.can	4 (April)	0.52	1	1.00	1.000
	lep.for	2 (February)	0.78	2	3.00	0.177
	lep.for	4 (April)	0.58	3	1.50	0.290
	osm.lan	3 (March)	0.86	2	3.50	0.085
	osm.lan	4 (April)	0.77	4	1.33	0.284
	tem.pro	1 (January)	0.62	4	3.00	0.351
	tem.pro	2 (February)	0.20	4	2.25	0.352
	tem.pro	3 (March)	0.42	2	3.00	0.164
Las Conchas	las.sp	2 (February)	0.28	2	2.50	0.170
	las.sp	3 (March)	0.72	1	2.00	0.189
	las.sp	4 (April)	0.55	5	1.43	0.175
	luc.ser	1 (January)	0.30	2	3.50	0.028
	luc.ser	2 (February)	0.46	1	5.00	1.000
	mel.var	1 (January)	0.77	4	2.00	0.327
	mel.var	2 (February)	0.60	3	2.75	0.121
	mel.var	3 (March)	0.84	3	2.40	0.243
	mel.var	4 (April)	0.76	2	1.25	0.166
	nom.dec	3 (March)	1.00	1	1.00	1.000
	nom.dec	4 (April)	0.99	1	1.00	1.000
	osm.lan	2 (February)	0.56	1	2.33	0.054
	osm.lan	3 (March)	0.78	2	2.60	0.229
	osm.lan	4 (April)	0.99	1	1.50	0.158
Cala Mesquida	acm.con	2 (May)	0.75	1	1.00	-
	acm.con	3 (June)	0.83	1	1.00	-
	cha.sic	1 (April)	0.72	1	2.50	0.006
	cha.sic	2 (May)	0.59	4	1.43	0.366
	cha.sic	3 (June)	0.95	3	1.00	0.407
	hop.leu	2 (May)	0.80	1	1.00	1.000
	hop.leu	3 (June)	0.80	1	1.00	1.000
	lep.anc	2 (May)	0.79	1	1.00	1.000
	lep.anc	3 (June)	0.58	1	1.00	1.000
	sar.unc	1 (April)	0.73	3	2.25	0.166
	sar.unc	2 (May)	0.82	4	2.25	0.205
Son Bosc	and.mic	2 (May)	0.56	2	1.00	0.586
	and.mic	3 (June)	1.00	2	2.00	0.004
	api.mel	1 (April)	0.93	5	1.17	-
	api.mel	2 (May)	0.78	9	1.70	0.073
	api.mel	3 (June)	0.82	7	1.89	0.101
	las.gri	3 (June)	0.83	4	1.00	0.887
	las.gri	4 (July)	0.94	4	1.00	0.861
	mel.sp	1 (April)	0.85	15	1.59	0.343
	mel.sp	2 (May)	0.61	10	1.06	-
	mel.sp	3 (June)	0.06	2	3.00	0.005
	mel.sp	4 (July)	0.71	3	1.00	-
	par.tib	2 (May)	0.98	4	1.20	0.405
	par.tib	3 (June)	0.67	5	1.20	0.229

Capítulo 3

Diferencias entre las redes de visitantes florales de una isla oceánica y una continental

Chapter 3

Differences in flower-visitation networks between an oceanic and a continental island

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Resumen

Dos diferencias biológicas importantes entre islas oceánicas y continentales son que las primeras tienen en general menor riqueza de especies y un mayor grado de disarmonía taxonómica que las segundas. Aunque existen algunas evidencias de redes de interacción planta/animal menos complejas en islas oceánicas, sólo unos pocos estudios comparan las comunidades insulares entre ellas o con comunidades continentales. En este trabajo se analiza la composición de especies y las propiedades estructurales de redes cuantitativas de visitantes florales en dos comunidades de cada tipo de islas: Islas Canarias (origen oceánico) e Islas Baleares (origen continental). Se compararon diferentes parámetros de red que nos informan sobre la vulnerabilidad frente a distintos tipos de perturbaciones. El número de especies total fue mayor en las redes de Baleares que en las de Canarias pero, contrariamente a lo esperado, el número total y la diversidad de interacciones no fue diferente entre ellas. Por otra parte, un mayor número de especies oportunistas sumado a la presencia de especies supergeneralistas en la isla oceánica dieron lugar a valores significativamente más altos de conectancia y anidamiento (ambos cuantitativos) en comparación con la isla continental. Dado que estos dos parámetros parecen estar asociados a la estabilidad de la red, nuestros resultados tienden a apoyar la hipótesis de que las comunidades insulares oceánicas de polinización son menos vulnerables a las perturbaciones que las comunidades de islas continentales, aunque se necesitan más estudios en islas con este tipo de enfoque de redes para determinar si se trata de un patrón general.

Differences in flower-visitation networks between an oceanic and a continental island

Introduction

Islands are ideal ecosystems for the study of certain ecological processes owing to their relatively low species richness, high level of endemicity and limited area relative to mainland regions. Two of the main types of island, based on their geological traits, are oceanic and continental islands (continental fragments *sensu* Whittaker & Fernández-Palacios 2007), which differ strongly in their initial resident biota: continental islands bear an initial biota that is identical to that of mainland areas (Thornton 2007), whereas oceanic islands, generally formed from submarine volcanic activity, are initially devoid of life and thus their biota is entirely the result of long-distance dispersal and *in situ* speciation.

The biota of oceanic islands also shows strong disharmony relative to that of mainland areas, containing different proportions of taxa found in the mainland source areas and lacking entire groups of taxa (*e.g.* large terrestrial mammals). This disharmony is mainly caused by the abilities of different species for long-distance dispersal and establishment on islands. For example, flower visitors with long proboscises, especially bees, are typically underrepresented in oceanic island environments (Inoue 1993), whereas small insects (flies, beetles, wasps and small moths) are over-represented, possibly because of their higher probability of arrival facilitated by strong winds (Barrett 1996). Therefore, oceanic island pollination networks show an impoverishment of potential animal pollinators (Gillespie & Roderick 2002), which results in a low ratio of animal to plant species (A:P; Trøjelsgaard & Olesen 2013). On continental islands, the disharmony in biota composition is less pronounced because of their mainland origin, although it may increase over time, depending on isolation, as a result of the extinction of ancestral taxa from the source (Gillespie & Roderick 2002). Another characteristic of oceanic communities is the presence of ‘super-generalist’ species (*sensu* Olesen *et al.* 2002), *i.e.* species with very high generalization levels (large number of interacting species) relative to co-occurring species (*e.g.* Kaiser-Bunbury *et al.* 2009; Padrón *et al.* 2009; Traveset *et al.* 2013).

No comparisons have been made between the two types of island with regard to the selectivity of species in the use of resources, which depends on their availability. The complementary specialization index *d'* (Blüthgen *et al.* 2006) provides this information. According to this parameter, a pollinator that visits a plant species proportionally to its availability in the community is considered to be opportunistic, whereas a pollinator that visits rare plants disproportionately more often than common ones is considered to be selective. We might expect that a pollinator reaching a new island, regardless of its origin (continental or oceanic), and assuming no morphological restrictions to interactions with flowers, will infiltrate the pollination network by linking to the most abundant plant species (thus acting as opportunistic, *i.e.* showing low selectivity). However, species might be expected to be more opportunistic on oceanic islands because of the phenomena of 'density compensation' and niche expansion, which are caused by the lower interspecific competition relative to continental islands or mainland areas (MacArthur *et al.* 1972; Blondel *et al.* 1988).

In the last decade, the application of network techniques to the study of community patterns has allowed the identification of some general properties, their ecological and evolutionary consequences and the role of each species in the community (Bascompte & Jordano 2007; Blüthgen *et al.* 2008; Ings *et al.* 2009; Vázquez *et al.* 2009). This network approach has also contributed to a realization of the importance of maintaining and restoring the integrity of species interactions if we wish to preserve the biodiversity on islands (Kaiser-Bunbury *et al.* 2010a), where species are more vulnerable to human disturbance because of their naturally small population sizes and ranges (Cox & Elmqvist 2000; Simberloff 2000). Despite the importance of a network approach, most conservation and restoration projects do not incorporate this information as indicators of community structure, ecosystem function and resilience of restored communities to future perturbations (Memmott 2009; Kaiser-Bunbury *et al.* 2010a; Menz *et al.* 2011; Devoto *et al.* 2012).

Here, we used this network perspective to compare species composition and the structure of different pollination communities between oceanic (Lanzarote) and continental (Mallorca) islands. We focused on coastal communities because they represent the habitat in which most immigrant species arrive (Whittaker & Fernández-Palacios 2007). Despite island differences in origin, area, age and colonization sources, we expected some similarities in species composition between communities, as a result of species adaptation to coastal habitats and the close proximity to a common source area (Africa), although strong differences in the predominant group of flower visitors could be hypothesized; specifically, we expected a higher fraction of bees in the Balearics and a higher fraction of small flies in the Canaries (Inoue 1993; Barrett 1996). We also predicted a greater diversity of interactions and more specialist (low linkage level) and selective (high *d′*) species in the Balearics (Trøjelsgaard & Olesen 2013). Moreover, because of the smaller communities on oceanic islands and the presumed presence of super-generalist species (Kaiser-Bunbury *et al.* 2009; Padrón *et al.* 2009; Traveset *et al.* 2013), we further envisaged higher connectivity and nestedness in the Canaries than in the Balearics, the latter with values probably more similar to those found in studies conducted on mainland areas (Trøjelsgaard & Olesen 2013). Comparison of patterns of plant-animal interactions between oceanic and continental islands have been performed only with seed dispersal communities (González-Castro *et al.* 2012); therefore, this is the first time that pollination networks have been contrasted between these two types of island.

Materials and methods

Study sites

The study was carried out in four coastal areas, two in Mallorca (continental island) and two in Lanzarote (oceanic island) (Fig. 3.1). The distance between each island and the mainland is rather similar (approximately 125 km for Lanzarote and 180 km for Mallorca), but an important biogeographical difference is the geographical location of the archipelagos. The Canary Islands are located in the Atlantic Ocean, Africa being the only nearby mainland, whereas the Balearic Islands are located in the western Mediterranean Sea and are surrounded by different nearby landmasses acting as potential sources of colonization (*e.g.* Africa, Iberian Peninsula). Moreover, the area and island age differ considerably between the two islands: Lanzarote has a surface area of 846 km^2 and its oldest volcanic areas are aged 15.5 Myr, whereas Mallorca has a surface area of 3625 km^2 and its age is c. 5 Myr.

On Mallorca, the largest of the Balearic Islands, the two study sites were Son Bosc (SB) (39°46′28.11″N, 3°07′45.34″E, 3.9 ha) and Cala Mesquida (CM) (39°44′37.63″N, 3°26′02.12″E, 1.4 ha). SB is a dune marshland (Fig. 3.2), located in the north of the island, with a high diversity of plants; the predominant vegetation consists of *Daucus carota* L. (Apiaceae), *Helichrysum stoechas* DC. (Asteraceae), *Lotus corniculatus* L. (Fabaceae), *Lotus cytisoides* L. (Fabaceae), *Scabiosa atropurpurea* L. (Dipsacaceae) and *Teucrium dunense* Sennen (Lamiaceae). CM, in the north-east, is one of the best preserved dune areas on Mallorca (Fig. 3.2); it is dominated by typical dune vegetation, including *Euphorbia* *paralias* L. (Euphorbiaceae), *Helichrysum stoechas*, *Scrophularia canina* L. (Scrophulariaceae), *Teucrium capitatum* L. (Lamiaceae) and *Lotus cytisoides*.

On Lanzarote, in the north-east of the Canary Islands, the study took place in Caletón Blanco (CB) (29°12′15.20″N, 13°25′26.07″W, 6 ha) and Las Conchas (LC) (29°16′32.13″N, 13°30′53.34″W, 4.3 ha). CB is also one of the best preserved dune areas of Lanzarote (Fig. 3.2), located in the north-east and included in the protected area of 'La Corona Natural Monument'. The dominant vegetation in this area consists of *Tetraena fontanesi* (Webb & Berthel.) Beier & Thulin (Zygophyllaceae), *Launaea arborescens* Murb. (Asteraceae), *Euphorbia paralias*, *Senecio leucanthemifolius* Poir. (Asteraceae) and *Polycarpaea nivea* Webb (Caryophyllaceae). LC is a dune area (Fig. 3.2) located in the north-west of La Graciosa islet (29.05 km^2), approximately 1.1 km from Lanzarote. This small island is a protected area included in the 'Archipiélago Chinijo' Natural Park. The vegetation is dominated by *Astydamia latifolia* Baill. (Apiaceae), *Launaea arborescens*, *Lotus lancerottensis* Webb & Berthel. (Fabaceae), *Ononis hesperia* (Maire) Förther & Podlech (Fabaceae) and *Polycarpaea nivea*.

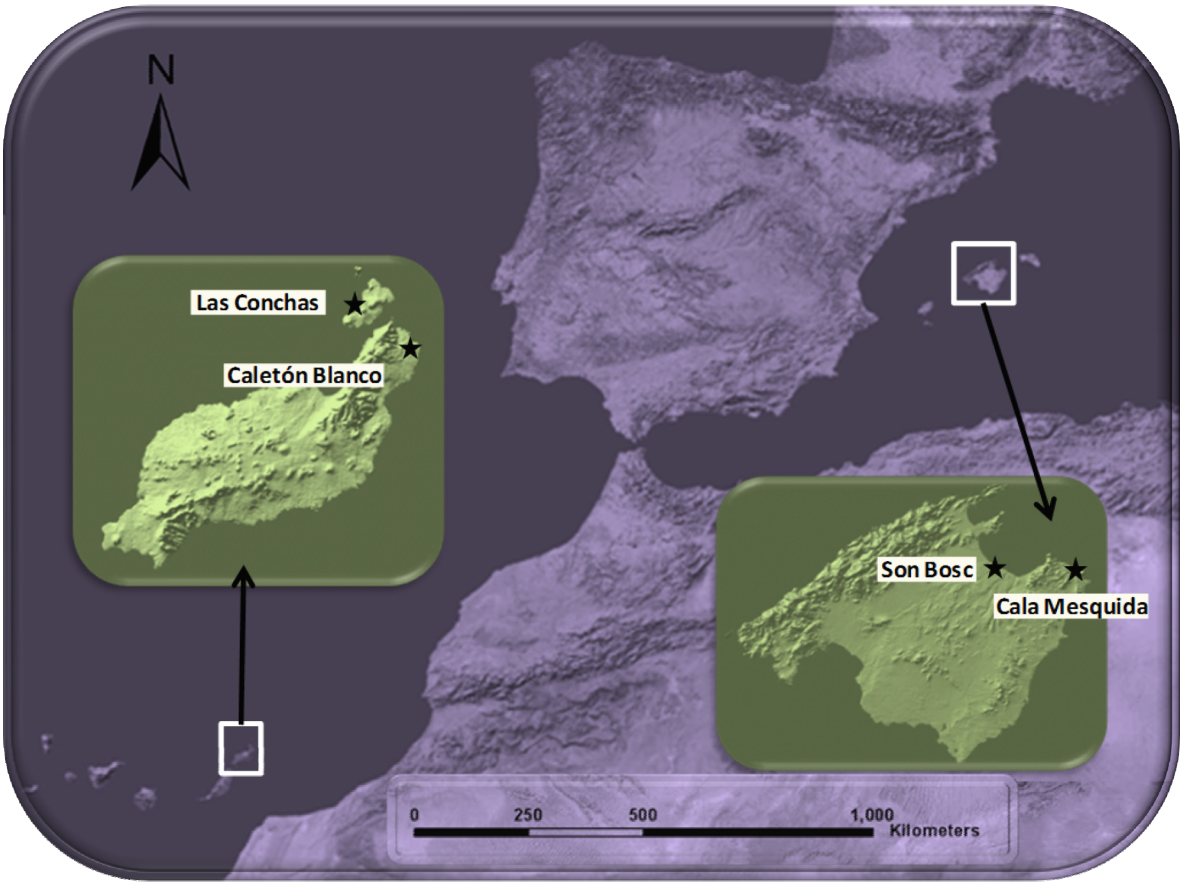

Figure 3.1. Map showing the location of the study sites.

The climatic conditions on the two study islands differ strongly. Mallorca has a mean annual temperature of 16 °C and a mean annual rainfall of 410 mm, occurring mostly from September to December. In contrast, Lanzarote has a mean annual temperature of 20.7 °C and a mean annual rainfall of 110 mm, occurring mostly from December to March (Agencia Estatal de Meteorología, AEMET).

Sampling procedure

Flower-visitor interactions were recorded in April-July 2010 on Mallorca and in January-April 2011 on Lanzarote, which covered the entire flowering spring season for both islands. Sampling started early in the year on Lanzarote because of the tight association between rainfall and plant flowering on this dry island.

Flower density was estimated every 2 weeks at each study site by counting the number of open flowers of each flowering plant observed along each of the ten (50×2 m^2) permanent belt transects established in SB and in each of the 30 (0.5×0.5 m^2) random plots located in the other three sites. Random plots instead of transects were used in

Figure 3.2. Images of each of the study coastal sites.

these sites to capture the high heterogeneity of each area. Flower density was calculated for each species as the number of open flowers divided by the total area surveyed. For species with tightly clustered inflorescences (*e.g.* Asteraceae), we scored each inflorescence as a flower.

On each census day at each community, all plants in bloom were observed, and censuses were performed once or twice a week at each site. We made randomized focal censuses, *i.e.* observing individuals of each flowering plant species at a time, between 10:00 and 17:00 h on sunny and low-wind days. Interactions were recorded from a distance of approximately 1 m from the focal plant species to minimize interference with insect behaviour during sampling. We recorded contacts between insects and flowers during 3-min periods at SB, 6-min periods at CM and 7.5-min periods in both sites on Lanzarote. Longer censuses were carried out in the last three locations because of the lower number of simultaneous species in bloom than at SB. During each census, we recorded: (1) the identity of flowering plant species; (2) the number of open flowers of each individual plant observed; (3) the identity of each flower visitor (species name if possible or morphotype otherwise); (4) the number of individuals of each species visiting flowers and (5) the number of flowers visited by each individual flower visitor. Insects that could not be identified in the field were collected for further identification by taxonomists.

The total time spent censusing flower-visitor interactions was 49:39 h at SB, 84:45 h at CM, 56:38 h at CB and 80:53 h at LC. Differences in total observation times among sites were a result of differences in the duration of the flowering period of their constituent plant species.

Species composition among sites

In order to assess the similarity in species composition among all study sites, we calculated the Bray-Curtis dissimilarity index (Bray & Curtis 1957), which ranges from zero, when species are very similar among sites, to unity, when no single species is shared among them. The Bray-Curtis dissimilarity was calculated for plants and animals separately, and at two different levels of species identification: species and genus level. Likewise, this index was calculated separately for each island, *i.e.* unifying information for the two sites.

Network parameters

Quantitative interaction networks were constructed using flower visitation rate (FVR) as the interaction weight, a measure of the intensity of mutual interaction strength between partners. The FVR of species was calculated as the number of flowers contacted by each flower visitor species during a census, standardized by the number of flowers observed, the total number of censuses per plant species and the specific flower abundance (Castro-Urgal *et al.* 2012).

We calculated quantitative network parameters, as they are more robust to sampling bias than qualitative ones (Dormann *et al.* 2009), and are thus more conservative for comparisons among different sites. We chose five parameters at the network level and three parameters at the species level which are often used to describe network structure.

At the network level, we calculated:

1. **Quantitative connectance** (C_q). This is the fraction of realized interactions in the network weighted by the interaction strength of each species, and was calculated following Bersier *et al.* (2002) (see also Kaiser-Bunbury *et al.* 2009). It is a measure of the network generalization level that tells us how connected all species in the community are. In contrast to the unweighted connectance, weighted connectance is robust against variation in sampling intensity, network size and level of asymmetry.

2. **Weighted *NODF*** (*WNODF*: Weighted Nestedness based on Overlap and Decreasing Fill; Almeida-Neto & Ulrich 2011). This is a measure of the degree of nestedness for quantitative data. Networks are nested if those species with fewer interactions are preferentially associated with a subset of species that interact with the most connected ones. It ranges from zero (not nested network) to 100 (highly nested network).

3. **Interaction evenness** (*IE*). This is a measure of the uniformity of interactions between species in a network, based on Shannon's evenness (Tylianakis *et al.* 2007). An uneven network has a high skewness in the distribution of interaction weights. It ranges from zero (completely uneven) to unity (completely uniform).

4. **Interaction diversity** (*ID*). This provides a measure of the complexity of associations in the community, separately for plants and flower visitors (*e.g.*

Albrecht *et al.* 2007). It is the Shannon diversity of interactions of a species averaged across all species, in our case flower visitors (ID_{fv}) or plant species (ID_p).

5. **Network specialization H_2'** (Blüthgen *et al.* 2006). This is a measure of the level of network selectiveness; it is also derived from Shannon entropy and is related to the weighted *d'* (described in detail below) across all species. It ranges between zero (opportunistic, high niche overlap) and unity (selective, high niche differentiation).

At the species level, we calculated:

6. **Species specialization *d'*** (Blüthgen *et al.* 2006). This is a measure of the level of selectiveness of a species. In contrast with the linkage level (see next parameter), it accounts for the available resources provided by its interaction partners. It also ranges from zero (highly opportunistic) to unity (highly selective). This index increases with the deviation from random selection of the available interaction partners based on their abundance. Thus, for instance, a flower visitor that visits flowering plant species proportionally to their availability in the community is considered to be opportunistic, whereas a flower visitor that visits rare plants disproportionately more often than common plants is considered to be selective. Given that *d'* is influenced by network asymmetry, which can be calculated as $(A-P)(A+P)^{-1}$, so that it ranges from zero (total symmetry) to unity (maximum asymmetry), where A is the number of animals and P is the number of plants in the network (Blüthgen *et al.* 2007), we used a corrected metric (d'_{corr}) (see Trøjelsgaard *et al.* 2013). This metric is derived from the residuals of the linear regressions of d'_p and d'_{fv} against network asymmetry in order to compare the four sites.

7. **Linkage level** (*L*). This tells us the level of generalization of each species, *i.e.* the number of species with which each species interacts. Although this is a qualitative parameter, we considered it here as it is frequently used when describing ecological networks, and mainly to compare it with other published pollination networks.

Finally, we also obtained a normalized linkage level (also named the normalized degree, *ND*), which is *L* divided by the number of possible partners. When calculating the mean of these two parameters, all flower visitors observed less than three times were not considered. The rationale was to avoid the overestimation of singletons and doubletons (species observed only once or twice, respectively) which might bias the true L and ND averages.

For each of the four networks, we also obtained the number of plant species (P), number of flower visitor species (A), total number of species (S), animal/plant ratio (A:P), total number of interactions (T_{int}), mean plant linkage level (L_p), mean flower visitor linkage level (L_{fv}), maximum number of partners of a plant species in each community (max. L_p) and maximum number of partners of a flower visitor species in each community (max. L_{fv}).

All network parameters and Bray-Curtis dissimilarity indices were calculated using the *bipartite* package version 1.17 (Dormann *et al.* 2009) run in R 2.11. Generalized linear mixed effect models were used to compare species specialization parameters across sites, employing site nested within island as a random factor. Tukey's test, with the general linear hypothesis function (glht; 'many-to-one comparison procedure' [Dunnett 1955]), was employed to detect differences among study sites. These analyses were performed using the packages *lme4* (Bates *et al.* 2011) and *multcomp* (Hothorn *et al.* 2008).

In order to confirm that our results described patterns that are different from random, we compared them with an appropriate null model (Dormann *et al.* 2009). We generated 1000 null versions (null model) of each community matrix using the *Patefield* algorithm implemented in the *bipartite* package with method *r2d* (Patefield 1981) (Table SM 3.1).

Results

Differences in species composition within and between islands

Species richness in the Balearic sites was more than twice as high as that in the Canarian sites. However, the total number of interactions (total number of insects observed visiting the flowers) was context dependent (Table 3.1). Thus, CM on Mallorca had fewer interactions than LC on Lanzarote, despite the fact that the number of species in the former was more than twofold higher than that in the latter. The ratio between flower visitors and plants also varied among sites and, on average, was higher on the oceanic than on the continental islands (Table 3.1).

Table 3.1. Qualitative web parameters for all studied sites: oceanic island (Lanzarote) and continental island (Mallorca). P (number of plant species), A (number of flower-visitor species), S (total number of species), A:P (animal to plant ratio), T_{int} (total number of interactions), L_p (mean plant linkage level ± SD), L_{fv} (mean flower-visitor linkage level ± SD), max. L_p (maximum number of partners of a plant species in each site), max. L_{fv} (maximum number of partners of a flower-visitor species in each site). The percentage of interactions of the most generalist species relative to the total number of interactions observed is shown in parentheses.

	Continental island		**Oceanic island**	
	Son Bosc	**Cala Mesquida**	**Caletón Blanco**	**Las Conchas**
P	69	42	18	25
A	143	131	62	62
S	212	173	80	87
A : P	2.07	3.12	3.44	2.48
T_{int}	2739	1466	1008	1913
L_p	7.33 ± 6.42	8.36 ± 7.97	7.61 ± 6.34	8.16 ± 6.84
Max L_p	28 (20%)	42 (32%)	24 (39%)	29 (47%)
L_{fv}	6.42 ± 6.4	4.76 ± 3.98	4.22 ± 3.16	4.33 ± 3.66
Max L_{fv}	32 (46%)	16 (38%)	13 (72%)	14 (56%)

The two islands differed significantly in species composition (Table 3.2); they had < 8% of species and < 30% of genera in common. At the island level, species similarity between sites was lower on Mallorca than on Lanzarote, but similarity between sites at the genus level was comparable between the islands (about 50% of genera were shared by the two sites on each island). Three plant species (*Cakile maritima* Scop., *Euphorbia paralias* and *Reichardia tingitana* (L.) Roth) were present in three of four study sites, and one bee (*Amegilla quadrifasciata*) and two butterflies (*Colias croceus* and *Vanessa cardui*) were present in all sites. At the genus level, species of *Euphorbia* L. and 12 flower visitors (five bees: *Amegilla* sp., *Andrena* spp., *Chalicodoma* spp., *Lasioglossum* spp., *Osmia* spp.; three beetles: *Dasytes* spp., *Meligethes* spp., *Mordellistena* sp.; two flies: *Sphaerophoria* spp., *Sarcophaga* spp.; and two butterfly taxa; *Vanessa* sp. and *Colias* sp.) were observed at all study sites.

Table 3.2. Bray-Curtis dissimilarity index for each two possible community combinations. This dissimilarity index ranges from zero, when species are similar among sites, to unity, when no single species is shared among them. Values in bold show the similarity in species composition between sites on the same island.

	Species-level		**Genus-level**	
	Plants	**Flower-visitors**	**Plants**	**Flower-visitors**
SB (Cont) *vs.* CM (Cont)	**0.73**	**0.55**	**0.59**	**0.44**
SB (Cont) *vs.* CB (Oce)	0.98	0.95	0.92	0.75
SB (Cont) *vs.* LC (Oce)	0.96	0.92	0.86	0.75
CM (Cont) *vs.* CB (Oce)	0.95	0.94	0.87	0.74
CM (Cont) *vs.* LC (Oce)	0.96	0.91	0.80	0.72
CB (Oce) *vs.* LC (Oce)	**0.55**	**0.51**	**0.54**	**0.44**
Continental *vs.* Oceanic	0.95	0.92	0.84	0.70

The main taxonomic group of flower visitors also varied between the two islands: bees were predominant on Mallorca (46 species (27.7%) at SB and 41 species (28.7%) at CM) and flies on Lanzarote (26 species (38.8%) at LC and 25 species (38.5%) at CB) (Fig. 3.3). With regard to plant taxa, Asteraceae was the family with the greatest species representation in all study sites: 17 species (54.8%) at CM, 12 species (35.3%) at SB, eight species (44.4%) at LC and four species (33.3%) at CB. This was followed by Fabaceae present in three of the sites: eight species (23.5%) at SB, six species (19.3%) at CM and four species (22.2%) at LC.

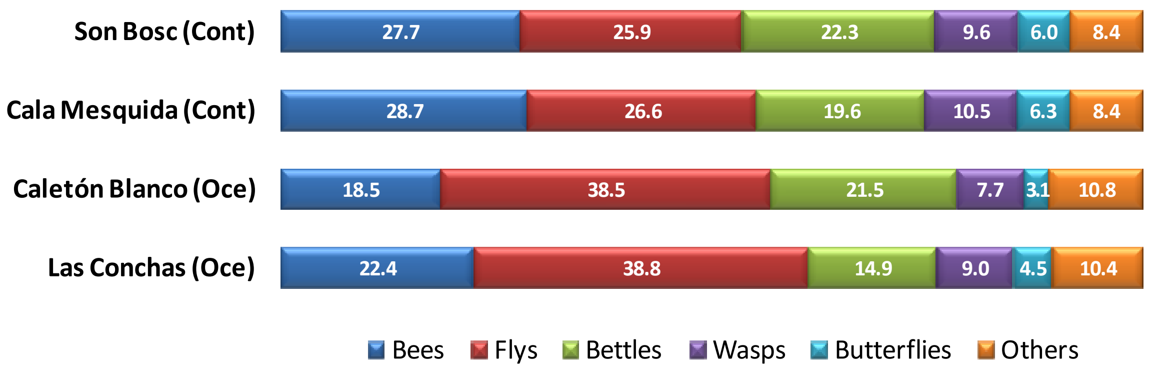

Figure 3.3. Proportions of flower visitor taxonomic groups at each study site.

Species specialization and selectivity

The plant linkage level (L_p) was rather similar among all four communities (Table 3.1). Likewise, the linkage level of flower visitors (L_{fv}) did not differ significantly between continental and oceanic communities, although SB (the most diverse area, with the largest number of species and interactions) showed higher L_{fv} than the other three communities (CM: $z = 3.85$, $p = 0.001$; CB: $z = 3.72$, $p = 0.01$; LC: $z = 4.42$, $p = 0.001$) (Table 3.1). When accounting for partner availability, and thus comparing *ND* among communities, similar results were obtained; however, in this case, SB only showed higher ND_{fv} than CB ($z = -2.74$, $p = 0.01$). The most generalist plant was *Euphorbia paralias* from CM on Mallorca, being visited by 42 different flower visitors, and the most generalist flower visitor was the beetle *Meligethes* sp. from the other Mallorcan community, SB, visiting 32 plant species.

On the Canaries, the most generalist species were native species, which had a disproportionately higher number of links than the rest, thus acting as super-generalist species. These were represented by two plants, *Euphorbia balsamifera* Aiton (Euphorbiaceae) at CB (with 24 links, involved in 39% of all network interactions) and *Astydamia latifolia* (Apiaceae) at LC (with 29 links, involved in 47% of all network interactions), and one flower visitor (a fly), *Tethina* sp. (Tethinidae), with 13 (72%) and 14 (56%) links at CB and LC, respectively.

With regard to species selectivity, both plants and flower visitors were overall more opportunistic (showed lower values of d' and H_2', Table 3.3) at the oceanic than at the continental sites. However, when using d'_{corr}, differences were significant only between the two Mallorcan sites and LC on Lanzarote for flower visitors (CM: $z = -4.17$, $p = 0.001$; SB: $z = 3.83$, $p = 0.001$) and between CM on Mallorca and the two sites on Lanzarote for plants (differences from CB: $z = 2.83$, $p = 0.05$; from LC: $z = -2.73$, $p = 0.01$). When we classified all species into different groups according to their d' value (highly selective, $d' > 0.75$; selective, $0.75 > d' > 0.5$; opportunistic, $0.5 > d' > 0.25$; highly opportunistic, $d' < 0.25$), we observed a clear predominance of selective species at the two Mallorcan sites and a predominance of opportunistic species at the two oceanic sites; on Lanzarote, highly selective species were almost absent (Fig. 3.4).

Table 3.3. Quantitative network parameters for all studied sites: oceanic island (Lanzarote) and continental island (Mallorca). d'_p (mean plant selectivity ± SD), d'_{fv} (mean flower visitor selectivity ± SD), H_2' (community-level selectivity), C_q (quantitative connectance), ID_p (plant interaction diversity), ID_{fv} (flower visitor interaction diversity), *IE* (interaction evenness), *WNODF* (Weighted Nestedness based on Overlap and Decreasing Fill).

	Continental island		Oceanic island	
	Son Bosc	**Cala Mesquida**	**Caletón Blanco**	**Las Conchas**
d'_p	0.56 ± 0.22	0.57 ± 0.14	0.41 ± 0.17	0.46 ± 0.18
d'_{fv}	0.54 ± 0.23	0.45 ± 0.20	0.37 ± 0.13	0.37 ± 0.18
H_2'	0.73	0.61	0.46	0.52
C_q	0.02	0.03	0.06	0.05
ID_p	0.39	0.46	0.35	0.51
ID_{fv}	1.01	1.20	1.14	1.22
IE	0.42	0.73	0.79	0.71
WNODF	10.41	11.66	19.91	21.73

Differences in network-level parameters within and between islands

The interaction diversity of both plants and flower visitors (ID_p, ID_{fv}) and the interaction evenness (*IE*) were similar for three of the four sites, which resulted in similar values for these parameters between islands (Table 3.3). The most uneven site and that showing a slightly lower interaction diversity, for either plants or flower visitors, was SB on Mallorca. By contrast, both quantitative connectance (C_q) and nestedness (*WNODF*) were almost twice as high at the oceanic than at the continental island sites (Table 3.3).

Discussion

Despite the greater species richness in the continental than oceanic pollination communities, A:P ratios were rather similar between Lanzarote (A:P = 2.96) and Mallorca (A:P = 2.60), reaching intermediate values to those previously reported from other islands (A:P = 2) and from mainland communities (A:P = 4) (Trøjelsgaard & Olesen 2013). The close proximity of our two study islands to the mainland source areas might partly explain the high pollination richness relative to other islands with a more depauperate pollinator

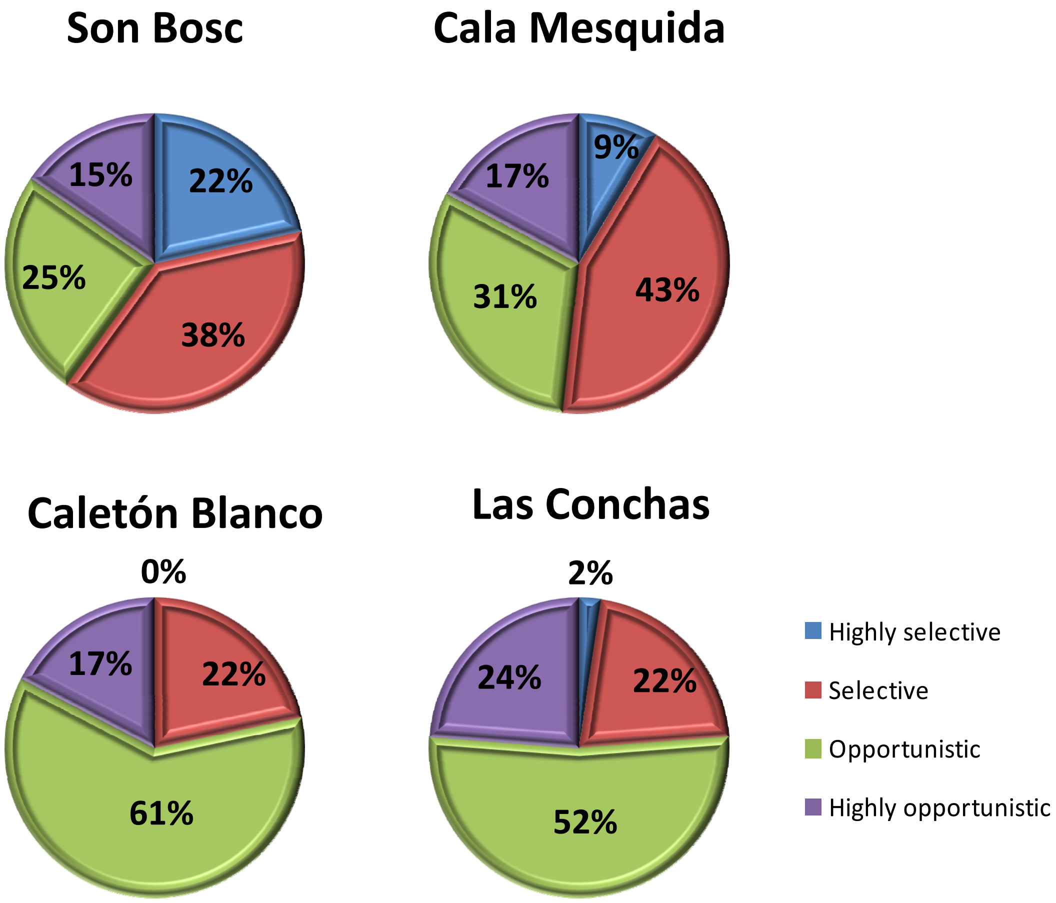

Figure 3.4. Proportions of species in the different categories of selectivity at each of the study sites. The degree of selectivity is calculated based on the *d'* parameter (highly selective, $d' > 0.75$; selective, $0.75 > d' > 0.5$; opportunistic, $0.5 > d' > 0.25$; highly opportunistic, $d' < 0.25$).

fauna. Probably because of this similar distance to the mainland, the coastal areas of Mallorca and Lanzarote analysed in this study shared up to 30% of the genera of flower visitors, a high value considering that the two sites within each island shared only 56% of the genera. By contrast, plants shared only 16% of genera between the two islands, possibly because of their lower capacity for dispersion and establishment than flower visitors.

Within islands, the two Canarian sites were more similar in species composition than the two Mallorcan sites. This translated into more similar qualitative parameters (total number of species, total number of interactions, mean and maximum species linkage level) and quantitative parameters (H_2' and *IE*) in the former. As expected, bees constituted the richest taxonomic group on the continental island, as found in continental communities (Kaiser-Bunbury *et al.* 2010a). By contrast, dipterans were the group with the largest number of species in the oceanic communities, a pattern commonly observed in island pollination assemblages (Kaiser-Bunbury *et al.* 2009; Padrón *et al.* 2009; Traveset *et al.* 2013).

Contrary to expectations (Barrett 1996; Padrón *et al.* 2009), we found that the number of links per species, for plants or flower visitors and accounting for partner availability or not, was rather similar between the two oceanic and continental island sites. Only flower visitors at SB tended to be more linked than those observed at the other three sites. Similar linkage levels between an oceanic and a continental island were also found by González-Castro *et al.* (2012) for vertebrate seed dispersal interactions. When contrasting our results with those obtained by Bartomeus *et al.* (2008), pooling all data from their coastal mainland study areas (which did not involve the entire community), we found that our island plants had lower linkage levels. However, accounting for the number of available partners (*i.e.* comparing normalized degrees; results not shown), these differences disappeared, being similarly generalized as continental plants.

Regardless of the lack of differences in the generalization level between the oceanic and continental island communities, we detected a small group of super-generalist species in the former. *Euphorbia balsamifera* and *Astydamia latifolia* are two such species, which have open flowers with nectar resources easily available for flower visitors and are widely distributed across all of the Canary Islands. All super-generalist species were involved in asymmetric interactions, *i.e.* links between specialist and generalist species, which are known to be common in small networks and important for the long-term survival of rare plant populations as they provide stable interaction partners (Bascompte *et al.* 2003; Kaiser-Bunbury *et al.* 2009; Memmott 2009). However, the loss of any of these native, highly connected species could be detrimental to overall network stability, causing possible secondary cascading extinctions and resulting in a decline of diversity (Memmott *et al.* 2004; Tylianakis *et al.* 2010). Thus, in a conservation context, the identification, management and restoration of species that interact strongly with others should be a principal objective (Dupont *et al.* 2003).

In contrast with the findings on the generalization level, differences in the level of species selectivity were detected between the two islands. The two Mallorcan networks were more selective, *i.e.* less opportunistic (higher H_2' values) than the two Canarian networks. In the latter, > 75% of species were opportunistic or highly opportunistic, but none was highly selective. These results contrast in part with those obtained by Trøjelsgaard *et al.* (2013), who found an increased d' for plants (but not for flower visitors) with island age in the Canaries. Using data from other coastal networks of another oceanic archipelago, the Galápagos (Traveset *et al.* 2013), we found that the oldest island, San Cristobal (2.4 - 4.0 Myr), showed the lowest *d'* values, with 70% of species also being opportunistic or highly opportunistic, whereas the youngest island, Fernandina (0.035 - 0.070 Myr), showed the highest *d'*, with 58% of species being selective or highly selective.

Data from more archipelagos are thus needed to assess how this index varies with island age and complexity of interactions. A higher proportion of opportunistic, generalized species on older islands might translate into a greater redundancy in species interactions, thus implying that they are less vulnerable to perturbations. In contrast, in the Mallorcan communities, > 50% of species was selective or highly selective, which might be associated with the higher niche competition described on continental islands (Whittaker & Fernández-Palacios 2007). This high level of selectiveness in continental island networks may indicate a reciprocal dependence between interacting partners, thus increasing the vulnerability of interactions to perturbations (Blüthgen *et al.* 2008).

Finally, the diversity of interactions in each community was similar between the two islands, despite their differences in species richness. However, a small oceanic network size with a large number of interactions, combined with the presence of opportunistic and also super-generalist species, results in a more connected community, as found on other oceanic islands (Kaiser-Bunbury *et al.* 2009). Greater connectivity may, in turn, result in greater nestedness (González-Castro *et al.* 2012; Trøjelsgaard & Olesen 2013; Traveset *et al.* 2013), which has been reported to provide stability and resistance to perturbations (Bascompte *et al.* 2003; Memmott *et al.* 2004; Burgos *et al.* 2007; Tylianakis *et al.* 2010).

Islands are of particular importance for the conservation of global diversity. However, the human pressure on ecosystems is likely to increase in the near future, as the introduction of invasive alien species and habitat alteration and destruction, the main threats to endemic biodiversity in many island ecosystems (Kaiser-Bunbury *et al.* 2010a), increase. The small population sizes and the high level of endemism make islands particularly susceptible to anthropogenic change. However, in the light of our results, small oceanic island communities might be less vulnerable to disturbance than previously thought, being buffered by some of the network traits (*e.g.* connectivity and nestedness) that provide stability to communities. Further research is certainly necessary from more archipelagos to establish the generality of our findings.

Supplementary Material

Table SM 3.1. Results of a null model analysis to confirm that our results described patterns that are different from random. Observed network parameter values were compared with the 1000 null version of each island community, calculated using the *Patefield* algorithm (method *r2d*) implemented in the *bipartite* package of R.

Son Bosc

	obs	null mean	lower CI	upper CI	*t*	*p*-value
WNODF	10.407	83.467	83.439	83.496	4983.9	0.000
ID_{fv}	1.010	2.069	2.069	2.070	3369.4	0.000
ID_{p}	0.389	1.327	1.327	1.328	2970.5	0.000
IE	0.418	0.427	0.427	0.427	988.9	0.000
H_2'	0.729	0.000	0.000	0.000	-3889593.9	0.000

Cala Mesquida

	obs	null mean	lower CI	upper CI	*t*	*p*-value
WNODF	11.661	83.856	83.828	83.883	5141.2	0.000
ID_{fv}	1.197	3.242	3.242	3.243	8439.0	0.000
ID_{p}	0.457	2.400	2.400	2.401	6902.2	0.000
IE	0.729	0.710	0.710	0.710	-1486.1	0.000
H_2'	0.614	0.001	0.001	0.001	-694634.5	0.000

Caletón Blanco

	obs	null mean	lower CI	upper CI	*t*	*p*-value
WNODF	19.911	77.525	77.458	77.591	1700.9	0.000
ID_{fv}	1.138	2.500	2.499	2.501	3625.6	0.000
ID_{p}	0.348	2.197	2.196	2.198	4306.0	0.000
IE	0.789	0.719	0.719	0.719	-2287.0	0.000
H_2'	0.464	0.002	0.002	0.002	-128751.2	0.000

Las Conchas

	obs	null mean	lower CI	upper CI	*t*	*p*-value
WNODF	21.729	84.682	84.636	84.727	2689.0	0.000
ID_{fv}	1.220	2.584	2.583	2.585	3626.0	0.000
ID_{p}	0.514	2.185	2.185	2.186	4562.0	0.000
IE	0.710	0.698	0.698	0.698	-460.7	0.000
H_2'	0.520	0.001	0.001	0.001	-607715.2	0.000

Capítulo 4

Efectos de la pérdida de hábitat sobre la estructura de la red de visitantes florales de una comunidad dunar

Chapter 4

Effects of habitat loss on the plant-flower visitor network structure of a dune community

El contenido de este capítulo está siendo preparado para su publicación como:

Traveset A, **Castro-Urgal R**, Rotllàn X, Lázaro A (In prep.) Effects of habitat loss on the plant-flower visitor network structure of a dune community

Resumen

Las interacciones entre las plantas y sus visitantes florales juegan un papel crucial en la conservación de la biodiversidad y el funcionamiento de los ecosistemas. La polinización es un valioso servicio ecosistémico, por lo que es muy importante conocer la forma en que estos patrones de interacción pueden ser modificados por los distintos componentes del cambio global. La destrucción del hábitat y los cambios en la calidad del mismo, constituyen las principales amenazas para dichas interacciones, así como para la supervivencia de las plantas y sus visitantes florales. El impacto que dichas perturbaciones tenga sobre las interacciones entre especies puede provocar cambios en toda la estructura de la red de visitantes florales. En este trabajo se evalúa el efecto de la pérdida de hábitat sobre los patrones de interacción entre las plantas y los insectos que visitan sus flores en una comunidad dunar situada en la isla de Mallorca. Con datos recolectados durante 4 años (2008-2011) se cuantifica el impacto de una gran perturbación sobre el área de estudio (justo después del período de floración del año 2010), que representó la pérdida de más de un 50% de la cubierta vegetal. Los resultados muestran que tras la perturbación se produce una disminución considerable tanto del número de especies y abundancia de visitantes florales como de interacciones en la red. Los escarabajos, las moscas y las hormigas fueron los visitantes florales más afectados, mientras que las abejas y las avispas fueron los menos afectados, probablemente debido a su menor capacidad de vuelo. El patrón anidado de interacciones fue menor después de la perturbación, posiblemente como consecuencia de la presencia de interacciones más especializadas entre las especies predominantes de la comunidad. También se produjo un incremento del nivel de la modularidad de la comunidad tras la pérdida de hábitat. Dichos resultados en conjunto indican que la red de visitantes florales será menos robusta y con menor grado de resiliencia ante futuras perturbaciones.

Effects of habitat loss on the plant-flower visitor network structure of a dune community

Introduction

The interactions between plants and their pollinators play a crucial role in biodiversity, conservation and ecosystem functioning. Habitat loss, fragmentation and changes in habitat quality, and in landscape structure in general, represent major threats to such interactions and thus to both plant and pollinator species persistence in the communities. Studies examining such threats at a community level, however, are still few and we thus have rather little empirical evidence on the final consequences of such habitat and landscape changes for the functioning of this important ecosystem service (Klein *et al.* 2007; Hagen *et al.* 2012; Ferreira *et al.* 2013; Nielsen & Totland 2014). Previous work has shown that a reduction in habitat quality and landscape heterogeneity cause species losses and lead to changes in the pattern of interactions among species, *i.e.* in the interaction network structure (Tylianakis *et al.* 2007; González *et al.* 2011). By reducing pollinator availability and diversity due to decreased floral resource supplies as well as nesting sites, habitat modifications can influence the levels of cross-pollination and, ultimately, fruit production (Aguilar *et al.* 2006; Winfree *et al.* 2011; Hagen *et al.* 2012; Viana *et al.* 2012; Ferreira *et al.* 2013; Vanbergen *et al.* 2014). Likewise, variation in conspecific plant densities may affect plant reproductive success by changing the pollinator-mediated connectivity between individuals in a plant population at different spatial scales, from meters to kilometers (Vanbergen *et al.* 2014). This indicates that, by altering interspecific interactions at a plant community-level, habitat disturbance can cascade down affecting the mating systems across levels of biological organization and potentially driving evolutionary changes (Eckert *et al.* 2010; Ferreira *et al.* 2013).

Rare and specialized interactions have shown to be the first to disappear after habitat reduction and thus an increase in the number of generalist plants and/or pollinators species is usually observed (Ashworth *et al.* 2004; Aizen *et al.* 2012; Vanbergen *et al.* 2014). Decreases in network nestedness in disturbed habitats have been also reported in different systems (Vanbergen *et al.* 2014; Moreira *et al.* 2015; Revilla *et al.* 2015), what has led authors to predict reductions in robustness and resilience of plant-pollinator networks to perturbations (Bascompte 2009; Fortuna *et al.* 2013), as well as decreases in the number of coexisting species (Bastolla *et al.* 2009). The loss of species and their interactions in a disturbed network can also lead to the formation of isolated compartments within the network (Spiesman & Inouye 2013) which run a higher risk of disappearing after future disturbances than if species are connected in a cohesive network. Different models have shown that the distribution in the number of interactions becomes very skewed when moving from pristine to perturbed areas and that mutualistic networks respond with a sudden collapse at critical habitat destruction thresholds (Keitt 2009; Kaiser-Bunbury *et al.* 2010b; Viana *et al.* 2012; Fortuna *et al.* 2013).

Habitat degradation may also cause homogenization of the plant-pollinator networks by promoting higher link-diversity but lower link-turnover in disturbed sites compared to undisturbed ones (Nielsen & Totland 2014). Moreover, the particular species' network functional role can change notably along a disturbance gradient, thus for instance a plant species can act as a hub (being at the network core) in one site but as a specialist (being at the network periphery) in another site (Campos-Navarrete *et al.* 2013; Nielsen & Totland 2014). Module and network hubs (*i.e.* species highly connected within their modules and with other species in other modules, respectively), together with connectors (species that link different modules), are considered keystone species for sustaining network structure and are thus the most vulnerable to disturbances (Olesen *et al.* 2007; Kaiser-Bunbury *et al.* 2010b; Fortuna *et al.* 2013).

Changes in pollinators' diversity are frequently reported mostly due to increased isolation of habitat patches and reduced landscape complexity caused by environmental simplification (Ferreira *et al.* 2013 and references therein). However, not all pollinator species respond similarly to habitat changes. Social bees, for instance, are known to be sensitive to changes in the distribution of nesting and foraging habitats in the landscape surrounding the nest (Williams *et al.* 2010; Carvell *et al.* 2012; Kennedy *et al.* 2013, Garibaldi *et al.* 2014) and, thus, proximal land cover changes can directly affect individual survival probability, locally reducing species abundance (Ferreira *et al.* 2015). Solitary bees, however, may be more affected by habitat destruction as they are more specialized than social bees (Williams *et al.* 2010; Ferreira *et al.* 2015). By contrast, non-social insects with free-living progeny (*e.g.* dipterans, coleopterans) are less affected by distance between resource patches (Jauker *et al.* 2009; Parsche *et al.* 2011). Moreover, flower-visitor abundance and species richness may be associated with floral abundance (Hegland & Boeke 2006; Hagen & Kraemer 2010) or with plant diversity (Potts *et al.* 2003; Ghazoul 2006; Blüthgen *et al.* 2007; Ebeling *et al.* 2008). In general, there is still scarce information on how different pollinator functional groups that coexist in a community respond to habitat disturbance (Burkle *et al.* 2013; Aguirre-Gutiérrez *et al.* 2015; Lázaro *et al.* 2016) and how they change their interaction patterns with plants (*e.g.* their rewiring capacity within functional groups).

In this study, we aimed at evaluating the impact of habitat disturbance (habitat loss, in particular) on the patterns of plant-flower visitor interactions in a coastal dune marshland community at the north of Mallorca (Balearic Islands, Western Mediterranean Sea). The plant-flower visitor network of this community was monitored for four consecutive years, from 2008 to 2011. After the flowering season of 2010, the study area was greatly disturbed due to the initial built of a golf course that caused the loss of c. 50% of the vegetation cover. This represented, thus, an opportunity to assess the extent to which such habitat loss altered the interactions between plants and their flower visitors.

Our specific questions were the following:

(1) Did network structural properties change after habitat disturbance more than the previous years?

(2) To what extent were floral resources, species richness and flower-visitor abundance affected by the disturbance?

(3) At the species level, how consistent across years were the degree, contribution to nestedness, *d'*, strength and weighted closeness centrality, and did these parameters change notably after the disturbance?

(4) Which flower-visitors' functional groups and which plant species (regarding traits such as flower abundance and floral symmetry) experienced the greatest changes in species level parameters after the disturbance?

(5) How consistent in time were the species' roles within the network, and did they change more after the disturbance relative to previous years?

Materials and methods

Study site

The study was carried out at Son Bosc (39°46'28.11''N; 3°07'45.34''E), a diverse dune in northern Mallorca, adjacent to S'Albufera Natural Park. The predominant vegetation consists of *Daucus carota* L. (Apiaceae), *Helichrysum stoechas* DC. (Asteraceae), *Lotus corniculatus* L. (Fabaceae), *Lotus cytisoides* L. (Fabaceae), *Scabiosa atropurpurea* L. (Dipsacaceae) and *Teucrium dunense* Sennen (Lamiaceae) and over 80 flowering species have been recorded in the area, mostly annual plants although also some shrubs like *Cistus salviifolius* L. (Cistaceae) and *Myoporum tenuifolium* G. Forster (Myoporaceae). Such a high diversity of flowers allows maintaining an also high diversity of flower-visiting insects (c. 125 spp), a good fraction of which nest in the sandy soils of this area. Specifically, this area bears the highest bee species richness of Mallorca island (D. Baldock, unpubl. data).

We performed censuses in Son Bosc during four consecutive years, from 2008 to 2011. During the summer of 2010, an area of 23402 m^2 was disturbed due to the construction of a golf course, representing 52.3% of the total area covered in our study, which encompassed 44710 m^2 (c. 4.5 ha; delimited in green in Fig. 4.1). Given that the largest disturbance occurred when most plants had already flowered in 2010, we expected the highest impact on the pollination network the following year. Thus, during 2011, we kept censusing all flowering plants both in the disturbed and in the remaining unaltered area.

Sampling methods

All plants in bloom were monitored throughout the flowering season, from early April to the end of July. Once or twice per week, we made insect censuses on flowers from haphazardly selected individuals from all flowering plant species. Censuses were done from 10:00 am to 17:00 pm on sunny and non-windy days. Insect visits to flowers were recorded from a distance of approximately 1 meter to minimize interference with insect behavior. We recorded contacts between insects and flowers during 3-5 minute periods. During each census we recorded: (a) identity of flowering plant species; (b) number of open flowers of each individual plant observed; (c) identity of each pollinator (species name if possible or morphotype otherwise); (d) number of individuals of each species visiting flowers and (e) number of flowers visited by each pollinator. Unidentified insects in the field were collected for further identification by taxonomists. We categorized flower-visitor species into the following functional groups (as done in previous studies; *e.g.* Fenster *et al.* 2004): ants, bees, beetles, hoverflies, flies (mainly muscoid flies), butterflies, wasps and others (mostly hemiptera).

Time spent censusing insects visiting flowers along the entire season was on average 36.3 hours. Most intensive sampling was from 2009 to 2011, when we also estimated flower abundance fortnightly at each site. In each flower census, we recorded the number of all open flowers of each flowering plant encountered within permanent belt transects; we surveyed 13 transects (50 x 2 m) in 2009 and 10 transects in 2010 and 2011, covering a total area of 1300 m^2 and 1000 m^2, respectively. Further details on sampling can be found in Castro-Urgal *et al.* (2012).

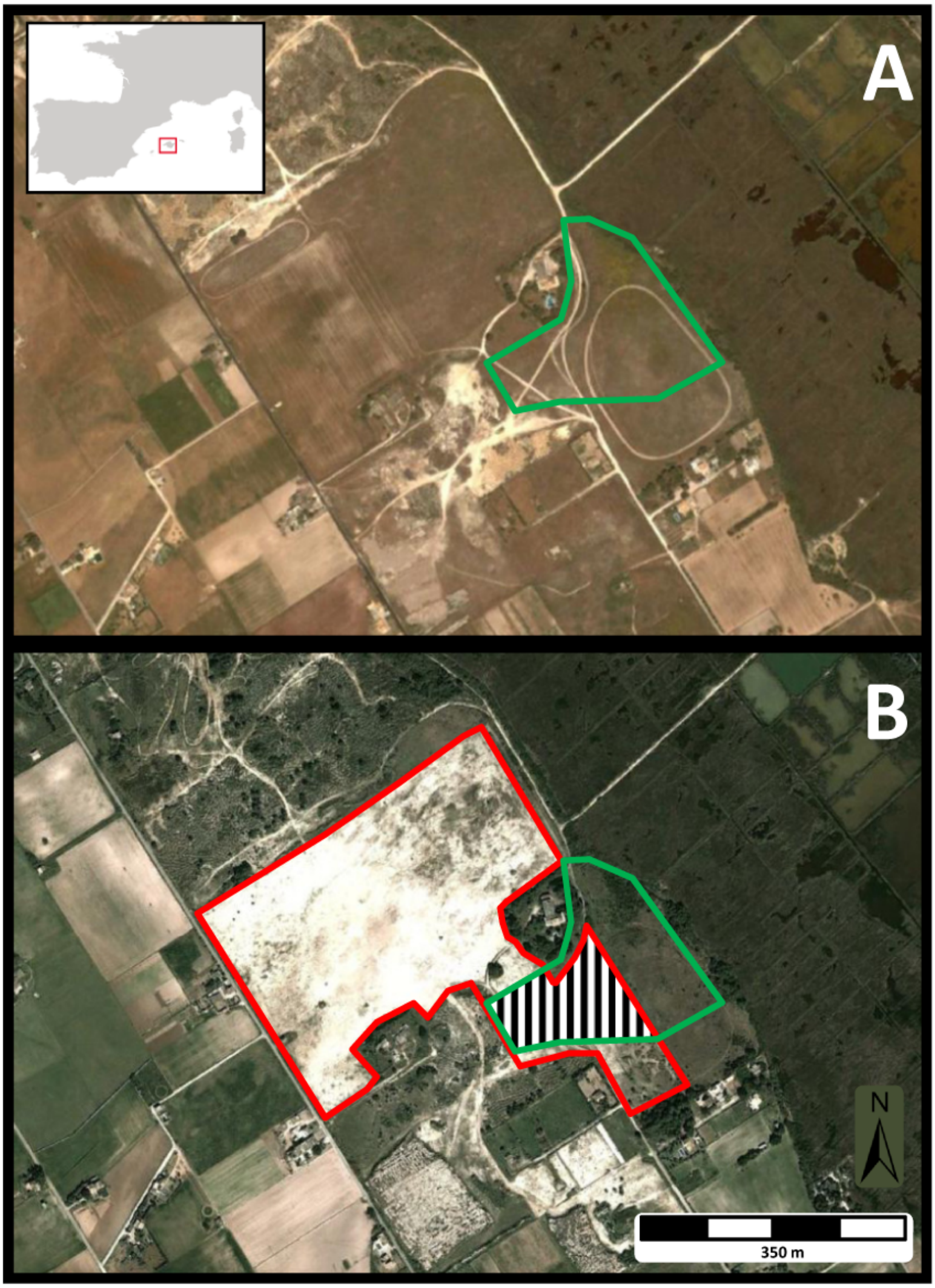

Figure 4.1. Aerial photograph showing Son Bosc study area before (A) and after (B) the disturbance (soil removal for a golf course construction). The green line marks the study area, the red line the disturbed area and the vertical black and white pattern the study area damaged.

Network parameters

We built four quantitative interactions matrices (one for each year) using the number of visits per unit time as link weight. For each network, we calculated the most widely used quantitative descriptors of the structure of weighted ecological interaction networks. At network level, these were: connectance (*C*), weighted nestedness (*WNODF*), complementary specialization H_2', interaction evenness (*IE*) and quantitative modularity (*Q*, *z*-scores; see below). At species level, we obtained the following metrics both for plants and pollinators: linkage level or degree, strength, species specialization (*d'*) as an index of selectiveness, weighted closeness centrality (*wCC*), contribution to nestedness n_i (see Supplementary Material for definitions of each parameter) and species' roles in the networks (*i.e.*, standardized connection "*c*" and participation values "*z*"; see below) for each plant and pollinator species in the networks. We used the bipartite package version 1.18 (Dormann *et al.* 2009) run in R to obtain all these network metrics, except *WNODF* and contribution to nestedness which were obtained with the software NODF version 2.0 (nestedness based on overlap and decreasing fill; Almeida-Neto & Ulrich 2011). The significance of *WNODF* values was assessed against 100 randomizations using the 'rc' and 'p' null models, as there were considered to be the most appropriate for our data.

Quantitative Modularity (*Q*) was estimated using the QuanBIMo algorithm (Dormann & Strauss 2014), which is implemented in R. It consists of a recurrent Markov chain Monte Carlo (MCMC) algorithm to find the best division of nodes (species) into modules. A total of 10^6 MCMC steps were used with a tolerance level of 10^{-10}. As *Q* values can vary among different runs, we repeated the calculations 100 times for each network (using the 'computemodules' function) and selected the iteration with maximum likelihood as the best estimation of *Q*. To account for *Q*'s dependence on network size and test the significance of modularity values, we calculated a *z*-score for each network. *Z*-scores were calculated by running the same algorithm in 100 random networks with identical marginal totals as the empirical network (Guimerà & Amaral 2005) and comparing the modularity values between random and empirical networks. Such tests were done using the null model "*r2d*" in the *bipartite* package (Dormann & Strauss 2014).

Following Guimerà & Amaral (2005), we identified species with important roles in the network by computing standardized connection and participation values (*c* and *z*, respectively). While *c* refers to the even distribution of links across modules, *z* refers to within-module degrees. The critical values suggested by those authors were *c* = 0.625 and *z* = 2.5. The 'hubs' of the networks are the species exceeding both of these values, as they link different modules as well as species within a module.

Statistical analysis

All analyses were conducted in R 3.1.2 (R Development Core Team 2008). To compare pollinator species richness among years we performed a generalized linear model (GLM) using a Poisson distribution and log as link function. In this analysis, year was included as a fixed categorical factor whereas the number of species in each flower-visitor functional group as sampling units. The interannual variations in species-level network parameters and abundances were analysed by means of generalized linear mixed models (GLMM, package *lme4*) that included species as a random factor to avoid pseudoreplication. We used separate models for plants and flower visitors and for each network parameter. The models for plants only included year as fixed categorical predictor variable, whereas those for flower visitors also included functional group and its interaction with year. All functional groups were included in the models, except for the 'others' group owing to its low species number. Due to the nature of the data we used: 1) Poisson distribution and log link functions for the degree analyses, after checking for the absence of overdispersed data (Zuur *et al.* 2009); 2) Gaussian distribution and log link function for the models of *d'* and 3) Gamma distribution and log link function for the rest of the variables. The consistency among years in species roles within the network was also analysed by means of GLMMs, including *c* and *z* as response variables, year as fixed factor and species as random factor. Plant species were the sampling units and data were adjusted to a gamma distribution in each model.

As we found significant differences in both plant degree and *d'* between 2011 and the average of the three previous years (see results), we further assessed whether such differences were associated to changes in the prevalence of plant species with different flower symmetry and different flower abundances. For this, we performed two separate GLMs to analyze the after-disturbance change in degree and *d'* (calculated as the difference between the degree/*d'* in 2011 and the average degree/*d'* in the previous years) as response variables, and flower symmetry (zygomorphic vs. actinomorphic) and flower abundance (average from 2009-2011) as independent predictor variables. Sampling units were the study plant species and data were adjusted to a Gaussian distribution in each model.

Post hoc analyses to test for differences among levels of a significant factor were conducted using Tukey a posteriori tests (package *multcomp*).

Results

Overall community structure

Table 4.1 shows the overall network properties for each study year. The number of flower-visitor species, number of links and weighted nestedness were much lower the year following habitat disturbance (2011) than the three previous years. The number of plants was also reduced after the disturbance but to a lower extent than the number of flower visitors. The networks showed a highly consistent connectance around 5%, which is a usual figure given the rather large network sizes. All networks were significantly nested ($p < 0.001$), meaning that the partners of the most specialized species are a subset of those that interact with the most generalist species. The lower nestedness in 2011 might thus result from the loss of some generalist species after the disturbance and/or from an increase in specialized interactions. The latter is actually supported by the higher H_2' value in 2011. The diversity of interactions was moderate (c. 0.50) across the four years of the study. Finally, the networks were significatively modular each year; however, while both modularity (Q) and the number of modules were higher in 2011 than the other years, this was not the case for *z*-scores (Table 4.1).

Overall, species richness per flower-visitor group was lower in 2011 (mean ± SE: 10.75 ± 3.65) compared to the previous years (14.71 ± 2.23) ($\chi_3^2 = 8.25$, $p = 0.046$). However, this difference was mostly due to a decrease in beetle and fly species richness (Table 4.2). The other groups barely changed across the four years of the study. Regarding flower-visitor abundance, the best model showed that it varied significantly among all the study years, consistently among pollinator groups (Year: $\chi_3^2 = 72.45$, $p < 0.0001$). It was lowest in 2011 (visits/min: 0.09 ± 0.02), highest in 2010 and 2009 (1.10 ± 0.11 and 1.12 ± 0.004, respectively) and intermediate in 2008 (0.18 ± 0.02).

Species-level network properties: plants

All the species-level network parameters differed significantly among years, except plants' strength (Table 4.3). In 2011, plants' degree was significantly lower (Fig. 4.2A) and *d'* was significantly higher (Fig. 4.2B) than the previous years; that is, the number of flower visitors per plant decreased after the disturbance and plants became more selective,

Table 4.1. Network parameters for each study year. *WNODF* (weighted nestedness), H_2' (index of specialization or selectiveness) and *IE* (interaction evenness). For modularity, the *z*-score is given, as the *Q* observed is compared to that expected with a null model based on marginal totals (representing abundance distributions of plants and pollinators; see Dormann & Strauss 2014 for further details).

Parameter	**2008**	**2009**	**2010**	**2011**
No. Plants	56	68	67	52
No. Pollinators	120	110	123	86
No. Links	347	390	494	248
Connectance	0.052	0.052	0.060	0.055
WNODF	7.698	8.670	9.412	5.456
H_2'	0.589	0.618	0.547	0.685
IE	0.532	0.529	0.514	0.497
Modularity (*Q*)	0.307	0.370	0.368	0.568
No. Modules	8	8	6	13
Modularity *z*-score	316.60	760.34	722.79	303.58

Table 4.2. Species richness in each flower-visitor group across the four study years. The groups in which species richness was considerably reduced after habitat disturbance are shown in bold.

Pollinator group	**2008**	**2009**	**2010**	**2011**
Ants	6	3	4	2
Bees	29	35	38	31
Beetles	25	24	29	**18**
Butterflies	7	5	3	3
Flies	25	18	23	**11**
Hoverflies	5	6	6	5
Wasps	13	13	14	15
Others	11	6	6	1

being visited by less abundant flower visitors. Significant differences among years were also observed in weighted closeness centrality and contribution to nestedness, but these did not seem to be related to the disturbance, as both parameters were significantly higher in 2008 (Fig. 4.2C-D) and the values in 2011 did not differ significantly from those in other years (Fig. 4.2C-D).

Table 4.3. Results of the Generalized Linear Models comparing species-level network parameters among the study years for plants and flower visitors. When the interaction between year and functional group was significant, the LRT for the interaction is given, but both factors were also included in the models.

Network index	**Plants** Year	**Pollinators** Year * Pollinator group
Degree	$\chi_3^2 = 55.14$, $p < 0.0001$	$\chi_{18}^2 = 36.34$, $p = 0.006$
Strength	$\chi_3^2 = 5.14$, $p = 0.162$	$\chi_{18}^2 = 36.40$, $p = 0.006$
d'	$\chi_3^2 = 27.59$, $p < 0.0001$	$\chi_{18}^2 = 64.09$, $p < 0.0001$
Weighted Closeness Centrality	$\chi_3^2 = 139.78$, $p < 0.0001$	$\chi_{18}^2 = 51.78$, $p < 0.0001$
Contribution to Nestedness	$\chi_3^2 = 15.4$, $p = 0.001$	$\chi_{18}^2 = 51.79$, $p < 0.0001$

Flower abundance positively influenced the after-disturbance change in plant species degree ($\chi_1^2 = 4.57$, $p = 0.03$) but not in *d'* ($\chi_1^2 = 0.60$, $p = 0.44$). In other words, those species producing more flowers were those most affected by the decrease in number of flower visitors after the disturbance, although they were not necessarily those showing a higher selectiveness. On the other hand, flower symmetry did not have a significant effect on either the after-disturbance change in degree ($\chi_1^2 = 0.82$, $p = 0.37$) or in *d'* ($\chi_1^2 = 0.81$, $p = 0.37$), *i.e.* both actinomorphic and zygomorphic species responded similarly to the disturbance regarding these two metrics.

Species-level network properties: flower visitors

For all species-level network parameters, a significant interaction was found between year and flower-visitor functional group (Table 4.3), indicating that such groups do not vary consistently along time. Ants, beetles and butterflies showed lower degrees in 2011 compared to the other years, whereas the other functional groups either showed no annual differences in their degree or these were not due to the disturbance (Fig. 4.3A). Ants also showed a reduced strength in 2011 compared to the other years (Fig. 4.3B), whereas the other groups showed either no variation among years or the variation was not related to the disturbance (Fig. 4.3B).

The effect of the disturbance on insect selectiveness was clearer, as practically all functional groups had higher *d'* in 2011 compared to the previous years (Fig. 4.3C). However, differences were significantly different from the rest of the years only for ants and beetles (Fig. 4.3C).

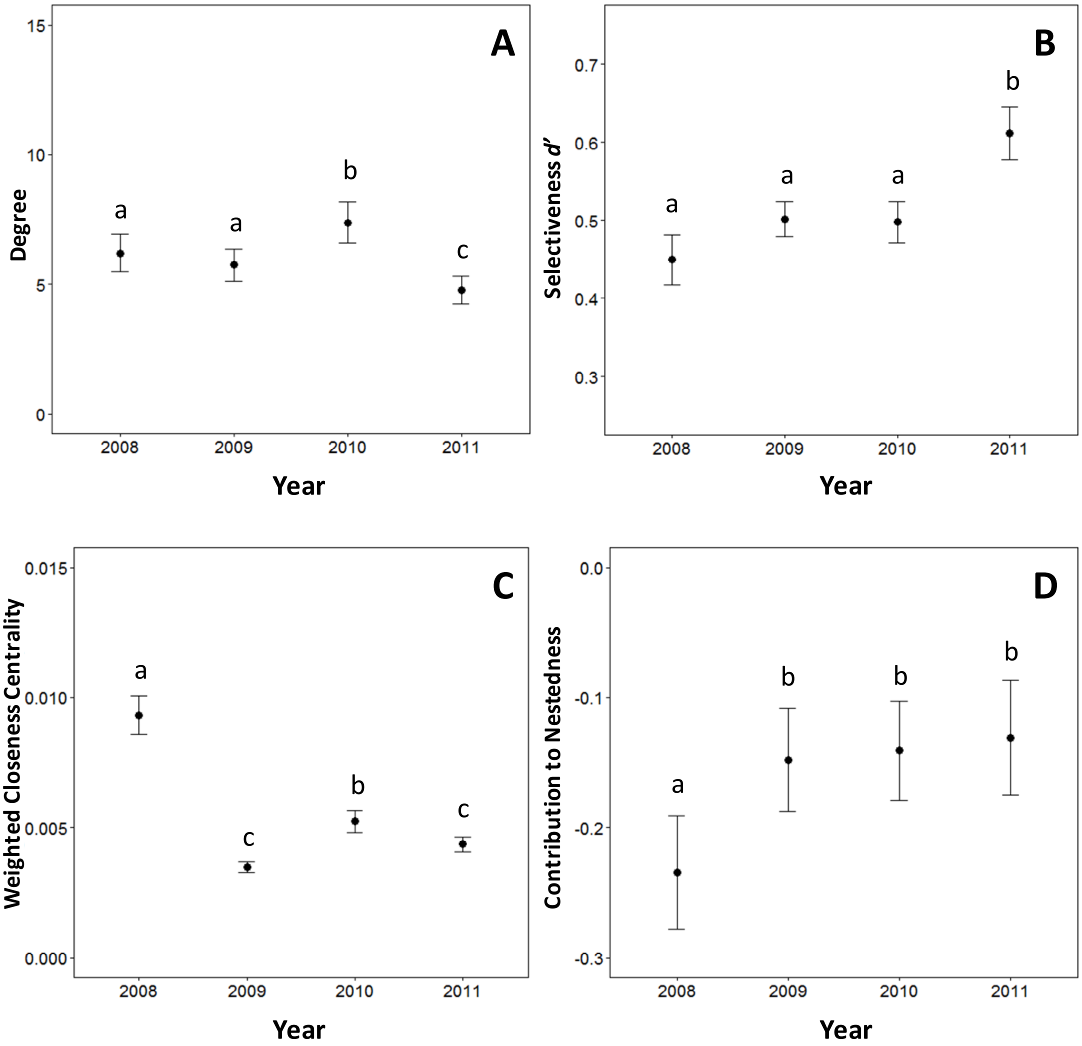

Figure 4.2. Mean (± SE) values of (A) Degree, (B) Selectiveness *d'*, (C) Weighted Closeness Centrality and (D) Contribution to Nestedness for plants across the study years. Different letters indicate significant differences among years.

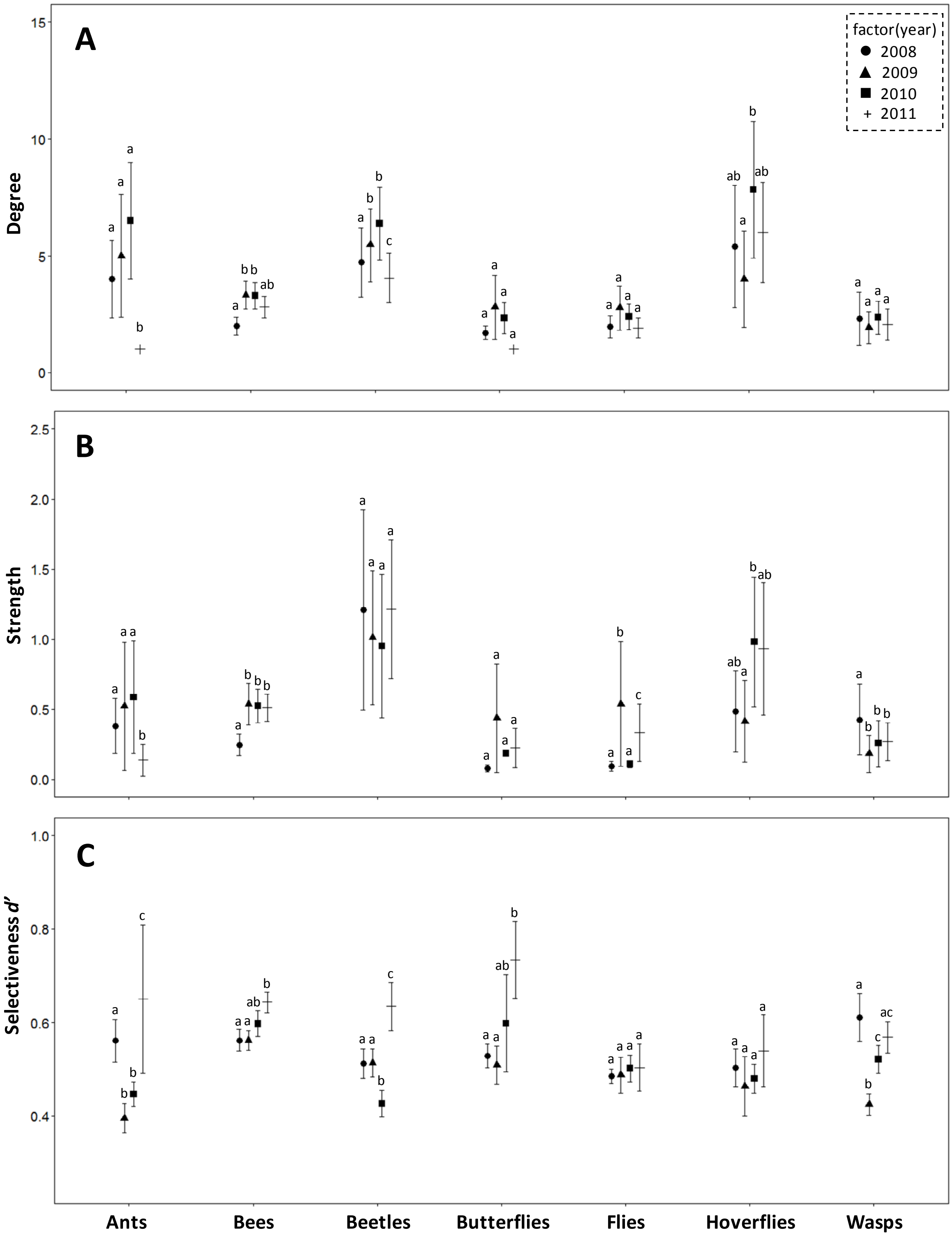

Figure 4.3. Mean (± SE) values of (A) Degree, (B) Strength and (C) Selectiveness *d’* across years for each pollinator group. In all cases, the interaction between year and flower-visitor group was significant at $p < 0.05$. Different letters indicate significant differences among years within each functional group.

Ants and butterflies showed lower weighted closeness centrality in 2011 than the previous years, whereas the opposite was found for bees, beetles and flies (Fig 4.4A). However, the differences between 2011 and the rest of the years were significant only for ants (Fig. 4.4A). The other insects groups showed interannual variations in this metric that were not related to the disturbance (Fig. 4.4A).

Lastly, flies and hoverflies tended to contribute more, but ants less, to nestedness in 2011 than the other years (Fig. 4.4B); however, differences were not significant. For the rest of groups, interannual variations were not related at all to the disturbance (Fig. 4.4B).

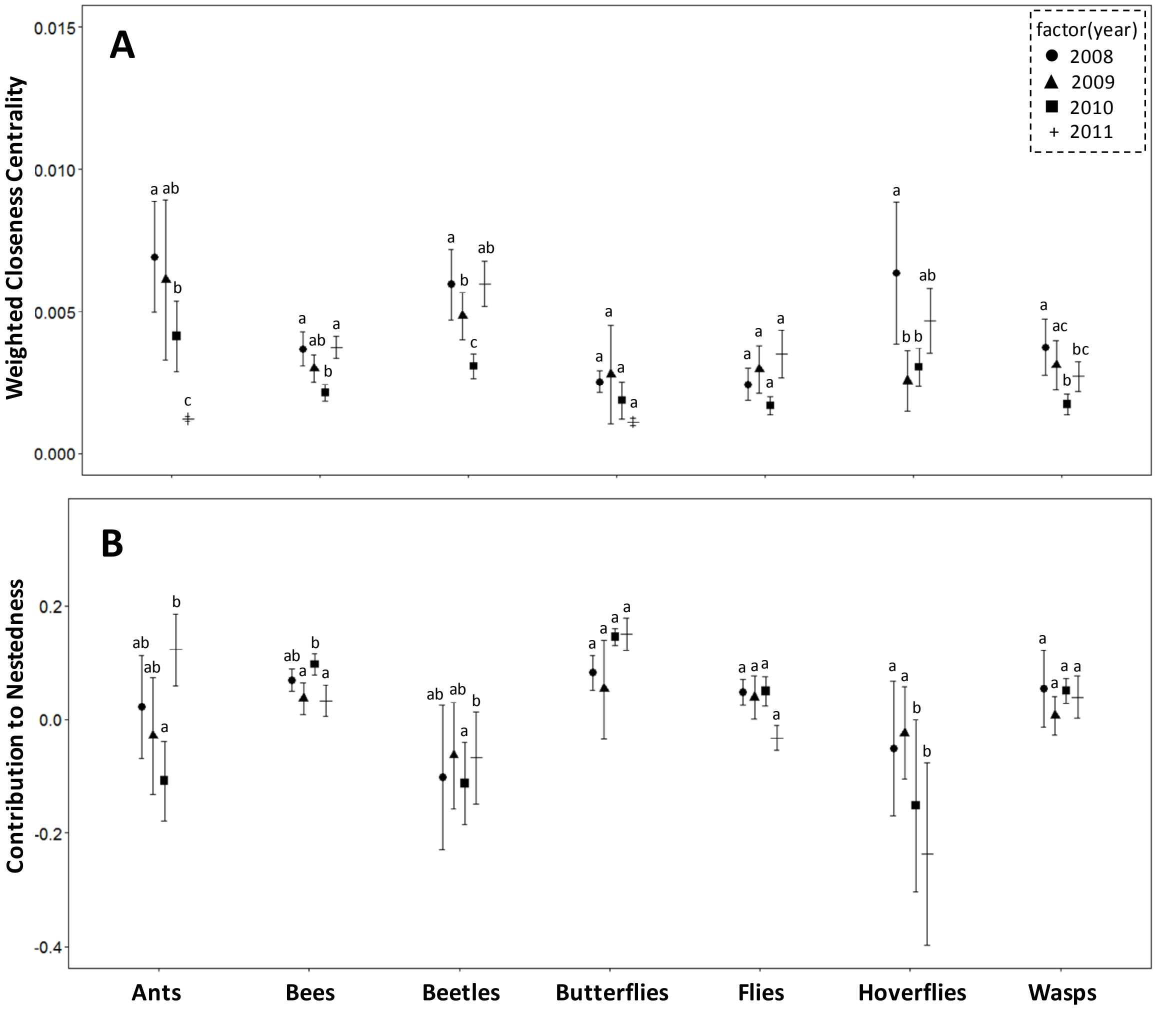

Figure 4.4. Mean (± SE) values of (A) Weighted Closeness Centrality and (B) Contribution to Nestedness across years for each flower visitor group. In all cases, the interaction between year and flower-visitor group was significant at $p < 0.05$. Different letters indicate significant differences among years within each functional group.

Species-level network properties: species roles

Standardized connection (c) varied among years for plant species ($\chi_3^2 = 10.55$, $p = 0.014$), although such variation was unrelated to the disturbance (Fig. 4.5A). Likewise, c varied among years for flower visitors, but in this case such variation depended on the functional group (interaction year x functional group: $\chi_{18}^2 = 34.99$, $p = 0.009$; Fig. 4.5B). Both ants and butterflies showed lower c in 2011 compared to the previous years whereas the other flower visitors showed either no significant variation across years or variation was independent of the disturbance (Fig. 4.5B).

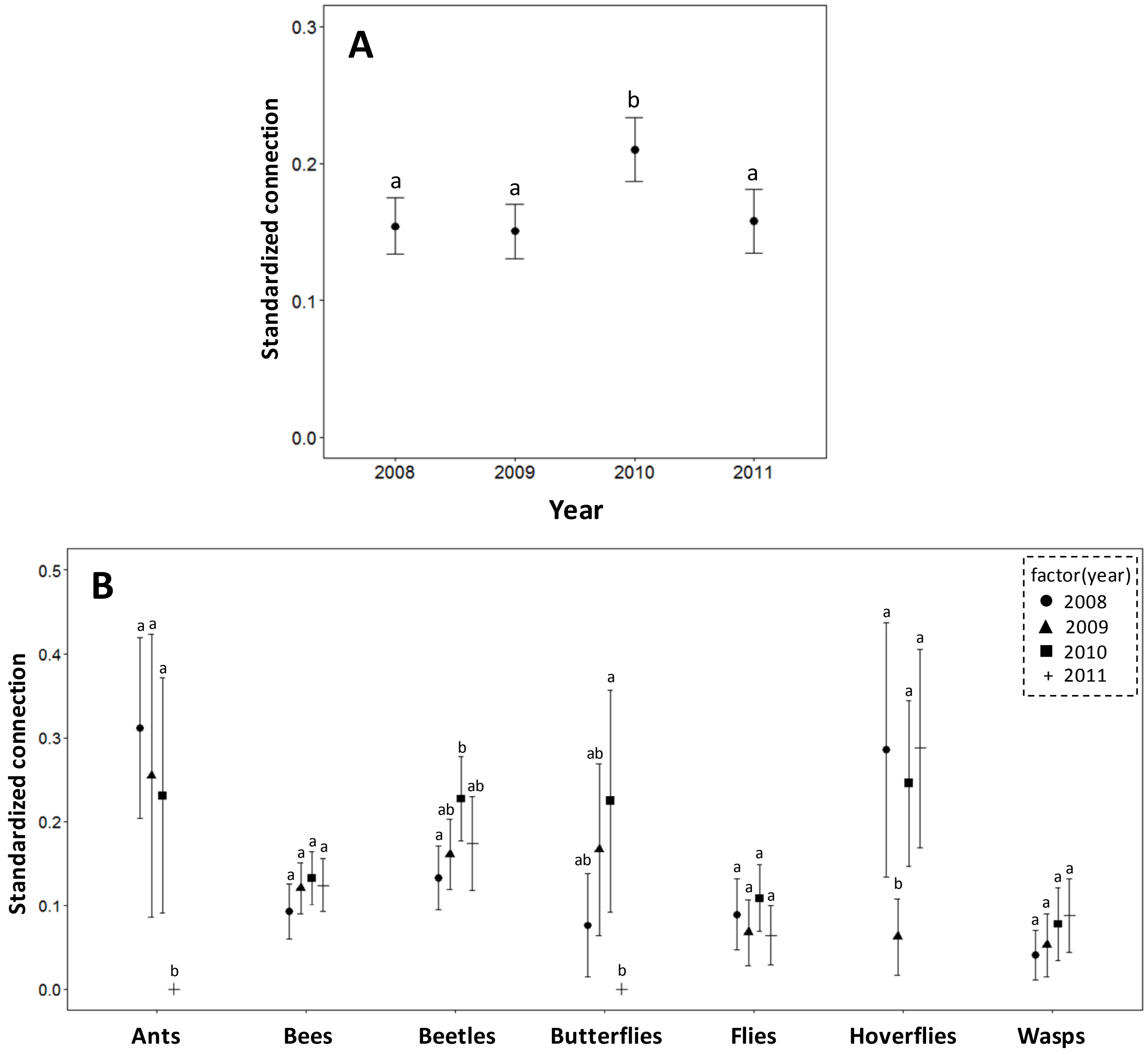

Figure 4.5. Mean (± SE) standardized connection across years in (A) plant species and (B) flower-visitor functional groups. The interaction between year and functional group was significant at $p < 0.05$. Different letters indicate significant differences among years (A) or among years within each functional group (B).

On the contrary, participation values (*z*) did not differ among years either for plants ($\chi_{3}^{2} = 4.07$, $p = 0.25$) or flower visitors (year: $\chi_{3}^{2} = 2.92$, $p = 0.40$; functional group: $\chi_{6}^{2} = 5.11$, $p = 0.53$; interaction year x functional group: $\chi_{1}^{2} = 20.37$, $p = 0.31$).

Discussion

The habitat loss in our study area showed to notably impact some of the structural properties of the plant-flower visitor network. Although most metrics varied across years, the number of flower visitors and the number of links in the network decreased more after the disturbance than the three previous years, despite network connectance was highly consistent in time. This is concordant with results from other studies showing a reduction in pollinator availability and diversity attributed to a decrease in floral resource supplies as well as nesting sites (Winfree *et al.* 2011; Hagen *et al.* 2012; Ferreira *et al.* 2013; Vanbergen *et al.* 2014). Moreover, the nested pattern of interactions was weaker the year following the disturbance, which suggests that generalist species (either plants or flower visitors) disappeared or were less abundant (and thus likely had fewer interactions) and/or that more specialized interactions appeared among the prevalent species in the community. The level of network specialization (H_2') in 2011 was in fact higher when compared to the previous years, what would support the lower nestedness values of that year. Other studies have also documented decreases in network nestedness in disturbed habitats (Vanbergen *et al.* 2014; Moreira *et al.* 2015; Revilla *et al.* 2015) though not always (Spiesman & Inouye 2013). A reduced nestedness is often associated to a lower stability and resilience of plant-pollinator networks to perturbations (Bastolla *et al.* 2009; Fortuna *et al.* 2013), although there is some controversy on this (James *et al.* 2013; Saavedra & Stouffer 2013; Rohr *et al.* 2014).

Greater modularity in disturbed habitats compared to undisturbed ones has also been reported (Spiesman & Inouye 2013). A more modular network is thought to reduce the opportunity of species to facilitate one another by sharing mutualistic partners and thus to have a destabilizing effect (Thébault & Fontaine 2010). Quantitative modularity (*Q*) has been found to be positively associated with complementary specialization H_2' using 22 quantitative pollination networks (Dormann & Strauss 2014). We thus expected that an increase in H_2' after habitat disturbance might result in a higher modularity. Both *Q* and the number of modules were actually higher in 2011 than the previous years, supporting the expectation. Nevertheless, when comparing the standardized values of *Q* (*i.e. z*-

scores), the differences disappeared and 2011 no longer showed higher modularity than previous year.

At the species level, most network metrics varied across years. For plants, only strength was found to be consistent in time, indicating that the relative importance of a particular plant species for flower visitors was rather constant across the four study years. This is indeed interesting as it suggests that despite some plants' traits can change in time (*e.g.* its abundance or its degree), the sum of dependencies of each flower-visitor species of that plant is not modified. The temporal changes in plant degree, weighted closeness centrality and contribution to nestedness indicate, by contrast, that a plant's position in the network will depend upon the number of its flower visitors as well as how generalist these are. Likewise, changes in plant *d'* across years show the different levels of 'selectiveness', *i.e.*, that plants were visited by either abundant (low *d'* values) or scarce (high *d'* values) flower visitors. Given the high temporal fluctuations in insect populations, such levels of selectiveness are indeed expected to vary much in time. The highest *d'* values observed in 2011 might actually reflect the lowest insect abundances found that year.

Regarding flower visitors, all species-level metrics varied across years, including species strength. In this case, the importance of a particular insect species for the entire plant community is likely to vary much depending upon its abundance and generalization level, which might be more variable than for plant species. We indeed found important differences across years in flower-visitor abundance the year after habitat disturbance showing the lowest values. Such disturbance not only influenced insect abundance but also species richness, although this was contingent upon functional group. Thus, species richness of beetles and flies were the most negatively affected. It is unknown why the other groups, especially bees and wasps, which are also abundant in the area, were not influenced much. One possible reason is that the nesting sites that these groups use, together with food resources, were not limiting enough and despite insect abundance was lowered, the disturbance did not lead any species to local extinction. In addition, bees and wasps might have a greater mobility (Torné-Noguera *et al.* 2014) and thus be less influenced by local disturbances. Moreover, ants were the functional group most negatively influenced by the disturbance regarding generalization level, strength, selectiveness and closeness centrality; they also played a less important role as module connectors after the disturbance. This might be mostly attributable to the lower foraging range, compared to the other functional groups, specifically flying insects. In general, there is still scarce information on how different pollinator functional groups that coexist in a community respond to habitat disturbance (Burkle *et al.* 2013; Aguirre-Gutiérrez *et al.* 2015; Lázaro *et al.* 2016) and on how they change their interaction patterns with plants (*e.g.* their rewiring capacity within functional groups). Even less information exists on the ultimate consequences of such changes for plant reproductive success. From a conservation viewpoint, monitoring these changes in natural communities could be highly relevant to the proposal of effective conservation strategies (Campos-Navarrete *et al.* 2013).

In short, our findings showed that the large disturbance occurred in the study area altered to a large extent the structure of the plant-flower visitor network, making it more vulnerable to future perturbations. The lower floral resources availability, together with a likely reduction in the nesting sites of some insect species, led to a reduction in species richness and flower-visitor abundance, translating in turn in a less nested and more modular network composed of more specialized interactions. Not all flower-visitor functional groups were similarly affected; beetles, flies and ants were more negatively influenced by the disturbance than other groups such as bees and wasps, what we attribute to their overall lower mobility.

Supplementary Material

Description of the network-level parameters calculated

Connectance (***C***; Dunne *et al.* 2002): the fraction of observed interactions relative to the total possible interactions within the network.

Weighted nestedness (***WNODF***; Almeida-Neto & Ulrich 2011): networks are nested if those species with fewer interactions are preferentially associated with a subset of species that interact with the most connected ones. The difference between presence-absence nestedness (*NODF*) and *WNODF* expresses how much of the nestedness in interaction composition looks like a gradient of abundances. A high value of nestedness indicates that the community is highly structured and organized.

Complementary specialization (H_2'; Blüthgen *et al.* 2006) characterizes the degree of complementary specialization in bipartite networks and it is derived from Shannon entropy. H_2' is related with weighted *d'* described in detail below, across all species. It ranges between 0 (no specialization, high niche overlap) and 1 (complete specialization, high niche differentiation).

Interaction Evenness (***IE***; Tylianakis *et al.* 2007) is a measure of the uniformity of interactions between species in a network based on Shannon's evenness. An uneven network has a high skewness in the distribution of interaction weights. It ranges from 0 (completely uneven) to 1 (completely uniform).

Quantitative modularity (***Q***; Dormann & Strauss 2014) is an algorithm to identify modules in quantitative bipartite (or two-mode) networks. It is based on the hierarchical random graphs concept of Clauset *et al.* (2008) and is extended to include quantitative information and adapted to work with bipartite graphs to compute modularity *Q* and detect modules in weighted bipartite networks.

Description of the species-level parameters calculated

Linkage level or degree is the number of species with which each species interacts. This index tells us the level of generalization of each species.

Species selectiveness (***d'***; Blüthgen *et al.* 2006) for plants and flower visitors measures the level of specialization of each species accounting for the available resources provided by the interaction partners (generally calculated as total number of realized interactions with other species of a given species in a bipartite network, *i.e.* its marginal total in the matrix). It ranges between 0 (no specialization) and 1 (complete specialization). This index increases with the deviation from random selection of the available interaction partners based on their abundance. Thus, a flower-visitor species that visits flowering plant species proportionally to their availability in the community is considered generalized, while a species that visits rare plants disproportionately more is considered specialized.

Strength (Bascompte *et al.* 2006) for plants and flower-visitors is the sum of dependencies of each plant or flower-visitor species, respectively. The dependence of a plant on a flower-visitor, for example, is the proportion of interactions between these two species out of the total interactions of a particular plant species. Therefore, the strength of a flower-visitor species is the sum of dependences of all plants interacting with this flower-visitor. It is a measure of the importance of this flower-visitor from the perspective of the plant set and *vice versa*.

Weighted Closeness Centrality (***wCC***; Opsahl *et al.* 2010) is a value describing the centrality of a species in the network but based on weighted representation of the network. Nodes with high *wCC* values can rapidly affect other nodes and *vice versa* by its path lengths to other nodes.

Contribution to nestedness ($\boldsymbol{n_i}$; Saavedra *et al.* 2011) estimates the degree to which the interactions of each row and column species increase or decrease community nestedness. The idea behind nestedness contribution is to determine how individual species' interactions change community nestedness compared to a random null model that is designed to control for the effect of differences in degree. For each row and column species, this function compares observed nestedness to an ensemble of nestedness values generated by randomizing the interactions of just that focal species. Nestedness contributions are the *z*-scores from this comparison. Therefore, a positive contributor to community nestedness (*i.e.*, a species whose interactions increase overall nestedness) will obtain values greater than 0 and negative contributors to nestedness will obtain values less than 0.

Resultados principales y discusión general

Resultados principales y discusión general

Efectos del uso de diferentes pesos de interacción en redes de visitantes florales

Para responder a las preguntas que se plantean los científicos, antes de empezar a recolectar datos de campo, es preciso pararse a pensar qué datos serán necesarios para los análisis que se quieren llevar a cabo para responder dichas preguntas. En el primer capítulo de esta tesis se investiga la gran variabilidad que existe a la hora de recopilar los datos de campo en estudios de polinización a nivel comunitario. Como consecuencia, existe también una gran variabilidad en la manera en la que finalmente se construyen las redes de visitantes florales. Estas diferencias metodológicas pueden llevar a interpretaciones ecológicas erróneas, sobre todo en aquellos estudios en los que se comparan redes elaboradas de maneras muy diversas. Siguiendo un aumento cada vez mayor en la complejidad del peso de interacción, nuestros resultados demuestran que el peso utilizado para cada interacción en las redes cuantitativas de visitantes florales afecta a la mayoría de las propiedades de la red.

El tiempo de muestreo de cada planta suele ser diferente debido a su corta o más prolongada fenología; por lo tanto, el número de visitas observadas podría depender del tiempo total de observación. Sin embargo, estandarizar por el tiempo total de censo provocó pocos cambios en los parámetros de red estudiados. Por lo general, los insectos más abundantes (es decir, con mayor número absoluto de visitas) mostraron también mayores tasas de visitas. Resultados similares fueron obtenidos por Vázquez & Simberloff (2003). Por otro lado, al añadir la información del número de flores observadas en el censo sí se encontraron diferencias significativas entre algunos de los parámetros estudiados. Por lo tanto, decidir añadir o no el número de flores observadas en cada censo a nuestro peso de interacción conlleva obtener conclusiones diferentes en nuestro estudio. Sorprendentemente, este no es el caso al incluir la información sobre el número de flores visitadas por cada especie de insecto en el peso de interacción, ya que esta información no provocó grandes cambios con respecto al peso anteriormente descrito. Consecuentemente, si comparamos estos dos últimos pesos podemos deducir que cuantas más visitas recibe una planta, mayor será el número de flores contactadas en cada visita. Finalmente, el último peso en el que se incluye la abundancia total de flores de cada especie de planta de la comunidad también generó resultados diferentes de los parámetros de red estudiados. A medida que el peso de interacción gana en complejidad se observa una clara tendencia hacia interacciones más especializadas, una mayor heterogeneidad en la frecuencia de las interacciones y un mayor anidamiento cuantitativo. La importancia de estas propiedades de la comunidad en relación a la estabilidad de la red y la resistencia de las especies y sus interacciones frente a posibles perturbaciones se discuten a lo largo de los siguientes apartados de esta discusión.

Se observó un mayor efecto del peso de interacción en aquellos parámetros relacionados con las plantas que en los relacionados con animales. Estas diferencias pueden ser atribuidas a tener una medida independiente de abundancia de flores pero no de insectos. La mayoría de las redes de visitantes florales se muestrean desde la perspectiva de las plantas, debido principalmente a las dificultades metodológicas de seguimiento de los visitantes florales. Avanzando en este sentido, cada vez más investigadores incluyen la perspectiva de los polinizadores en las interacciones planta-polinizador a nivel comunitario, por ejemplo mediante la exploración de la estructura de las redes de transporte de polen (Gibson *et al.* 2006; Bosch *et al.* 2009; Alarcón 2010; Tur *et al.* 2014, 2016).

El peso más apropiado para un estudio de redes ecológicas en particular dependerá del objetivo de la investigación, del método de muestreo utilizado en el trabajo de campo y de los índices calculados para describir la estructura de la red. Sin embargo, si nuestro objetivo es avanzar hacia una descripción funcionalmente más relevante de la estructura de las redes ecológicas, necesitamos pesos de interacción que sean lo más precisos posible para evitar sesgos y errores de interpretación y que estén estandarizados en toda la red. Obtener una estructura lo más relacionada posible con su función ecosistémica nos puede ayudar, por ejemplo, a predecir mejor los impactos del cambio global en toda la comunidad, como pueden ser las invasiones biológicas o las consecuencias de la pérdida de especies/interacciones en la comunidad (Schleuning *et al.* 2015).

Características de las especies con las que interactúan los más generalistas y especialistas de una comunidad

Gran parte de la investigación ecológica se focaliza en tratar de entender por qué las especies son generalistas o especialistas en sus interacciones y cómo las redes de interacciones evolucionan en un entorno determinado. Para comprender el comportamiento de estas especies (generalistas/oportunistas y especialistas/selectivas) es preciso conocer también las características de las especies con las que interactúan (sus "parejas") y si estas parejas difieren en determinados rasgos. Los resultados del segundo capítulo muestran que las especies más generalistas de una comunidad (aquellas que interactúan con un mayor número de especies) visitan (en el caso de visitantes florales) o son visitadas (en el caso de las plantas) por una amplia gama de diferentes especies pertenecientes a diferentes grupos funcionales de insectos o diferentes familias de plantas con gran heterogeneidad en sus abundancias.

Sin embargo, las especies especialistas tienden a visitar o ser visitadas, en su mayoría, por especies comunes (con similar abundancia entre ellas) que pertenecen a la misma familia de plantas o grupo funcional de visitantes florales, evitando o disminuyendo el riesgo de extinción debido a la pérdida de interacciones mutualistas provocada por diferentes impulsores del cambio global (Kiers *et al.* 2010). Este hallazgo concuerda con resultados previos que demuestran que la especialización recíproca entre las especies es bastante rara y que las interacciones entre mutualistas es altamente asimétrica, un patrón que contribuye a aumentar el anidamiento en la comunidad (Vázquez & Aizen 2004; Bascompte *et al.* 2006). Se ha demostrado que este patrón también disminuye la competencia interespecífica en aquellas comunidades con mayor solapamiento de nicho, anidadas o con redes muy conectadas (Bastolla *et al.* 2009; Valdovinos *et al.* 2013).

El peso de interacción más complejo y detallado (capítulo 1) nos permite alcanzar un mejor conocimiento del nivel de selectividad (índice cuantitativo) de las especies en una comunidad. Ambos tipos de especies, oportunistas y selectivas, interactúan con una alta riqueza funcional de especies. Este resultado es particularmente interesante, ya que muestra que las especies selectivas, consideradas hasta el momento más vulnerables a las perturbaciones, podrían ser mantenidas en la comunidad mediante la interacción con una amplia gama de diferentes especies pertenecientes a distintas familias (en el caso de las plantas) o a distintos grupos funcionales (en el caso de los visitantes florales). Interactuar con especies escasas pero diversas podría de hecho ser una "estrategia" de las especies selectivas para evitar la competencia por los recursos abundantes y asegurar su mantenimiento en la comunidad.

Algunos estudios han mostrado una alta variabilidad en la presencia de especies y de interacciones en la misma estación y entre estaciones (Herrera 1988; Alarcón *et al.* 2008; Olesen *et al.* 2008; Dupont *et al.* 2009; Fang & Huang 2012), pero poco se sabe sobre los mecanismos que producen tales cambios (Trøjelsgaard *et al.* 2015). Dichos cambios en las interacciones pueden ser consecuencia de cambios en la abundancia de las especies con las que se interactúa o por la presencia de nuevas especies en la comunidad. Por lo tanto, la decisión de con quién interactuar puede depender de la dinámica temporal de la comunidad. Esta fluctuación temporal de las especies y de las interacciones podría ser amortiguada si la especie que se pierde es sustituida por otra con las mismas o similares características (Fang & Huang 2012).

Los resultados muestran que, de hecho, éste es el caso para casi todas las especies estudiadas en el segundo capítulo. A pesar de las nuevas especies de visitantes florales que aparecen y desaparecen a lo largo de la estación y a pesar de los cambios en sus abundancias, todas las plantas seleccionadas (generalistas, especialistas, oportunistas y selectivas) fueron muy constantes en las características de las especies con las que interactuaron en toda la temporada. Acorde con nuestros resultados, Fang & Huang (2012) encontraron que durante su estudio de 4 años, la mayoría de las plantas interactuaban con los mismos grupos funcionales de polinizadores. Del mismo modo, las especies de visitantes florales especialistas, selectivas y oportunistas no cambiaron sus preferencias a través del tiempo. Por el contrario, las especies de visitantes florales generalistas si cambiaron sus preferencias en función de la dinámica temporal de las plantas en la comunidad a lo largo de la temporada. Se sabe que la amplitud de la dieta de los polinizadores generalistas es un rasgo flexible resultante de la adaptación a las diferentes opciones de alimentación relacionada con la disponibilidad de recursos (Fontaine *et al.* 2008; Valdovinos *et al.* 2013).

Aunque nuestros hallazgos se basan en una sola temporada, creemos que nos ofrecen una visión bastante clara de las interacciones entre pares de especies ya que analizamos aquellas especies que coexisten en el tiempo y analizamos sus características en el momento de la interacción. Sin embargo, para la generalización de nuestros resultados, es necesario el estudio de otras comunidades y datos de más temporadas. Por otra parte, es necesario considerar otras características de las especies, tales como el tipo de recompensa ofrecida por las flores (Petanidou *et al.* 2006), el tipo y tamaño de flores e insectos (Stang *et al.* 2006, 2007), el color (Whitney *et al.* 2009) o los aromas (Junker *et al.* 2010) para entender todos los posibles mecanismos que influyen en la microestructura de las redes de visitantes florales.

Similitudes y diferencias en redes de visitantes florales en islas de diferente origen

Las islas son de particular importancia para la conservación de la diversidad global. Sus pequeños tamaños de población y el alto nivel de endemismos las hacen particularmente susceptibles a cambios antropogénicos. Los resultados del tercer capítulo nos muestran las diferencias entre una isla de origen oceánico y otra de origen continental. A pesar de la mayor riqueza de especies en las comunidades de islas continentales con respecto a las oceánicas, el ratio animal/planta fue similar entre Lanzarote (A:P = 2,96) y Mallorca (A:P = 2,60), alcanzando valores intermedios de los observados en otras islas (A:P = 2) y en comunidades de la zona continental (A:P = 4) (Trøjelsgaard & Olesen 2013). La proximidad de nuestras dos islas de estudio a las áreas de origen continental podría explicar, en parte, la alta riqueza de polinizadores en relación con otras islas más empobrecidas. Probablemente debido a esta distancia similar a la parte continental, las zonas costeras estudiadas de Mallorca y Lanzarote comparten hasta el 30% de los géneros de visitantes florales, un valor alto teniendo en cuenta que las dos zonas de estudio dentro de cada isla sólo comparten el 56% de los géneros. Por el contrario, las plantas comparten sólo el 16% de los géneros entre las dos islas, posiblemente debido a su menor capacidad de dispersión y establecimiento.

Dentro de las islas, los dos sitios canarios fueron más similares en la composición de especies que los de Mallorca. Esto se tradujo en parámetros cualitativos y cuantitativos más similares en la primera. Como era de esperar, las abejas constituyeron el grupo taxonómico más rico en la isla continental, al igual que en las comunidades continentales (Kaiser-Bunbury *et al.* 2010a). Por el contrario, los dípteros fueron el grupo con el mayor número de especies en las comunidades oceánicas, patrón observado comúnmente en redes de visitantes florales en islas oceánicas (Kaiser-Bunbury *et al.* 2009; Padrón *et al.* 2009; Traveset *et al.* 2013).

Contrariamente a lo esperado (Barrett 1996; Padrón *et al.* 2009), se encontró que el nivel de generalismo (número de especies con las que interactúan), de plantas y visitantes florales, era bastante similar entre las zonas insulares oceánicas y continentales. Valores similares de generalismo entre un isla oceánica y una isla continental también fueron encontrados por González-Castro *et al.* (2012) para las interacciones de dispersión de semillas por vertebrados. En las comunidades oceánicas se detectó un pequeño grupo de especies nativas supergeneralistas, todas ellas involucradas en interacciones asimétricas, es decir, interacciones entre especies especialistas y generalistas. Estas interacciones asimétricas son comunes en redes pequeñas y son importantes para la supervivencia a largo plazo de las poblaciones de especies raras, ya que proporcionan interacciones estables (Bascompte *et al.* 2003; Kaiser-Bunbury *et al.* 2009; Memmott 2009). La pérdida de cualquiera de estas especies supergeneralistas nativas podría ser perjudicial para la estabilidad general de la red, causando posibles extinciones secundarias en cascada y disminuyendo la diversidad. Por lo tanto, en un contexto de conservación, la identificación, manejo y restauración de especies nativas que interactúan fuertemente con otras deben ser un objetivo principal (Dupont *et al.* 2003; Memmott *et al.* 2004; Tylianakis *et al.* 2010).

En contraste con los resultados en el nivel de generalización, sí se detectaron diferencias en el nivel de selectividad de especies entre las dos islas. Las dos redes mallorquinas fueron más selectivas, (valores superiores de H_2') que las dos redes canarias. Este resultado difiere del obtenido en un reciente estudio en el que se analizan redes de visitantes florales de todo el mundo (Traveset *et al.* 2016). En dicho estudio no se encontraron diferencias entre el nivel de selectividad de las comunidades de islas oceánicas, islas continentales y del continente. Esta diferencia puede ser debida a la alta variabilidad en el nivel de selectividad de las especies, por ejemplo, en un mismo archipiélago en función de la edad de las islas (Trøjelsgaard *et al.* 2013). En las comunidades canarias, más del 75% de las especies fueron oportunistas o altamente oportunistas, pero ninguna altamente selectiva. Estos resultados contrastan en parte con los de Trøjelsgaard *et al.* (2013), quienes encontraron un aumento en el nivel de selectividad de las plantas en relación a la edad de las islas en Canarias. Utilizando datos de otras redes costeras de otro archipiélago oceánico, las Galápagos (Traveset *et al.* 2013), se encontró que, en la isla más antigua, San Cristóbal (2.4 - 4.0 Ma), el 70% de las especies eran oportunistas o altamente oportunistas, mientras que en la isla más joven, Fernandina (0.035 - 0.070 Ma) un 58% de las especies eran selectivas o altamente selectivas.

Una mayor proporción de especies oportunistas y generalistas en las islas de mayor edad podría traducirse en una mayor redundancia en las interacciones entre especies, lo que implica, por lo tanto, que son menos vulnerables a las perturbaciones (Schleuning *et al.* 2015). Por el contrario, en las comunidades de Mallorca, más del 50% de las especies fueron selectivas o altamente selectivas, lo que podría estar asociado a la mayor competencia por nicho descrito para islas continentales (Whittaker & Fernández-Palacios

2007). Este alto nivel de selectividad en las redes de islas continentales puede indicar una dependencia recíproca entre las especies que interactúan, lo que aumenta la vulnerabilidad de las interacciones a las perturbaciones (Blüthgen *et al.* 2008). Sin embargo, como hemos visto anteriormente, estas especies selectivas pueden presentar estrategias alternativas al resto de especies para mantenerse en la comunidad.

Efecto de una gran perturbación en una comunidad dunar

La pérdida del hábitat es uno de los impulsores del cambio global, un fenómeno de rápido crecimiento en todo el mundo que puede afectar severamente a las redes ecológicas (Hagen *et al.* 2012). La construcción de zonas recreativas para el disfrute del ser humano ocasiona, la mayoría de las veces, un gran daño en el ecosistema. Como pudimos observar en los resultados del cuarto capítulo, la pérdida de alrededor del 50% del hábitat en el área de estudio provocada por la construcción de un campo de golf mostró un impacto sobre algunas de las propiedades estructurales de la red de la polinización estudiada. El número de polinizadores y el número de interacciones en la red disminuyeron después de la perturbación. Sin embargo, la conectancia de la red fue muy consistente en el tiempo. Estos resultados concuerdan con los obtenidos en otros estudios, mostrando una reducción en la disponibilidad y diversidad de los polinizadores como resultado de una disminución de los recursos florales y de sitios de anidación (Winfree *et al.* 2011; Hagen *et al.* 2012; Ferreira *et al.* 2013; Vanbergen *et al.* 2014).

Por otra parte, el patrón anidado de las interacciones fue menor el año siguiente a la perturbación, lo que sugiere interacciones más especializadas entre las especies predominantes en la comunidad, resultado apoyado por los valores más altos del nivel de especialización de la red (H_2') en 2011. Otros estudios también han documentado disminuciones del anidamiento de redes de hábitats perturbados (Vanbergen *et al.* 2014; Moreira *et al.* 2015; Revilla *et al.* 2015), aunque no siempre (Spiesman & Inouye 2013). Como hemos visto anteriormente, un menor anidamiento a menudo se asocia a una menor estabilidad y menor resistencia de las redes planta-polinizador a las perturbaciones (Bastolla *et al.* 2009; Fortuna *et al.* 2013).

Se ha observado también una mayor modularidad en hábitats perturbados en comparación con los no perturbados (Spiesman & Inouye 2013). Una red más modular puede reducir la capacidad de algunas especies de ayudarse recíprocamente mediante el intercambio de las especies con las que interactúan y, por lo tanto, puede tener un efecto desestabilizador (Thébault & Fontaine 2010). Tanto la modularidad como el número de módulos fueron mayores después de la perturbación aunque estas diferencias no fueron significativas al estandarizar los análisis por el tamaño de la red.

A nivel de especie, la fuerza de interacción (*strength*) de las plantas fue el único parámetro en el que no se observaron cambios durante los 4 años de estudio. Por lo tanto, la importancia relativa de una especie particular de plantas para la comunidad de visitantes florales fue constante. Esto es realmente interesante, ya que sugiere que, a pesar de que los rasgos de algunas plantas pueden cambiar en el tiempo (por ejemplo, su abundancia o su nivel de generalismo), la suma de las dependencias de cada uno de los visitantes florales de esa planta no se modificó. Los cambios temporales en el nivel de generalismo de las plantas, su proximidad central ponderada y su contribución al anidamiento indicaron, por el contrario, que la posición de una planta en la red dependerá de la cantidad de visitantes florales que tenga y del nivel de generalismo de éstos. Con respecto al nivel de selectividad (*d'*) de las plantas, se encontraron los valores más altos (mayor selectividad) el año posterior a la perturbación probablemente como consecuencia de la menor abundancia de insectos encontrada ese mismo año.

En cuanto a los visitantes florales, todos los parámetros estudiados a nivel de especie variaron entre años. La importancia de una especie de visitante floral en particular para toda la comunidad de plantas dependió de cómo de abundante y de generalista fuese ese visitante floral. La perturbación no sólo influyó en la abundancia de insectos, sino también en la riqueza de especies, siendo los escarabajos y las moscas los grupos más perjudicados. En relación al nivel de generalización, la fuerza de interacción, la selectividad y la proximidad central ponderada, las hormigas fueron el grupo funcional más afectado, disminuyendo incluso su papel como conectores de la red después de la perturbación. Sin embargo, otros grupos funcionales, especialmente abejas y avispas (muy abundantes en la zona) resultaron menos afectados. Una posible explicación es que la mayor movilidad de abejas y avispas (Torné-Noguera *et al.* 2014) les proporciona mayor flexibilidad a la hora de encontrar nuevos recursos y, por lo tanto, las hace menos vulnerables a perturbaciones locales.

En general, todavía hay poca información sobre cómo los diferentes grupos funcionales de visitantes florales que conviven en una comunidad responden a las perturbaciones del hábitat (Burkle *et al.* 2013; Aguirre-Gutiérrez *et al.* 2015, Lázaro *et al.* 2016). Es interesante también conocer la forma en la que cambian sus patrones de interacción con las plantas. Existe incluso menos información sobre las consecuencias de estos cambios para el éxito reproductivo de las plantas, por lo que queda un largo e interesante camino en el estudio de todos estos cambios producidos como consecuencia, no sólo de las alteraciones del hábitat, sino de todos los procesos impulsores del cambio global. Desde un punto de vista de conservación, el seguimiento de estos cambios en las comunidades naturales podría ser de gran importancia para la propuesta de estrategias efectivas de conservación (Campos-Navarrete *et al.* 2013).

Resistencia de las redes de interacción de visitantes florales frente al cambio global

El concepto de especialización en sistemas planta-polinizador está conectado inevitablemente a la noción de cascadas de extinción en los ecosistemas naturales, es decir, a la idea de que si el polinizador de una planta especialista se extingue, entonces la planta también se extinguirá. Sin embargo, como se ha expuesto en el segundo capítulo, las especies más especialistas interactúan con especies abundantes en la comunidad, lo que da robustez a las redes de visitantes florales (debido al aumento del anidamiento) de cara a posibles perturbaciones que impliquen la pérdida de especies (Bascompte *et al.* 2003; Memmott *et al.* 2004; Fortuna & Bascompte 2006; Saavedra *et al.* 2011). Del mismo modo, las especies selectivas visitan o son visitados por especies que pertenecen a diferentes familias de plantas o diferentes grupos funcionales de insectos y esto puede darles una mayor resistencia para hacer frente a la extinción de alguna de las especies con las que interactúan.

En todo caso, basándonos en nuestros resultados, podemos predecir que la gran mayoría de las especies de plantas y visitantes florales encontrarán nuevas especies con las que interactuar con rasgos similares a las que podrían desaparecer y, por lo tanto, la probabilidad de cascadas de extinción podría ser menor a la que se había pensado inicialmente (Petanidou *et al.* 2008; Burkle & Alarcón 2011). Sin embargo, como comentamos anteriormente, son muy necesarios estudios que incorporen medidas de los servicios ecosistémicos de los visitantes florales para determinar cómo estos cambios en las especies con las que interactúan podrían afectar a la reproducción y supervivencia de las plantas.

Por otro lado, debido al pequeño tamaño de las redes de visitantes florales y al alto nivel de endemismo en comunidades de islas oceánicas, éstas son también consideradas particularmente susceptibles a perturbaciones debidas al cambio global. La presión humana sobre estos ecosistemas es probable que aumente en un futuro próximo, como la introducción de especies exóticas invasoras y la alteración y destrucción del hábitat, principales amenazas para la biodiversidad endémica en muchos ecosistemas insulares (Kaiser-Bunbury *et al.* 2010a; Hagen *et al.* 2012). Los resultados del tercer capítulo muestran que, aunque pequeñas, las redes de visitantes florales en islas oceánicas están muy conectadas gracias a la presencia de especies oportunistas y especies supergeneralistas (Kaiser-Bunbury *et al.* 2009). Mayor conectividad puede, a su vez, dar lugar a una mayor anidamiento (González-Castro *et al.* 2012; Traveset *et al.* 2013; Trøjelsgaard & Olesen 2013), proporcionando estabilidad y resistencia a las perturbaciones (Bascompte *et al.* 2003; Memmott *et al.* 2004; Burgos *et al.* 2007; Tylianakis *et al.* 2010). Por lo tanto, a la luz de estos resultados, las pequeñas comunidades de las islas oceánicas podrían ser menos vulnerables a las perturbaciones de lo que se pensaba hasta ahora.

Sin embargo, la pérdida del 53% del área de la zona de estudio en Son Bosc (capítulo 4), produjo una disminución en el número y riqueza de polinizadores y en el número de interacciones en la red. Una alta diversidad de los roles funcionales de animales mutualistas, promovido por una gran diversidad de grupos funcionales, asegura una mayor diversidad de interacciones a través de toda la comunidad de plantas. Esto concuerda con la idea de medir la redundancia de los servicios mutualistas de los animales a las plantas debido a la diversidad funcional de las especies con las que interactúan (Albrecht *et al.* 2013). Esta alta diversidad funcional y diversidad de interacciones entre animales mutualistas promueve el aprovisionamiento y la estabilidad de las funciones ecosistémicas (Schleuning *et al.* 2015). Por lo tanto, menor anidamiento, mayor modularidad, mayor número de especies especialistas y menor número y riqueza de polinizadores hace que esta zona de estudio sea más vulnerable a futuras perturbaciones.

En conclusión, gracias a las técnicas de análisis de redes complejas utilizadas en esta tesis damos un paso adelante en el conocimiento tanto de las particularidades como de las características globales de las redes de visitantes florales en comunidades costeras insulares. Utilizar un peso de interacción adecuado a la hora de construir las redes de interacción nos conduce a que estas sean cada vez más realistas y completas. Hemos podido entender con mayor profundidad el dinamismo y la capacidad de la especies de asegurar su supervivencia en las diferentes comunidades utilizando distintas estrategias. Hemos observado la resistencia de la mayoría de las especies a una gran perturbación, aunque todavía desconocemos sus efectos a largo plazo. Estudios de este tipo son extremadamente necesarios para intentar proteger, en la medida de lo posible, los ecosistemas naturales frente a la gran cantidad de perturbaciones provocadas por el ser humano. Toda esta información es imprescindible a la hora de realizar proyectos de conservación y restauración de ecosistemas insulares exitosos.

Conclusiones principales y perspectivas futuras

Conclusiones principales

- El peso utilizado para construir las matrices de interacción entre las plantas y sus visitantes florales influye en los parámetros de red estudiados. Por lo tanto, es importante considerar cuidadosamente el peso de interacción más apropiado en cada caso, haciendo hincapié en que las comparaciones entre redes que utilizan diferentes pesos podrían dar lugar a resultados erróneos y, en consecuencia, a interpretaciones ecológicas equivocadas.

- Cuando el peso de interacción gana en complejidad, se observa una clara tendencia hacia interacciones más especializadas, mayor heterogeneidad en la frecuencia de las interacciones y mayor anidamiento cuantitativo. Para avanzar hacia una descripción más funcional de la estructura de las redes ecológicas, se necesitan pesos de interacción detallados que nos proporcionen información realista de las características de la comunidad de estudio.

- Las especies especialistas (con pocas parejas) y selectivas (que visitan especies poco abundantes o escasas), consideradas las más vulnerables frente a perturbaciones, interactúan principalmente con especies abundantes y/o con parejas funcionalmente diferentes, respectivamente. Este comportamiento les proporciona resistencia frente a posibles cambios y les ayuda a mantenerse en la comunidad.

- Las únicas especies que muestran cambios a lo largo de la temporada en los rasgos de sus parejas, impulsados a su vez por los cambios en la composición de especies de la comunidad, son las especies de visitantes florales generalistas.

- Las cascadas de extinción causadas por la pérdida de especies pueden no ocurrir tan rápidamente como se pensaba. La gran mayoría de plantas y visitantes florales suelen encontrar nuevas especies con las que interactuar, con rasgos similares a los de las especies con las que interactuaban inicialmente.

- Las redes de visitantes florales de Mallorca (isla continental) poseen un mayor número de especies que las de Lanzarote (isla oceánica). Sin embargo, esto no se traduce ni en un mayor número de interacciones ni en una mayor diversidad de las mismas, probablemente debido a la presencia de especies supergeneralistas.

- A pesar de las diferencias de origen, área, edad y fuentes de colonización, las zonas costeras de Mallorca y Lanzarote comparten hasta un 30% de los géneros de visitantes florales y un 16% de los géneros de plantas. Las abejas constituyen el grupo taxonómico más rico en la isla continental mientras que los dípteros fueron el grupo con mayor número de especies en las comunidades oceánicas.

- Las especies de las comunidades mallorquinas son más selectivas (> 50% son selectivas o altamente selectivas) que las especies de las comunidades canarias (> 75% son oportunistas o altamente oportunistas). El alto nivel de selectividad en las redes de la isla continental podría indicar una mayor dependencia recíproca entre las especies interactuantes, lo que aumentaría su vulnerabilidad a las perturbaciones. Por otro lado, una mayor proporción de especies oportunistas podría traducirse en una mayor redundancia en las interacciones, lo que implicaría una menor vulnerabilidad de las comunidades oceánicas frente a perturbaciones.

- Los valores más altos de conectancia y anidamiento en las redes de visitantes florales costeras en islas oceánicas, resultado de la presencia de un mayor número de especies oportunistas y de especies supergeneralistas, proporcionan también mayor resistencia a las perturbaciones en comparación con las redes de visitantes florales de las islas continentales.

- La pérdida del 53% del área de la zona de estudio en Son Bosc tuvo como consecuencia la disminución del número de polinizadores y el número de interacciones en la red. Los movimientos de tierra realizados para la construcción del campo de golf afectaron en mayor medida a los escarabajos, las moscas y las hormigas. Las abejas y las avispas se vieron menos afectadas, probablemente debido a una mayor capacidad de vuelo con respecto a otros grupos funcionales, característica que les puede proporcionar mayor resistencia frente a perturbaciones locales.

- El nivel de especialización y selectividad de las plantas de la comunidad de Son Bosc aumentó como consecuencia tanto de factores propios (menor abundancia floral) como de factores externos (menor riqueza y abundancia de polinizadores) en 2011, un año después de la perturbación.

- La pérdida de gran parte del hábitat se tradujo en una disminución del anidamiento y un aumento de la modularidad de la red de visitantes florales. Además, conllevó una mayor proporción de especies especialistas, lo que provoca que la comunidad sea más vulnerable frente a futuros cambios consecuencia del cambio global.

Perspectivas futuras

Generalmente, los proyectos de investigación contribuyen a despejar algunas incógnitas sobre el tema abordado pero, simultáneamente, generan nuevas preguntas, nuevas ideas y/o abren nuevas vías de trabajo. La labor llevada a cabo tanto en el laboratorio de nuestro grupo de investigación como junto a otros grupos de investigación nos permite aprender nuevas técnicas y colaborar en diferentes estudios que, aunque no formen parte de la línea de investigación principal de la tesis doctoral, suelen ser de gran utilidad en el desarrollo profesional de los estudiantes de doctorado. En mi caso personal, si bien estoy satisfecha por haber logrado culminar varios estudios que han visto la luz en forma de publicaciones en revistas especializadas, también han surgido otras preguntas que podrían dar lugar a nuevas líneas de investigación. Este camino que vamos recorriendo, aunque puede ser frustrante en ocasiones, es sin duda la mejor y única manera de seguir avanzando y profundizando en el conocimiento de cada disciplina científica.

Durante mi estancia en Mendoza (Argentina) en el laboratorio dirigido por el Dr. Diego P. Vázquez, tuve la oportunidad de realizar tanto trabajo de laboratorio como de campo, tomando parte de los datos de las redes de plantas y visitantes florales en la zona de Villavicencio. Participé en un proyecto en el que se tomaron datos morfométricos tanto de las flores como de los insectos de la misma comunidad. Utilizando toda esta información, tenemos en marcha un estudio sobre la posible coevolución entre el largo de la corola y del aparato succionador de los insectos a nivel comunitario. La red de visitantes florales utilizada en este proyecto abarca 5 años y 20745 interacciones entre 38 especies de plantas y 71 especies de visitantes florales. Sabemos que las redes mutualistas suelen ser bastante generalistas y la fuerza de interacción (y, por tanto, las presiones de selección) es a menudo asimétrica, por lo que la coevolución podría no ser tan importante a nivel de toda la comunidad. Lo que esperamos observar es que las interacciones más frecuentes y simétricas coevolucionen en mayor medida. Los resultados preliminares de este estudio apuntan a la idea de que los rasgos estudiados no están coevolucionando. Solo cuando eliminamos de la red las interacciones más frecuentes aparece una tendencia, aunque no significativa, hacia la evolución conjunta de los rasgos. Este resultado puede responder al hecho de que las interacciones más frecuentes se dan entre los organismos más generalistas. Seguimos trabajando para incluir la simetría de la interacción y el nivel de generalización de los participantes en las mismas en los siguientes análisis. Dichos resultados preliminares apoyan la idea hoy más generalizada de que la coevolución a nivel comunitario tiende a ser difusa y difícilmente cuantificable, al menos con los métodos utilizados hasta ahora en este proyecto.

Siguiendo una metodología similar a la aprendida durante la estancia en Mendoza, hemos tomado datos morfométricos de todas las especies vegetales y gran parte de las especies de visitantes florales de una de las comunidades estudiadas en Mallorca, concretamente la de la zona de Cala Mesquida. Con esta información y usando un enfoque similar al del segundo capítulo de la presente tesis doctoral, se pueden estudiar las diferencias morfométricas entre las especies con las que interactúan los más generalistas/oportunistas o especialistas/selectivos de la comunidad. En dicho capítulo hemos podido observar cómo las especies más especialistas visitan en mayor medida a las especies más abundantes de la comunidad. A su vez, las especies más abundantes suelen ser más generalistas y, por tanto, podríamos esperar dos cosas. Por un lado, que los insectos especialistas interactúen con especies abundantes con una simetría floral actinomorfa y menores restricciones a la hora de alcanzar la recompensa floral buscada, ya sea polen o néctar. Por otro lado, en el caso de las plantas especialistas, que los visitantes florales con los que interactúan sean de menor tamaño o grandes pero con probóscides largas. Similares características se podrían esperar para aquellas especies que interactúan con las más generalistas y oportunistas de la comunidad. Sin embargo, las especies con las que interactúan las más selectivas de la comunidad sí podrían presentar unas características morfométricas más restrictivas.

Por último, en la zona de estudio de Son Bosc, que ha sido afectada por una gran perturbación como hemos visto en el manuscrito correspondiente al cuarto capítulo de esta tesis doctoral, se han tomado datos durante este mismo año 2016. Disponiendo de más datos de la misma zona de estudio será posible evaluar, con mayor detalle, el efecto causado sobre las plantas y los visitantes florales por dicha perturbación ocasionada por los movimientos de tierra realizados con la intención de construir un campo de golf. De igual manera, se podrá observar si existe una recuperación en la zona o si, por el contrario, el impacto fue tan grande que continúa la caída en el número de especies y de interacciones. Otro factor importante e interesante a tener en cuenta es el cambio de las interacciones entre las especies y así comprobar cómo ante un acontecimiento de tal magnitud la comunidad se reestructura para poder seguir sobreviviendo.

Estas cuestiones son solo algunos ejemplos que sirven para ilustrar este proceso continuo de avance en el conocimiento de las diferentes disciplinas científicas del que hablamos anteriormente. Al comienzo de los proyectos de investigación nos planteamos una serie de preguntas, que vamos respondiendo poco a poco. Durante dicho proceso siempre van surgiendo otros interrogantes que nos van guiando hacia una comprensión más profunda de los sistemas naturales que estudiamos. Es, ni más ni menos, que lo que vamos haciendo en nuestro día a día. Vamos acercándonos con paso firme hacia una meta clara y objetiva, que no es otra que intentar conocer lo mejor posible nuestro entorno, su funcionamiento y su dinámica. Por el camino vamos entendiendo algunas cuestiones y otras nos van indicando la dirección de los siguientes pasos. Así, entendiendo lo que sucede en los lugares que nos rodean, quizás algún día podamos tomar más conciencia del valor que realmente tienen los ecosistemas que, en muchas ocasiones, ocupamos y afectamos gravemente sin ser realmente necesario.

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03. Rasmussen C, Carrión AL, **Castro-Urgal R**, Chamorro S, Gonzalez VH, Griswold TL, Herrera HW, McMullen CK, Olesen JM, Traveset A (2012) *Megachile timberlakei* Cockerell (Hymenoptera: Megachilidae): Yet another adventive bee species to the Galápagos Archipelago. *The Pan-Pacific Entomologist* 88(1): 98-102. DOI: http://dx.doi.org/10.3956/2012-04.1

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10. Traveset A, Tur C, Trøjelsgaard K, Heleno R, **Castro-Urgal R**, Olesen JM (2016) Global patterns of mainland and insular pollination networks. *Global Ecology and Biogeography 25*(7): 880-890. DOI: http://dx.doi.org/10.1111/geb.12362

11. Traveset A, **Castro-Urgal R**, Rotllàn X, Lázaro A (*In prep.*) Effects of habitat loss on the plant-flower visitor network structure of a dune community

12. Lomáscolo SB, Chacoff NP, Vázquez DP, Giannini N, **Castro-Urgal R** (*In prep*) Coevolution in a plant-pollinator network

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Tesis Doctoral UIB 2016 Patrones emergentes en redes de polinización en comunidades costeras de Baleares y Canarias Rocío Castro Urgal