

On the Structure and Dynamics of Ecological Networks

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MADRID-SEVILLA
2000-2005



Universidad
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HACE CONSTAR:

Que el texto adjunto corresponde a la Tesis Doctoral: **On the Structure and Dynamics of Ecological Networks**, de la que es autor el licenciado en Ciencias Ambientales D. Carlos J. Melián Peñate.

Esta Tesis reúne los requisitos necesarios para su defensa y aprobación para optar al grado de Doctor por la Universidad de Alcalá.

Alcalá de Henares, Diciembre de 2004

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The original papers on which this PhD. is based are downloadable from <http://www.bascompte.org>. All this document is downloadable from <http://ieg.ebd.csic.es/melian>.

The following articles will be presented in this PhD. (chronological order):

Melián, C. J. and Bascompte, J. (2002). Food web structure and habitat loss. *Ecology Letters*, **5**:37-46.

Melián, C. J. and Bascompte, J. (2002). Complex networks: two ways to be robust? *Ecology Letters*, **5**:705-708.

Melián, C. J. and Bascompte, J. (2004). Food web cohesion. *Ecology*, **85**:352-358.

Melián, C. J., Bascompte, J. and Jordano, P. (2005). Spatial structure and dynamics in a marine food web. In “Belgrano, A., Scharler, U., Dunne, J., and Ulanowicz, R. E.”, *Complexity in Aquatic Food Webs: an Ecosystem Approach*. Oxford Univ. Press, pp 19-24, (in press).

Bascompte, J., Melián, C. J. and Sala, E. Interaction strength motifs and the overfishing of marine food webs. *Submitted*.

Melián, C. J., Bascompte, J., and Jordano, P. The structure and dynamics of the antagonistic-mutualistic Doñana Ecological Network. *Submitted*.

Thank you!

The present document would had been impossible to develop without direct and indirect help of many people. The following people helped me either during all the process or as an important step of it. I would like to sincerely thank all of them:

My fathers, Paco Melián and Mariquilla Peñate, My partner and scientific collaborator Mayte Valenciano for her patience, Antonio Gómez Sal and Miguel A. Rodríguez for continuous discussions and facilities in the department of Ecology at Alcalá University, José M^a Montoya for his philosophical and scientific suggestions, José Manuel Nicolau, Antonio López Pintor, and Jesús Martínez for interesting discussions, Louis-Félix Bersier, Raphael Boulay, Rafa Bravo, Dani Cabello, Manolo Carrión, Antonio Gómez, Roger Jovani, Bartolo Luque, Fátima Marrero, Eduardo Perero, and Sergio Tirado for comments and debates, George Sugihara and Joel E. Cohen for helpful discussions on food webs and for allowing me to visit their labs in San Diego, California (Summer 2002), and New York (Summer 2003) respectively, Specific thanks are introduced in the section **Acknowledgements** of each manuscript, Pedro Jordano and Miguel A. Fortuna for their conceptual and technical suggestions, Special thanks to Jordi Bascompte for his continuous ideas, support, and for helping me both to understand science as an open process, and more broadly the current state of the world.

Overview

An important fraction of my time during this PhD has been devoted to develop ideas, algorithms and models based on empirical data with scientists from different areas of ecology. During this process, I have learnt that there are lots of 'dead' data dealing with species in different ecosystems all around the world collected along the last 50 years. Each study follows different methods, and interprets results according with each authors' personal or group skills. In this context the main two goals of the present PhD have been: (1) to analyze the most large and resolved data sets of food webs from the literature and new synthesized data using both static null models and dynamic simulations, and (2) to synthesize fragmented studies within the ecological network framework. The resulting work is an improved Caribbean Coral Reef food web, and a completely new Doñana food web. The specific goals in the present study are: (a) to detect new structural patterns in a set of qualitative food webs (chapter 2), (b) to link structure and dynamics in the quantitative Caribbean food web (chapter 3), (c) to extend food webs in space (chapter 4), and (d) to explore the effect of structure on the dynamics of a species-rich community with two types of ecological interactions (chapter 5).

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0.1 Introducción

Durante el desarrollo de la presente investigación (2000-2004), mi visión de la ecología ha cambiado. En principio consideraba a la ecología una disciplina joven e inmadura. Tras pasar por un proceso corto e intensivo de investigación, de leer y pensar sobre artículos y debatir con científicos de diferentes campos, ahora miro a la ecología con otros ojos. Creo que a pesar de su juventud la ecología tiene partes maduras. En los siguientes párrafos intentaré exponer esta sensación.

El 12 de Diciembre de 1999, escribí una carta al prof. R. E. Ulanowicz y le comenté que me gustaría trabajar en análisis de redes en su grupo. Había leído uno de sus libros, *Ecology, the Ascendent Perspective*, el cual me sorprendió tanto por su visión de conjunto, como por continuar desarrollando ideas de ecólogos que habían trabajado en ecología de comunidades desde los años 70 (el prof. Ramón Margalef entre otros). El prof. Ulanowicz me respondió muy claramente, haciendo notar que su grupo de investigación era muy pequeño, consistiendo en un postdoctorado, un estudiante de doctorado y él mismo. La razón de ese tamaño, comentaba, era el poco dinero que se dedicaba en los Estados Unidos a la ecología teórica. Además me comentó que en un futuro próximo recibiría dinero para otro doctorado, y el único requisito era tener una gran base en matemáticas. Por supuesto, le respondí que no tenía una base muy fuerte en matemáticas y que esa plaza estaba fuera de mis posibilidades. En ese periodo dedicaba el tiempo a leer trabajos que se consideraban clásicos en ecología (Elton, Lindeman, Hutchinson, MacArthur, Odum y Margalef, entre otros). La ecología era para mí una disciplina marginal, y consideraba que todos los conceptos y métodos que ella usaba procedían de otras disciplinas.

El 24 de Agosto del 2002, durante una estancia con el prof. George Sugihara y junto a Jordi Bascompte en el *Scripps Institution of Oceanography*, San Diego, California, nos percatamos de que uno de los referees de nuestro trabajo *Complex Networks: two ways to be robust?*, era el prof. R. E. Ulanowicz. El prof. Ulanowicz fué un revisor realmente constructivo, y sus sugerencias ayudaron a mejorar la versión final del trabajo.

Alguno de sus comentarios sobre la ecología fueron

muy claros para mí¹:

I do apologize if any emotion crept into my review concerning the history of networks in ecology. It is just back in May there was a "Perspectives" article in the journal Nature, extolling some new work on quantitative ecosystem networks as the beginning of a new discipline, when I and several others had been working in the field for well over 20 years now!. Also, none of the contemporary literature on networks in science seem to mention anything we accomplished. So I am very sensitive at this point. As my career comes toward its end, it is a bit discouraging to realize that one's entire career will probably be neglected, but such is life.

Y continuó como sigue:

I was quite pleased with the ms. that Wilfried Wolff and I put together. We were able to show rather convincingly (I think) that the magnitudes of ecosystem transfers are Cauchy-distributed (now called scale-free). It did not appear to us that the topological (binary) food webs were distributed in the same way. When interest in scalefree networks broke, I was waiting for someone to cite our earlier work, but I have yet to find any mention of it anywhere. I would be grateful if you could cite in your rewrite.

Después de recibir esta carta, he procurado criticar mi idea de madurez, primero porque había estado más de un año leyendo en la primera parte de mi tesis en la Universidad de Alcalá artículos clásicos sobre redes tróficas (desde 1998 hasta el 2000), pero en menos de tres años (verano del 2002), había olvidado completamente el trabajo del prof. Ulanowicz y Wolff, entre otros, y segundo, porque empezaba a ver que la ecología no era tan inmadura como yo pensaba. Quizás lo inmaduro estaba en como entendía yo la práctica científica. Las distribuciones de flujos tipo *Cauchy* y la distribución de conexiones por nodo habían sido estudiadas por trabajos pioneros en ecología y muy posiblemente en otras disciplinas científicas, mientras el "renacimiento" de las redes complejas y su gran esfuerzo en unificar diferentes disciplinas (Evans 2002) no estaba capturando esta peculiaridad. El prof. Ulanowicz entre otros, forman la parte madura de la ecología. Yo me considero en la parte inmadura. Inevitablemente, desde una per-

¹El prof. R. E. Ulanowicz ha aceptado que su texto sea citado en la presente introducción.

spectiva sucesional, ambas partes son esenciales para la estructura y dinámica de la ciencia. Sin embargo, es necesario reconocer que los avances conceptuales, metodológicos y los resultados mostrados por la parte madura no están siendo correctamente registrados por la parte inmadura dentro de la estructura del proceso científico, al menos dentro del estudio de redes ecológicas.

De forma similar, una gran variedad de modelos nulos tanto cualitativos como cuantitativos están siendo introducidos dentro del marco de las redes complejas. Algunos de los modelos nulos han sido previamente estudiados en ecología de comunidades (para el *algoritmo swap* ver Connor and Simberloff 1979; Artzy-Randrup et al. 2004). Sin embargo, si miramos en detalle el proceso que ha sufrido este algoritmo, podemos encontrarnos con que el matemático D. Gale lo había desarrollado formalmente en 1957 (Gale 1957), y en las décadas siguientes fué usado en diferentes disciplinas (ver Maslov et al. 2002). Trazar hacia atrás en detalle el origen y la evolución de los conceptos y los métodos dentro y entre las disciplinas científicas, es sin lugar a dudas, uno de los más importantes, y difíciles aspectos para preservar el cuerpo de una disciplina, y de la ciencia. Específicamente, la parte inmadura de una disciplina, o de la ciencia en su conjunto, deben ser muy sensibles en este punto.

¿Cómo han cambiado estos hechos parciales mi visión de los conceptos y métodos usados en ecología para detectar propiedades estructurales y dinámicas en redes tróficas?. Mi visión ha pasado a una madurez fuerte (Margalef 1963; Eldredge 1986; Cohen 1995). Sin embargo, a pesar de la mejora de los datos tanto en número de especies y detalles de su biología como en resolución, nuestro entendimiento de las redes tróficas no está necesariamente creciendo. Mientras la idea de progreso está más relacionada con la racionalidad limitada, las restricciones y la fragmentación de la información manejada por grupos de diversa ideología, la idea de madurez está relacionada con la forma en la que los individuos y los grupos acumulan, intercambian, sintetizan y generan información a partir de datos y métodos aislados.

En este contexto, el método usado aquí ha pretendido trabajar conjuntamente con datos, algoritmos y modelos dinámicos. Gran parte del presente trabajo ha estado dedicado a reunir datos históricos y recientes de diferentes fuentes para mejorar datos previamente existentes, como es el caso de la red trófica marina del Caribe, para introducir en la literatura ecológica un nuevo trabajo de síntesis como

es el caso de la red trófica de Doñana, o para simplemente analizar las nuevas redes más resueltas y de mayor tamaño que ofrece la literatura en ecología. El uso e incorporación de modelos nulos y simulaciones numéricas para testar propiedades estructurales y dinámicas en dichos datos han ocupado el resto del tiempo.

¿Cuales han sido las principales aproximaciones a la idea de estructura en las redes tróficas?. La ecología tiene una larga tradición estudiando la estructura de las comunidades (Camerano 1880; Forbes 1887; Elton 1927; Lindeman 1942; MacArthur 1955; Hutchinson 1959; Margalef 1963; Cohen 1968; Odum 1968; Polis and Strong 1996). La idea de estructura ha sufrido y sigue sufriendo cambios dramáticos en perspectivas y resultados. La estructura de las comunidades ha sido vista como una entidad compleja, con una miríada de detalles por explorar (Elton 1927; Lindeman 1942; Margalef 1963), como un mundo de subredes aisladas o “perspectiva microscópica” (Paine 1966), como una entidad organizada explorada a través de la estructura de nicho de las especies o “perspectiva mesoscópica” (Cohen 1968; Cohen 1978; Sugihara 1983), como una “propiedad macroscópica” (May 1973; Martinez 1991), describible a través de la conectividad global, de nuevo como una entidad compleja, donde se duda de estructura (Polis and Strong 1996), visión que ha promovido un vivo debate sobre conceptos tradicionalmente aceptados como parte del cuerpo de la ecología (Hairston and Hairston 1997). Nuevos y mejores datos, así como trabajos de síntesis se necesitan actualmente.

Sin embargo, el estudio de la estructura en redes tróficas ha estado compartimentalizado, centrándose independientemente en subredes aisladas, en la estructura que surge cuando se estudian los nichos de muchas especies, o en la conectividad global de las redes. ¿Cómo están conectadas estas perspectivas tradicionalmente aisladas?. El incremento en calidad y cantidad de los datos y su resolución, así como el despegue de metodologías provenientes del estudio de redes complejas, podría potencialmente proveernos de patrones más precisos y principalmente centrados en el nivel de interdependencia entre las tres escalas previamente comentadas. En el segundo capítulo hemos intentado unir las aproximaciones de subredes tradicionales y la conectividad global de una red trófica. Esta perspectiva nace en un intento de aprender de dos de los trabajos que han marcado tanto un gran nivel de calidad en los datos como una reflexión autocrítica de sus limitaciones (Lindeman 1942; Po-

lis and Strong 1996). Específicamente, hemos testado con las redes tróficas más largas y resueltas la clásica dicotomía entre estructura compartimentalizada o aleatoria.

¿Cómo insertar la estructura en la dinámica de las redes tróficas?. El entendimiento de la dinámica de las comunidades ecológicas es más reciente (Lewontin 1969; May 1973; Levins 1975), y después del reconocimiento de problemas con la estabilidad local en sistemas muy fluctuantes (Lewontin 1969; Lawlor 1977; Cohen and Newman 1984; Cohen and Newman 1985), diferentes variantes de estabilidad han surgido (Pimm 1982), pero aún existen problemas con la estabilidad de comunidades ricas en especies (Berlow et al. 2004; Emmerson and Raffaelli 2004). Sin embargo, creo que lo realmente importante al estudiar la dinámica es que la estructura está incorporada. Por ejemplo, el modelo de ecosistema de May (1973), asumía una estructura totalmente aleatoria en redes tróficas de pequeño-mediano tamaño.

Se han realizado muchos estudios que incorporan propiedades estructurales de las redes reales en las matrices de los modelos dinámicos (DeAngelis 1975; Yodzis 1981; Pimm 1982; Cohen et al. 1990; Caldarelli et al. 1998; Chen and Cohen 2001; Kondoh 2003). Sin embargo, la exploración de propiedades estructurales introduciendo información biológica de las especies tanto cualitativa como cuantitativa, y sus consecuencias dinámicas permanecen poco exploradas (Schaffer 1981; Emmerson and Raffaelli 2004). ¿Cómo integrar información biológica en la búsqueda de patrones estructurales y dinámicos en las redes tróficas?. El capítulo tres explora la presencia de cadenas y módulos cuantitativos con omnivoría en la red trófica del Caribe, y estudia las implicaciones dinámicas de la sobrexplotación parametrizando el modelo con los ratios de tamaño entre depredadores y presas, sus abundancias y tasas metabólicas.

La mayoría de las aproximaciones sobre la estructura y dinámica de las redes tróficas se han realizado asumiendo un área local y homogéneo y considerando un sólo tipo de interacción ecológica (p.e., antagonistas, mutualistas ó competitivas). Sin embargo, datos cada vez más detallados están mostrando tanto la importancia de la estructura espacial de las comunidades como el elevado número de tipos de interacción ecológica que afectan a sus propiedades (Thompson 2002; Berlow et al. 2004). ¿Cómo integrar la estructura y dinámica de las redes tróficas en el espacio?. El capítulo cuatro es un intento de extender en el espacio diferentes subredes con inter-

acciones antagonistas y competitivas, comprender su estructura y dinámica y predecir cómo responden a la destrucción del hábitat. Para ello se han planteado dos cuestiones básicas, (1) ¿Cómo afecta la estructura de las subredes la respuesta de las especies a la destrucción del hábitat?, y (2) ¿Cual es la interdependencia entre la estructura y la dinámica en subredes con dos tipos de interacción en un conjunto de comunidades locales unidas por procesos de dispersión?

El capítulo cinco representa para mi el trabajo sistemático más importante. El trabajo sintetiza estudios de diferentes grupos de investigación llevados a cabo en la Reserva Biológica de Doñana durante 10 años (1975-1985). Específicamente estudiamos los efectos de la estructura de la comunidad de Doñana con dos tipos de interacciones ecológicas (herbivoría y mutualismo con aproximadamente 400 especies) sobre su dinámica.

En resumen, la presente tesis analiza conjuntamente propiedades estructurales y dinámicas en redes ecológicas uniendo bases de datos con modelos nulos y simulaciones numéricas. De los seis trabajos presentados (ver en Tabla 1 la escala objeto de estudio en cada capítulo), cinco usan datos empíricos de síntesis, de los cuales dos estudian propiedades estructurales (*capítulo dos*), y los otros tres integran propiedades estructurales y dinámicas (*capítulo tres, segundo trabajo del capítulo cuatro, y capítulo cinco*). Sólo un trabajo explora mediante simulación numérica subredes en el espacio (*primer trabajo del capítulo tres*). La tabla 2 sintetiza para cada capítulo la forma en la que hemos combinado bases de datos y síntesis de nuevos datos con los algoritmos y simulaciones numéricas. He incluido en la parte final de cada capítulo dos apéndices. Con el primero *¿Qué es nuevo?* intentaré revisar de forma breve y crítica que se resuelve de las cuestiones planteadas y que se añade. Con el segundo, *Trabajo actual y futuro*, intentaré mostrar nuestro trabajo actual, relacionarlo con trabajos recientes y sugerir y especular sobre posibles nuevos trabajos y conexiones entre ellos.

Chapter 1

Introduction

During the time this research has been developed (2000-2004), my view of ecology has drastically changed. Initially I regarded ecology as a very young and immature discipline. After the research process presented here, reading and thinking on ecology, and debating with scientists from different fields, I now guess that ecology, regardless of its youth is becoming a mature science. Let me try to argue this point.

On December 12, 1999 I wrote a letter to Prof. R. E. Ulanowicz asking him the possibility to work in network analysis within his group. I had read one of his books, *Ecology, the Ascendent Perspective*, which it seemed to me really intriguing, both for his systemic perspective and because he extended some methods and ideas from previous community ecologist (Prof. R. Margalef among others). He answered me very clearly, noticing that his working group was very small, consisting of one postdoctoral associate and one graduate student, and himself, and his reason was that little money was available in the USA to support theoretical ecology. He told me that in a foreseeable future he would receive support for another graduate student, and the only requisite was a very strong mathematical background. Of course I answered him that I was not that strong at mathematics and this position was out of my reach. At that time I was reading classic works in ecology from Elton, Lindeman, Hutchinson, MacArthur, Odum, Margalef, among others, and I thought that ecology was a marginal discipline, and almost all concepts and methods it used came from other disciplines.

On August 24, 2002, during my stay with George Sugihara and Jordi Bascompte at *Scripps Institution of Oceanography*, San Diego, California, we noticed that one of the referees of our work *Complex Net-*

works: two ways to be robust?, was R. E. Ulanowicz. He was really a constructive referee, and his suggestions helped us to improve the final version of the manuscript. Some of his comments about ecology were very straightforward to me. I reproduce his comments here¹:

I do apologize if any emotion crept into my review concerning the history of networks in ecology. It is just back in May there was a "Perspectives" article in the journal Nature, extolling some new work on quantitative ecosystem networks as the beginning of a new discipline, when I and several others had been working in the field for well over 20 years now!. Also, none of the contemporary literature on networks in science seem to mention anything we accomplished. So I am very sensitive at this point. As my career comes toward its end, it is a bit discouraging to realize that one's entire career will probably be neglected, but such is life.

And he continued as follows:

I was quite pleased with the ms. that Wilfried Wolff and I put together. We were able to show rather convincingly (I think) that the magnitudes of ecosystem transfers are Cauchy-distributed (now called scale-free). It did not appear to us that the topological (binary) food webs were distributed in the same way. When interest in scalefree networks broke, I was waiting for someone to cite our earlier work, but I have yet to find any mention of it anywhere. I would be grateful if you could cite in your rewrite.

After this letter, I have tried to self-criticize my view of maturity first, because I had been more than one year reading classic papers about food webs (from 1998 to 2000) but after less than three years (summer

¹Prof. R. E. Ulanowicz accepted the quotation of his text in this introduction.

2002) I had forgotten completely the Prof. Ulanowicz and Wolff's study, among other works, and second, because I realized that ecology was not as young as I thought. Cauchy-distributed transfers and degree distributions were studied by pioneering works in ecology, but the "renaissance" of complex networks unifying different disciplines (Evans 2002) from a graph perspective was not capturing this feature. Prof. Ulanowicz among others, are to me the mature side of ecology. I form the immature side. Inevitably from a successional point of view both parts are essential to the structure and dynamics of science. At this point some conceptual and methodological advances made by the mature part are not being correctly registered by ourselves in the scientific process, specifically in the ecological network approach.

Similarly a lot of qualitative and quantitative null models are now being introduced in the framework of large matrices when exploring complex networks. Some of the null models have been largely explored and debated in community ecology (for the *swap algorithm* see Connor and Simberloff 1979; Artzy-Randrup et al. 2004). However, if we examine in detail the previous use of this algorithm we can find that the mathematician D. Gale developed its factorial formalism (Gale 1957), and the next decades was used in different fields (see Maslov et al. 2002 for a small review). Tracing back the origin and evolution of ideas, concepts, and methods within and between scientific disciplines is undoubtedly one of the most important and difficult things to do to preserve the historical background of a discipline, and science as a whole. Specially the immature part of a discipline must be sensitive at this point.

How did these partial processes change my view of the concepts and methods used in ecology to detect the structure and dynamics of food webs? My view of the concepts and methods used to detect structure and dynamics have changed from a weak to a partially strong maturity (Margalef 1963; Eldredge 1986; Cohen 1995). However, regardless the improvement of ecological data both in size and resolution, our cumulative understanding on food webs is not necessarily increasing. While the idea of progress is more related with bounded rationality, and information restriction and fragmentation used by diverse ideological groups, the idea of maturity is related with the way individuals and groups freely accumulate, synthesize, interchange and generate information from isolated data and methods. In this context, the methods used here have been intended to work together with data, algo-

rithms and dynamical models.

An important part of this work has been devoted to integrate historical and current data from different sources to improve previous data, as in the Caribbean coral reef food web, to introduce a new synthetic work, as the Doñana ecological network, or simply to analyze the current most resolved and biggest food webs from the ecological literature. The rest of this work concerns the introduction and use of null models and numerical simulations to test the structural and dynamical properties of these data.

What have been the major contributions to food web structure? Ecology has a long tradition studying the structure of food webs (Camerano 1880; Forbes 1887; Elton 1927; Lindeman 1942; MacArthur 1955; Hutchinson 1959; Margalef 1963; Cohen 1968; Odum 1968; Polis and Strong 1996). Structure has suffered and still is suffering dramatical changes in perspectives and results. Food web structure has been seen as a complex entity (Elton 1927; Lindeman 1942; Margalef 1963), as simplified and isolated subwebs or "microscopic perspective" (Paine 1966), as organized entities by exploring combinatorial properties of real niche spaces or "mesoscopic perspectives" (Cohen 1968; Cohen 1978; Sugihara 1983), as a "macroscopic property" (May 1973; Martinez 1991), again as a complex entity where the idea of structure need improvements with the new high quality data (Polis and Strong 1996). Results from these data promoted a debate on the trophic level dynamics and other traditional properties in food webs (Hairston and Hairston 1997). New synthesis with improved data sets are needed at this point.

However the study of structure in food webs has been compartmentalized, dealing with the *microscopic*, *mesoscopic*, and *macroscopic* properties independently one of the others. What new and larger food webs could show us? Increasing size and resolution of different food webs could potentially provides more accurate patterns, and more important, they could show us the level of interdependence between different scales. The second chapter tries to fill the gap between traditional subweb approaches and the macroscopic structure of large matrices. This perspective try to learn from two of the previous studies showing data quality and self-criticism in food web approaches (Lindeman 1942; Polis and Strong 1996). Specifically, we have tested the traditional trade-off between compartments or randomly assembled food webs in the largest and most resolved data. .

How to integrate structure in the dynamics of food

webs? The understanding of the dynamics of ecological communities is more recent (Lewontin 1969; May 1973; Levins 1975), and after the recognition of problems with local stability (Lewontin 1969; Lawlor 1977; Cohen and Newman 1984; Cohen and Newman 1985), different variants of stability emerged (Pimm 1982), but problems remain regarding the stability of species-rich communities (Berlow et al. 2004; Emmerson and Raffaelli 2004). However, the important thing studying dynamics is that structure is directly incorporated. For example, May’s model ecosystem assumed a total randomly structured in a small-medium size food web (May 1973).

Many efforts have been made towards incorporating structural features of real food webs into the pool of community matrices of dynamic models (DeAngelis 1975; Yodzis 1981; Pimm 1982; Cohen et al. 1990; Caldarelli et al. 1998; Chen and Cohen 2001; Kondoh 2003). However, the exploration of structural features of real data in small and large qualitative and quantitative food web dynamics remains open (Schaffer 1981; Emmerson and Raffaelli 2004). How to integrate structure and dynamics of quantitative subwebs introducing biological features of species in a large food web? Chapter three integrates structure (by calculating the number of quantitative trophic chains and omnivore modules), and dynamics in an overfished ecosystem (by parameterizing with body size ratios and metabolic rates).

Most approaches on community structure and dynamics have been done within a local area using a single interaction type (i.e., antagonistic, mutualistic or competitive). However, current ecological data is showing that food webs are structured in space and composed by several types of ecological interactions (Thompson 2002; Berlow et al. 2004). How to integrate the structure and dynamics of food webs in space?, What is the spatial structure and dynamics of a large food web?, and How to integrate structure and dynamics in a large community with two types of ecological interactions? Chapter four is a first attempt to extend in space different subwebs with trophic and competitive interactions. Chapter five represents to me the most important effort in the present thesis. The work presented in this chapter synthesizes studies from different groups during approximately ten years (1975-1985) in the Doñana ecological network, southern Spain. Specifically we study the effect of structure on the dynamics of a rich-species community with two interaction types.

The present PhD. contains six works (see Table

1 for the approach used in each chapter), five using empirical data, from which only two study structural properties (*chapter two*), and the other three integrate structural properties and dynamical modelling (*chapter three, four, and five*). Only one work explores a set of subwebs in space from a theoretical perspective (first work in *chapter three*). Table 2 shows how we have combined data sets and synthesis of new data with algorithms and numerical simulations in each chapter. I have included in the final part of each chapter two appendices. Firstly *What is New?* through which I will try to observe in detail what is really new showing up results of related studies, which implies a constructive self-criticism of each work presented here, and secondly, *Current and Future Work* in which I will try to briefly explore our current work and relate it with recent studies, suggesting and speculating about possible new works and links among them.

Literature Cited

- Albert, R., Barabási, A.-L. (2002). Statistical mechanics of complex networks. *Rev. Mod. Phys.*, **74**:47, *cond-mat/0106096*.
- Artzy-Randrup, Y., Fleishman, S. J., Ben-Tal, N., and Stone, L. (2004). Comment on “Network motifs:simple building blocks of complex networks” and “Superfamilies of evolved and designed networks”, *Science*, **305**:1107.
- Berlow, E. L., Neutel, A.-M., Cohen, J. E., DeRuiter, P. C., et al. (2004). Interaction strengths in food webs: issues and opportunities. *J. Anim. Ecol.*, **73**:585-598.
- Caldarelli, G., Higgs, P. G., and McKane, A. J. (1998). Modelling coevolution in multispecies communities. *J. theor. Biol.*, **193**:345-358.
- Camerano, L. (1880). Dell’equilibrio dei viventi mercè la reciproca distruzione. *Atti della Reale Accademia delle Scienze di Torino*, **15**:393-414.
- Chen, X., and Cohen, J. E. (2001). Global stability, local stability, and permanence in model food webs. *J. theor. Biol.*, **212**:223-235.
- Cohen, J. E., (1968). Interval graphs and food webs: a finding and a problem. RAND Corporation Document D-17696-PR, 30.
- Cohen, J. E. (1978). *Food webs and niche space*. Princeton University Press, Princeton, New Jersey, USA.
- Cohen, J. E. and Newman, C. M. (1984). The stability of large random matrices and their products.

- Ann. of Prob., **12**:283-310.
- Cohen, J. E. and Newman, C. M. (1985). When will a large complex system be stable? *J. theor. Biol.*, **113**:153-156.
- Cohen, J. E., Luczak, T., Newman, C. M., and Zhou, Z.-M. (1990). Stochastic structure and non-linear dynamics of food webs: qualitative stability in a Lotka-Volterra cascade model. *Proc. Roy. Soc. (London)*, Series B, **240**:607-627.
- Cohen, J. E. (1995). Random graphs in ecology. In *Topics in contemporary probability and its applications*, L. Snell ed, CRC Press.
- Connor, E. F., and Simberloff, D. (1979). The assembly of species communities: chance or competition? *Ecology*, **60**:1132-1140.
- DeAngelis, D. L. (1975). Stability and connectance in food web models. *Ecology*, **56**:238-243.
- Eldredge, N. (1986). Information, economics and evolution. *Ann. Rev. Ecol. Syst.*, **17**:351-369.
- Elton, C. S. (1927). *Animal ecology*. The Macmillan Co., New York.
- Emmerson, M. C., and Raffaelli, D. (2004). Predator-prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.*, **73**:399-409.
- Evans (2004). Complex networks. *cond-mat/0405123*
- Forbes, C. A. (1887). The lake as a microcosm. Republished 1925. *Illinois Nat. Hist. Survey Bull.*, **15**:537-550.
- Hutchinson, G. E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.*, **93**:145-159.
- H Hairston, N. G., and Hairston, N. G. (1997). Does food web complexity eliminate trophic-level dynamics? *Am. Nat.*, **149**:1001-1007.
- Gale, D. (1957). A theorem on flows in networks. *Pac. J. Math.*, **7**:1073-1082.
- Kondoh, M. (2003). Foraging adaptation and the relationship between food web complexity and stability. *Science*, **299**:1388-1391.
- Lawlor, L. R. (1977). A comment on randomly constructed model ecosystems. *Am. Nat.*, **112**:445-447.
- Levins, R. (1975). Evolution in communities near equilibrium. In: Cody, M. L., and Diamond, J. M., eds. *Ecology and Evolution of Communities*. Harvard Univ. Press. Cambridge, Massachusetts, USA.
- Lewontin, R. C. (1969). The meaning of stability. In *Diversity and Stability in Ecological Systems. Symposium 22. Brook Haven National Laboratory* (Woodwell, G. M., and Smith, H. H. eds), pp. 13-24. New York.
- Lindeman, R. L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, **23**:399-418.
- MacArthur, R. H. (1955). Fluctuations of animal populations, and a measure of community stability. *Ecology*, **36**:533-536.
- Martinez, N. D. (1991). Artifacts or attributes? effects of resolution on the Little Rock Lake food web. *Ecol. Monogr.*, **61**:367-392.
- Margalef, R. (1963). On certain unifying principles in ecology. *Am. Nat.*, **97**:357-374.
- Maslov, S., Sneppen, K., and Zaliznyak, A. (2002). Detection of topological patterns in complex networks: correlation profiles of the Internet. *cond-mat/0205379*.
- May, R. M. (1973). Will a large complex system be stable? *Nature*, **238**:413-414.
- Odum, E. P. (1968). Energy flow in ecosystems: a historical review. *Am. Zool.*, **8**:11-18.
- Paine, R. T. (1966). Food web complexity and species diversity. *Am. Nat.*, **100**:65-75.
- Pimm, S. L. (1982). *Food Webs*. London: Chapman and Hall.
- Polis, G. A., and Strong, D. R. (1996). Food web complexity and community dynamics. *Am. Nat.*, **147**:813-846.
- Schaffer, W. M. (1981). Ecological abstraction: the consequences of reduced dimensionality in ecological models. *Ecol. Monogr.*, **51**:383-401.
- Sugihara, G. (1983). Holes in niche space: a derived assembly rule and its relation to intervality. Pages 25-35 in D. L. DeAngelis, W. Post, and G. Sugihara, editors. *Current trends in food web theory*. Report 5983. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- Thompson, J. N. (2002). Plant-animal interactions: future directions. In: Herrera, C., and Pellmyr, O. eds. *Plant-animal interactions. An evolutionary approach*. Blackwell, Oxford.
- Ulanowicz, R. E., and Wolff, W. F. (1991). Ecosystem flow networks: loaded dice? *Math. Biosci.*, **103**:45-68.
- Ulanowicz, R. E. (1997). *Ecology, the Ascendent Perspective*. Columbia University Press, New York.
- Yodzis, P. (1981). The stability of ecosystems. *Nature*, **289**:674-676.

	Unit of Study	ql (1 i.t.)	qt (1 i.t.)	ql(2+ i.t.)	qt(2+ i.t.)	Structure	Dynamics
	subweb		Chapter 3(1)	Chapter 5(1)		subwebs (Chapter 3) subwebs (Chapter 5) cohesion (Chapter 2)	subwebs (Chapter 3) food web (Chapter 5)
One community	intermediate	Chapter 2(2)					
	subweb				Chapter 4(2)	subwebs (Chapter 4)	subwebs (Chapter 4)
Set of communities	intermediate						

Table 1 represents the scale of the approach of each chapter. Chapter two integrates subwebs in an intermediate scale by defining an operative concept of subweb (ql. (1 i.t.) means qualitative matrix with one interaction type). Chapter three explores subweb structure (simple trophic chain and omnivory) in a large and quantitative food web, and introduces a bioenergetic model to explore its dynamical consequences (qt. (1 i.t.) means quantitative matrix with one interaction type). Chapter four extends in space subwebs with two types of ecological interactions (qt. (2 i.t.) means quantitative matrix with two interaction types). Chapter five integrates the structure of a large community with two types of interactions and its dynamical consequences. The number of articles of each chapter is within brackets.

	Data Sets Analysis	Synthesis of New Data	Null Models	Numerical Simulations
Chapter 2	*	*	*	
Chapter 3		*	*	*
Chapter 4		*	*	*
Chapter 5		*	*	*

Table 2 represents the different methodological approaches in each chapter.

Chapter 2

Qualitative Food Web Structure

This chapter tries to link the concepts of subweb and compartment in qualitative species-rich communities. Random assembly or compartmentalization have been the traditional approaches to food webs patterns. However, with the current most resolved data, food webs are neither randomly assembled nor compartmentalized but highly cohesive. Different ways to detect this cohesive pattern and its ecological implications are outlined in this chapter. The chapter contains two papers. The first one (*Complex Networks: Two ways to be robust?*) introduces a measure of correlation between the number of links of each species and the average number of links of its neighbors. The second work (*Food web Cohesion*) introduces an operational measure of subweb in the five largest food webs.

2.1 Complex Networks: Two Ways to be Robust?

Complex networks: two ways to be robust?

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Abstract

Recent studies of biological networks have focused on the distribution of the number of links per node. However, the connectivity distribution does not uncover all the complexity of their topology. Here, we analyse the relation between the connectivity of a species and the average connectivity of its nearest neighbours in three of the most resolved community food webs. We compare the pattern arising with the one recently reported for protein networks and for a simple null model of a random network. Whereas two highly connected nodes are unlikely to be connected between each other in protein networks, the reverse happens in food webs. We discuss this difference in organization in relation to the robustness of biological networks to different types of perturbation.

Keywords

Complex networks, food webs, protein networks, randomly assembled networks, topology.

Ecology Letters (2002) 5: 705–708

INTRODUCTION

With the recent growth of empirical information, biological networks are becoming better resolved. This empirical work is providing insight into how these complex networks are assembled and how they remain stable to deleterious perturbations (Albert *et al.* 2000; Williams & Martinez 2000; Solé & Montoya 2001). Previous studies of biological networks have focused on the connectivity distribution, that is, the probability density distribution of the number of links per node. This connectivity distribution has been shown to have longer tails than would be expected for an exponential distribution, meaning that some species may be extremely connected and that the network is very heterogeneous (Ulanowicz & Wolff 1991; Amaral *et al.* 2000; Jeong *et al.* 2000; Montoya & Solé 2002; Jordano, Bascompte & Olesen, unpublished Ms; see however, Camacho *et al.* 2002 and Dunne *et al.* 2002a). However, the connectivity distribution does not necessarily capture all the topological complexity of biological networks (Dorogovtsev & Mendes 2002). A first step towards a more detailed characterization of biological networks concerns the study of connectivity correlation, that is, the relation between the number of interactions of a node and the average connectivity of its nearest neighbours (Krapivsky & Redner 2001).

Recently, Internet and protein networks have been analysed by plotting their connectivity correlation (Pastor-Satorras *et al.* 2001; Maslov & Sneppen 2002), a method

never used before in ecology. Two types of protein networks have been analysed: physical interaction, and transcription regulatory networks. Protein connectivity represents the fraction of pairs of proteins that interact, forming a network with functional and structural relationships (Maslov & Sneppen 2002). Here, we analyse the connectivity correlation in three of the most resolved community food webs to date and compare the arising pattern with that recently reported for protein networks. Protein networks show an inverse relationship between the connectivity of a node and the average connectivity of its nearest neighbours. That is, neighbours of highly connected proteins have low connectivity and, similarly, low connected proteins are connected with highly connected proteins. This means that links between highly connected proteins are systematically suppressed. That is, the network is compartmentalized in sub-networks organized around a highly connected node with few links among such sub-networks (Maslov & Sneppen 2002).

In this paper we first study the connectivity correlation in food webs, and compare the observed pattern with characteristic values for protein networks. We discuss differences between both types of networks in relation to their robustness to perturbations.

METHODS

Connectivity correlation (Fig. 1a) is best represented by the conditional probability $P_c(k'|k)$, which defines the

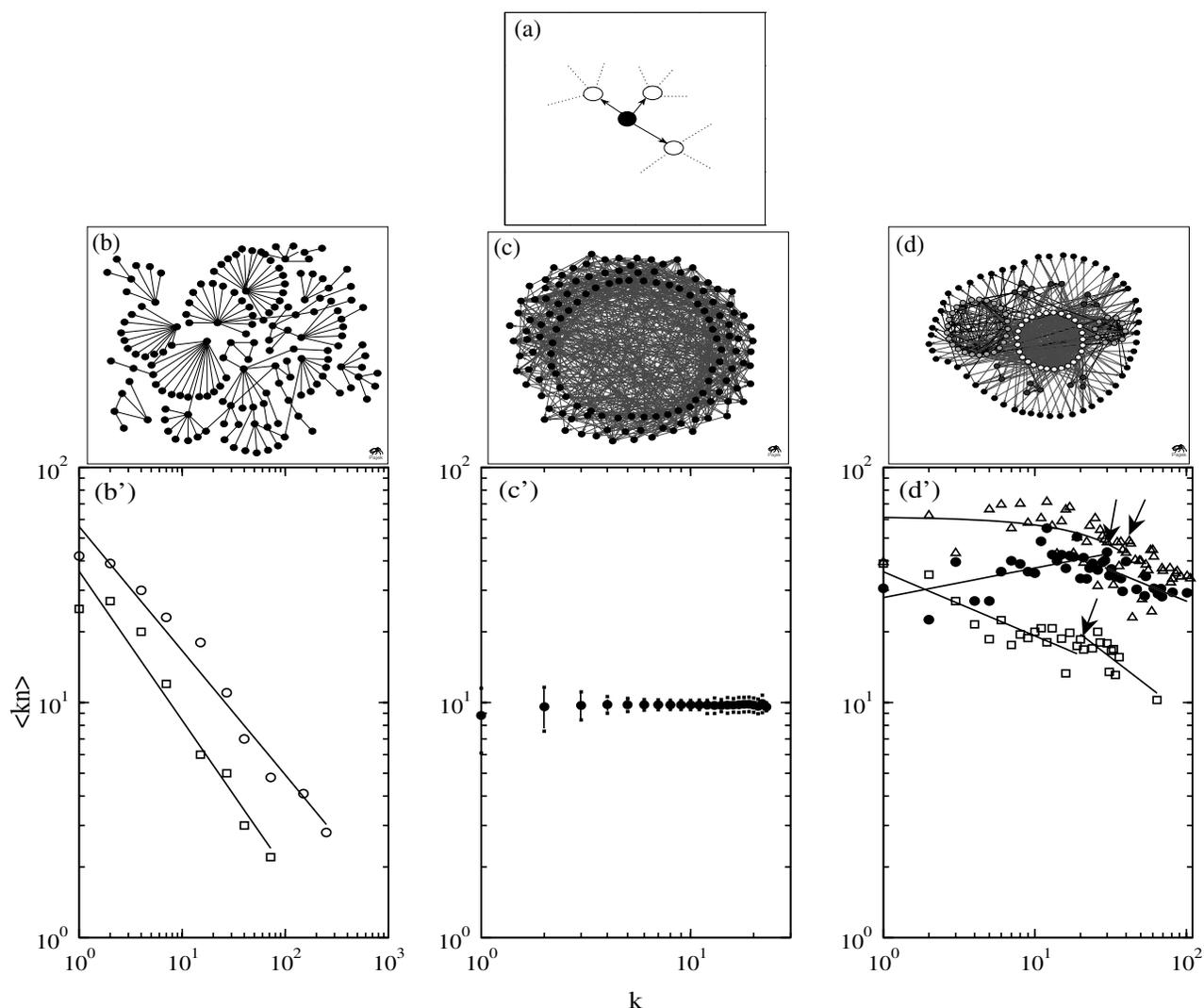


Figure 1 (a) A hypothetical food web graph. The average connectivity of the neighbours of the black node with $k = 3$ links is $\langle k_n \rangle = 4$. (b) A subset of the network of physical interactions between nuclear proteins (modified from Maslov & Sneppen 2002); (c) a single random replicate of the Ythan Estuary food web, and (d) the graph of the Ythan Estuary food web. (b') The average connectivity $\langle k_n \rangle$ of the neighbours of a link with connectivity k as a function of k in interaction (\circ) and regulatory (\square) protein networks; (c') the average and standard deviation of 1000 randomly assembled networks; and (d') the average connectivity of food webs (Little Rock Lake (Δ) (Martinez 1991); El Verde (\bullet) (Reagan & Waide 1996); and Ythan Estuary (\square) (Huxham *et al.* 1996)). Arrows point to the threshold in connectivity (k_c) where a significant shift in the relationship appears. Note that links between highly connected proteins are systematically suppressed, generating a compartmentalized network (b and b'), whereas links between highly connected species are common in food webs, generating a cohesive network (d and d'). Randomly assembled networks show uncorrelated connectivity (c and c'). The network visualization was carried out using the PAJEK program for large network analysis: <http://vlado.fmf.uni-lj.si/pub/networks/pajek/pajekman.htm>.

probability that a link belonging to species with connectivity k points to a species with connectivity k' . If $P_c(k'|k)$ is independent of k , there is no correlation among species' connectivity. The average connectivity ($\langle k_n \rangle$) of the species directly connected (nearest neighbours) to a species with connectivity k can be expressed as:

$$\langle k_n \rangle = \sum_{k'} k' P_c(k'|k). \quad (1)$$

To detect shifts in the relationship between the connectivity of a node (k) and the average connectivity of its nearest neighbours ($\langle k_n \rangle$) we used split-line regression

(Schmid *et al.* 1994; Bersier & Sugihara 1997). Provided that a shift was detected in the slope of the regression, the threshold value (k_c) was calculated, and the data were divided into two groups: one including the data with values below the threshold, and the other including the rest of the data. Different subsets are thus determined in base to significant differences in the slope of the regression. As a benchmark to compare the connectivity correlation pattern we generated 1000 randomly assembled networks with the same number of species and connectivity in a similar way to Newman *et al.* (2001). For species with connectivity k we calculated the average connectivity and standard deviation of the nearest neighbours across all generated networks. The basic rules operating in the assemblage process were as follows.

- 1 At time $t = 0$, n_o nodes with $n_o - 1$ links each were created.
- 2 At each time step, a new node was added to the network, and ingoing and outgoing links with nodes already present were established with the same probability. That is, a link between two nodes was treated as a random event, independent of the presence of other links.

Although some patterns may depend on the choice of the nature of the links considered (ingoing links, outgoing links, or both; Camacho *et al.* 2002; Montoya & Solé 2002), in this paper we consider both ingoing and outgoing links following the analysis by Maslov & Sneppen (2002). We can thus directly compare our results with the ones observed for protein networks. Also, the results presented here are based on binary interactions. Future work will determine to what extent results based on binary interactions stand when quantitative information (i.e. interaction strength) is incorporated (Ulanowicz & Wolff 1991; Ulanowicz 2002).

RESULTS

The three types of network compared here differed in their internal topology (see Fig. 1). For both interaction and regulatory protein networks (Fig. 1b) correlation existed across all domains of connectivity (k), with connectivity correlation ($\langle k_n \rangle$) decaying as a power law $\langle k_n \rangle \propto k^{-0.6}$ (Maslov & Sneppen 2002; Fig. 1b'). On the other hand, randomly assembled networks (Fig. 1c) showed uncorrelated connectivity across all the domain of connectivity, that is, an absence of correlation between a species connectivity and the average connectivity of its nearest neighbours (Fig. 1c').

In contrast to protein and random networks, food webs (Fig. 1d) showed a connectivity threshold k_c in the response of $\langle k_n \rangle$ with increasing k ($k_c=19$ interactions for Ythan Estuary; $k_c=39$ for Little Rock Lake; and $k_c=28$ for El

Verde, Fig. 1d'). That is, food webs had two different domains with significantly different slopes across the range of values of species' connectivity. Specifically, both of Ythan Estuary's subsets best fit a power law ($P < 0.05$), with slopes of -0.27 and -0.49 above and below the threshold, respectively; Little Rock Lake's first subset best fits a linear regression ($P < 0.05$) with a slope of -0.48 ; the relationship is nonsignificant below the threshold; El Verde best fits a power law ($P < 0.05$) in both subsets with slopes of 0.12 and -0.26 above and below the threshold, respectively.

The above pattern suggests the existence of two assembly patterns at different scales of connectivity. In the first domain, connectivity of the nearest neighbours either decays very slowly or does not decay at all with k . In the second domain, $\langle k_n \rangle$ decays with k in a similar way to that found for protein networks. Globally, the average connectivity of the nearest neighbours does not decay as fast with the connectivity of a focal node as in protein networks.

SUMMARY AND DISCUSSION

The internal topology of the two types of biological network compared here depart from randomly assembled networks. Interaction and regulatory protein networks are structured so that two highly connected nodes are not connected to each other. The distribution of connections is highly heterogeneous, the network being organized as a series of highly connected nodes isolated from each other. In other words, the network is compartmentalized.

Recent papers on complex networks have studied the robustness of a network with regard to two different types of perturbation: robustness to the spread of a deleterious mutation (Maslov & Sneppen 2002), and robustness to the fragmentation of the network as an increasing number of nodes is deleted (Albert *et al.* 2000; Solé & Montoya 2001; Dunne *et al.* 2002b). How is the connectivity correlation pattern observed for food webs related to these two types of robustness?

As suggested by Maslov & Sneppen (2002) the compartmentalized pattern observed in protein networks increases the overall robustness of the network by isolating the cascading effects of deleterious mutations. In contrast, the food webs studied here have a pattern that is neither similar to the structure of randomly assembled webs, nor similar to protein networks. Food webs show two well-defined domains in the connectivity correlation distribution. In contrast to protein networks, two highly connected species within a food web are likely to interact among each other. This is likely to decrease the level of compartmentalization, a traditional concept in food web studies (Pimm & Lawton 1980). In this regard, food webs are likely to be more susceptible to the spread of a contaminant. However, the connectivity correlation pattern here described for food

webs, with their low level of compartmentalization (densely connected species connected to each other), may confer on them a higher resistance to fragmentation if a fraction of the species were removed. Thus, there are different ways of being robust related to different types of perturbations.

Previous authors have explored the effect of the connectivity distribution on the resistance of complex networks to fragmentation (Albert *et al.* 2000; Solé & Montoya 2001; Dunne *et al.* 2002b). However, a given connectivity distribution may be organized in different patterns of connectivity correlation. Our results build on previous work focusing on connectivity distribution patterns by pointing out that the pattern of connectivity correlation may also be important for understanding how food webs respond to perturbations. We suggest that the connectivity correlation provides an additional characterization of both the structure of food webs and their susceptibility to perturbations. Further work based on assembly models of biological networks incorporating both qualitative and quantitative information (Ulanowicz 2002) will give more insight into the relationship between connectivity distribution, connectivity correlation, and their importance to network responses to disturbances.

Through this and related papers we have looked at structural properties of food webs and their influence on the network response to perturbations. This work complements traditional theoretical approaches based on the stability of linearized dynamical systems (May 1972; Rozdilsky & Stone 2001). Further work is needed to integrate these two perspectives.

In summary, the pattern of connectivity correlation of complex networks reveals intrinsic features of their topology. The suppression of links between highly connected proteins, but their presence in food webs, reflects both differences in their structure and in their response to different perturbations.

ACKNOWLEDGEMENTS

We thank Pedro Jordano, Sandy Liebhold, and Miguel Angel Rodríguez for useful comments on a previous draft. Funding was provided by the Spanish Ministry of Science and Technology (Grant BOS2000-1366-C02-02 to J. B and Ph.D. Fellowship FP2000-6137 to C. J. M).

REFERENCES

- Albert, R., Jeong, H. & Barabasi, A.-L. (2000). Error and attack tolerance of complex networks. *Nature*, 406, 378–382.
- Amaral, L.A., Scala, A., Barthélemy, M. & Stanley, H.E. (2000). Classes of small-world networks. *Proc. Nat. Acad. Sci.*, 97, 11149–11152.
- Bersier, L.-F. & Sugihara, G. (1997). Scaling regions for food web properties. *Proc. Nat. Acad. Sci.*, 94, 1247–1251.
- Camacho, J., Guimera, R. & Amaral, L.A. (2002). Robust patterns in food web structure. *Phys. Rev. Lett.*, 88, 228102.
- Dorogovtsev, S.N. & Mendes, J.F.F. (2002). Evolution of networks. *Adv. Phys.*, 51, 1079.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002a). Small networks but not small worlds: unique aspects of food web structure. *Proc. Nat. Acad. Sci.*, in press.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002b). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.*, 5, 558–567.
- Huxham, M., Beaney, S. & Raffaelli, D. (1996). Do parasites reduce the changes of triangulation in a real food web? *Oikos*, 76, 284–300.
- Jeong, H., Tombor, B., Albert, R., Oltvai, Z.N. & Barabasi, A.-L. (2000). The large-scale organization of metabolic networks. *Nature*, 407, 651–654.
- Krapivsky, P.L. & Redner, S. (2001). Organization of growing random networks. *Phys. Rev. E*, 63, 066123.
- Martinez, N.D. (1991). Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecol. Monogr.*, 61, 367–392.
- Maslov, S. & Sneppen, K. (2002). Specificity and stability in topology of protein networks. *Science*, 296, 910–913.
- May, R.M. (1972). Will a large complex system be stable? *Nature*, 238, 413–414.
- Montoya, J.M. & Solé, R.V. (2002). Small world pattern in food webs. *J. Theor. Biol.*, 214, 405–412.
- Newman, M.E.J., Strogatz, S.H. & Watts, D.J. (2001). Random graphs with arbitrary degree distributions and their applications. *Phys. Rev. E*, 64, U153–U168.
- Pastor-Satorras, R., Vazquez, A. & Vespignani, A. (2001). Dynamical and correlation properties of the Internet. *Phys. Rev. Lett.*, 87, 258701.
- Pimm, S.L. & Lawton, J.H. (1980). Are food webs divided into compartments?. *J. Anim. Ecol.*, 49, 879–898.
- Reagan, D.P. & Waide, R.B. (1996). *The Food Web of a Tropical Rain Forest*. University of Chicago Press.
- Rozdilsky, I.D. & Stone, L. (2001). Complexity can enhance stability in competitive systems. *Ecol. Lett.*, 4, 397–400.
- Schmid, B., Polasek, W., Weiner, J., Krause, A. & Stoll, P. (1994). Modeling of discontinuous relationships in biology with censored regression. *Am. Nat.*, 143, 494–507.
- Solé, R.V. & Montoya, J.M. (2001). Complexity and fragility in ecological networks. *Proc. Roy. Soc. B*, 268, 2039–2045.
- Ulanowicz, R.E. (2002). The balance between adaptability and adaptation. *BioSystems*, 64, 13–22.
- Ulanowicz, R.E. & Wolff, W.F. (1991). Ecosystem flow networks: loaded dice?. *Math. Biosci.*, 103, 45–68.
- Williams, R.J. & Martinez, N.D. (2000). Simple rules yield complex food webs. *Nature*, 404, 180–183.

Editor, P. J. Morin

Manuscript received 25 May 2002

First decision made 22 August 2002

Manuscript accepted 28 August 2002

2.2 Food Web Cohesion

FOOD WEB COHESION

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Abstract. Both dynamic and topologic approaches in food webs have shown how structure alters conditions for stability. However, while most studies concerning the structure of food webs have shown a nonrandom pattern, it still remains unclear how this structure is related to compartmentalization and to responses to perturbations. Here we build a bridge between connectance, food web structure, and compartmentalization by studying how links are distributed within and between subwebs. A “ k subweb” is defined as a subset of species that are connected to at least k species from the same subset. We study the k subweb frequency distribution (i.e., the number of k subwebs in each food web). This distribution is highly skewed, decaying in all cases as a power law. The most dense subweb has the most interactions, despite containing a small number of species, and shows connectivity values independent of species richness. The removal of the most dense subweb implies multiple fragmentation. Our results show a cohesive organization, that is, a high number of small subwebs highly connected among themselves through the most dense subweb. We discuss the implications of this organization in relation to different types of disturbances.

Key words: cohesion; compartmentalization; connectance; food web structure; null model; subweb.

INTRODUCTION

The structure of food webs is an important property for understanding dynamic (May 1972, DeAngelis 1975, Pimm 1979, Lawlor 1980) and topologic (Pimm 1982) stability. Both theoretical and empirical approximations have represented food web structure with guilds (Root 1967), blocks and modules (May 1972), cliques and dominant cliques (Cohen 1978, Yodzis 1982), compartments (Pimm 1979), subwebs (Paine 1980), block submatrices (Critchlow and Stearns 1982), and simplicial complexes (Sugihara 1983). From these studies it is well known that food webs are not randomly assembled. However, it still remains unclear how the nonrandom structure of food webs is related to compartmentalization and its topologic and dynamic implications for stability following perturbations (Pimm and Lawton 1980, Polis 1991, Raffaelli and Hall 1992, Strong 1992, Solow et al. 1999). This is especially relevant after studies that show a much larger complexity of food webs than previously expected (Polis 1991, Strong 1992, Hall and Raffaelli 1993, Polis and Strong 1996).

Current studies show that groups of species are more connected internally than they are with other groups of species (Solow and Beet 1998, Montoya and Solé 2002). However, these studies do not make explicit reference to the number of modules and their heterogeneity (see Ravasz et al. 2002). Here, we build a bridge between connectance, food web structure, and compartmentalization by studying how links are dis-

tributed within and between subsets of species in twelve highly resolved food webs.

Specifically, we address the following questions: (1) How are subwebs structured within highly resolved food webs? (2) What is the relation between food web structure and compartmentalization? (3) What are the implications of subweb structure for responses to perturbations? In order to answer these questions we develop an operative definition of subweb.

MEASURES OF FOOD WEB STRUCTURAL ORGANIZATION

The k subweb

A k subweb is defined here as a subset of species which are connected to at least k prey species and/or predator species within the same subset. A k subweb has the following features: (1) Subwebs are defined using only information on the presence and absence of interactions. (2) Each species belongs only to one subweb, the subset where each species has the highest k value. (3) Each subweb contains species from different trophic levels.

Fig. 1 makes explicit this concept. As noted, different subwebs with the same k value are disjointed in the web. The sum of the total number of disjointed subwebs with at least k interactions represents the frequency of k subwebs. If we denote by S_T and S_k the total number of subwebs and the number of k subwebs, respectively, the frequency distribution of k subwebs is thus $p(S_k) = S_k/S_T$. (Note that, throughout this paper, $p(S_k)$ represents cumulative distribution.)

The most dense subweb

The most dense subweb is the subset of connected species with the largest number of interactions per spe-

Manuscript received 15 October 2002; revised 7 May 2003; accepted 13 May 2003; final version received 5 June 2003. Corresponding Editor: W. S. C. Gurney.

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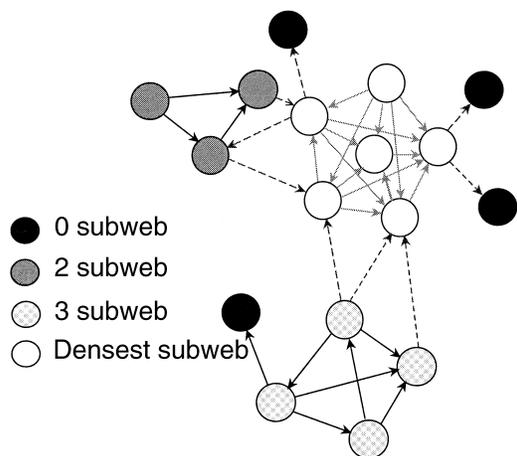


FIG. 1. A hypothetical food web graph. A subset of vertices is called a k subweb if every species within the subset is connected to at least k prey and/or predators from the same subset. We can observe the following subwebs: four separate 0 subwebs (i.e., species have no links with other species within the same subset, but have one or more links with other k subwebs of higher degree; black nodes); one 2 subweb; one 3 subweb; and one 5 subweb, the most dense subweb (white nodes). The links within the most dense subweb are represented as gray lines. The density of such interactions represents the connectance of the most dense subweb (C_d). Broken lines represent the interactions between the densest subweb and the rest of the web. The density of such interactions represents the intersubweb connectance between the most dense subweb and the rest of the web. Note that the web becomes fragmented in five parts if we eliminate the densest subweb.

cies (white circles in Figs. 1 and 2). In order to get a measure of cohesion, we calculate and compare connectance for the twelve food webs studied here (see Table 1). If real food webs are cohesive, we will find that the value of connectance of the most dense subweb is significantly larger than both global connectance and the connectance of the most dense subweb for a series of food web models. Global connectance is defined as

$$C = \frac{L}{S^2} \quad (1)$$

where L is the number of links in the web and S^2 is the maximum number of possible links, including cannibalism and mutual predation (Martinez 1991). Similarly, we can define the connectance of the densest subweb (C_d) as

$$C_d = \frac{L_d}{S_d^2} \quad (2)$$

where L_d is the number of interactions within the most dense subweb, and S_d^2 is the maximum number of possible interactions within the most dense subweb.

Null models of food web structure

Can this most dense subweb observed in food webs be reproduced by models with different levels of com-

plexity? To answer this question, five food web models were tested. We generated 50 replicates of each model with the same number of species and global connectance as the real food webs. Our statistic (P) is the probability that a random replicate has a C_d value equal or higher than the observed value (Manly 1998).

In the first model, the basic null model, any link among species occurs with the same probability, equal to the global connectance (C) of the empirical web (Cohen 1978). The second model (Cohen et al.'s 1990 cascade model), assigns each species a random value drawn uniformly from the interval $[0,1]$ and each species has the probability $P = 2CS/(S - 1)$ of consuming only species with values less than its own. The third model is the niche model by Williams and Martinez (2000). This model assigns a randomly drawn "niche value" to each species, similarly to the cascade model. Species are then constrained to consume all prey species within one range of values whose randomly chosen center is less than the consumer's niche value. In the preferential attachment model (Barabási and Albert 1999), the probability that a new species will be connected to a previous species is proportional to the connectivity of the later (both for resources and predators (j) of each new species), so that $P(k_i) = k_j/\sum_i(k_i)$. Finally, the local rewiring algorithm randomizes the empirical data yet strictly conserves ingoing and outgoing links (Connor and Simberloff 1979, Gotelli 2001). In this algorithm, a pair of directed links $A-B$ and $C-D$ are randomly selected. They are rewired in such a way that A becomes connected to D , and C to B , provided that none of these links already existed in the network, in which case the rewiring stops, and a new pair of edges is selected (Maslov and Sneppen 2002). We used a library of codes in *Matlab* to generate these matrices (C. J. Melián and J. Bascompte, unpublished data).

RESULTS

For the five largest food webs, we calculated the k subweb frequency distribution. The distribution was found to be strongly skewed with the best fit following a power law in all webs (see cumulative distribution in Fig. 2). The mean, ± 1 SD, of the exponent (γ) for the five food webs was -1.34 ± 0.57 . This means that subwebs show an extreme heterogeneity, with most subwebs with a small number of interactions per species and a unique most dense subweb.

In Silwood Park (Fig. 2a), species belonging to the most dense part (9% of species in the web) embody 70% of the interactions (26% of interactions among the species of the most dense subweb and 44% among these species and the rest of the web). In Ythan Estuary (Fig. 2b), the most dense subweb (21% of species in the web) holds 74% of all the links in the web (30% among

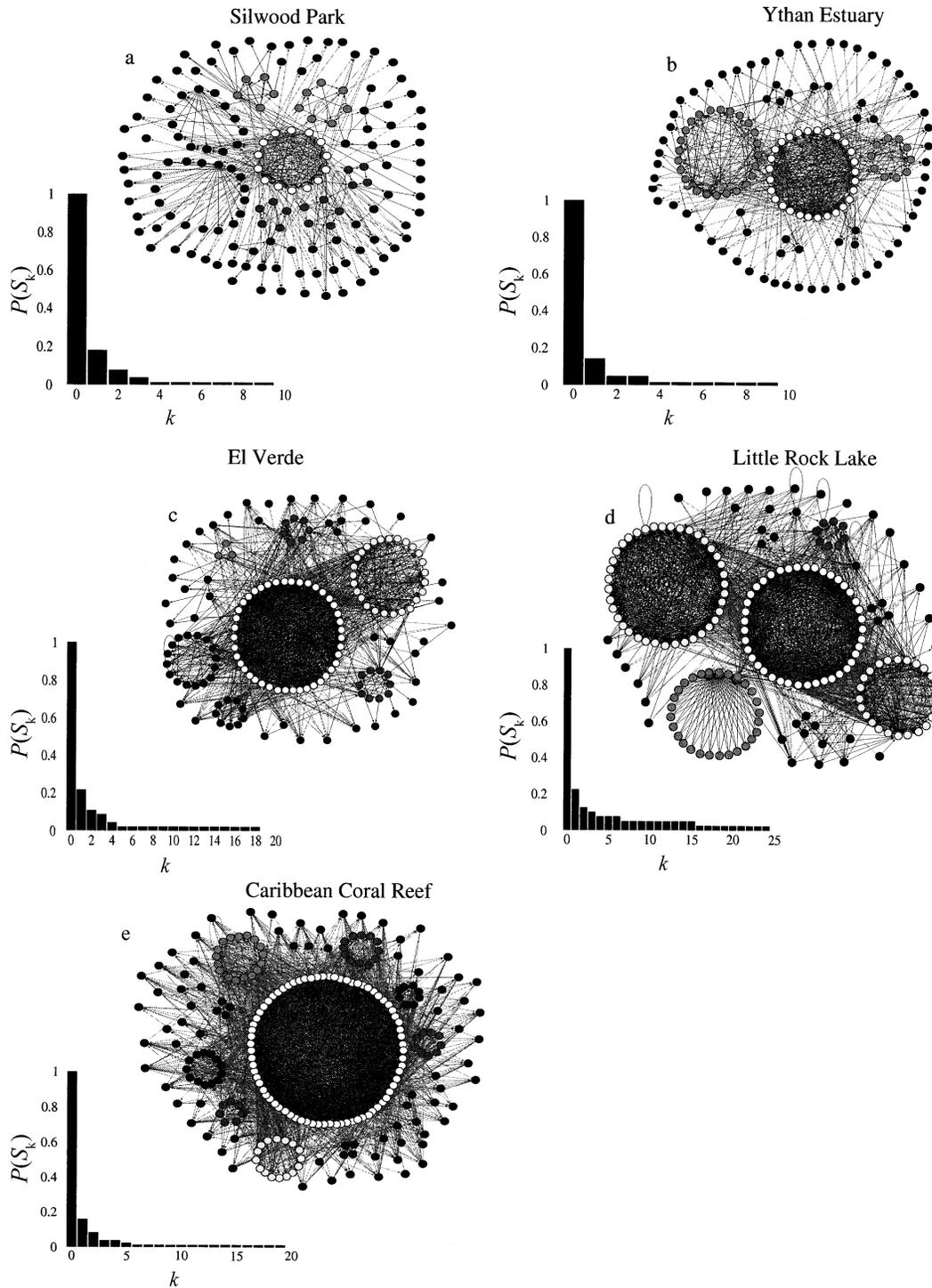


FIG. 2. Food web structure and k subweb frequency distribution (represented as the cumulative distribution $P(S_k)$) for (a) Silwood Park, (b) Ythan Estuary, (c) El Verde, (d) Little Rock Lake, and (e) the Caribbean. Gray level and line type are as in Fig. 1. As noted, the k subweb frequency distribution is highly skewed, decaying in all cases as a power law with a mean (± 1 SD) exponent $\langle \gamma \rangle = -1.34 \pm 0.57$. The network visualization was done using the Pajek program for large network analysis (available online).²

² URL: <http://vlado.fmf.uni-lj.si/pub/networks/pajek/pajekman.htm>

TABLE 1. Food webs studied and their statistical properties.

Food web	S	$k \pm 1$ SD	C	C_d	$\langle C_{db} \rangle$	$\langle C_{dc} \rangle$	$\langle C_{dn} \rangle$	$\langle C_{lra} \rangle$	$\langle C_{dpa} \rangle$	Distribution
MAS	23	6 ± 3	0.13	0.26	0.16**	0.17**	0.32 ^{NS}	0.24 ^{NS}	0.39 ^{NS}	†
BEN	29	14 ± 6	0.24	0.34	0.26**	0.26**	0.38 ^{NS}	0.32 ^{NS}	0.36 ^{NS}	†
COA	30	19 ± 8	0.32	0.47	0.34**	0.35**	0.47 ^{NS}	0.44*	0.42 ^{NS}	†
CHE	36	5 ± 3	0.06	0.14	0.08**	0.09**	0.18 ^{NS}	0.15 ^{NS}	0.33 ^{NS}	†
SKI	37	21 ± 9	0.27	0.51	0.28**	0.29**	0.4†	0.43*	0.39 ^{NS}	†
STM	44	10 ± 6	0.11	0.16	0.13**	0.13†	0.22 ^{NS}	0.17 ^{NS}	0.29 ^{NS}	†
UKG	75	3 ± 3	0.02	0.26	0.03**	0.04**	0.14†	0.14†	0.16†	†
YE	134	9 ± 10	0.03	0.23	0.04**	0.04**	0.12 ^{NS}	0.19†	0.12†	PL ($\gamma = -1.87$)
SP	154	5 ± 7	0.02	0.38	0.02**	0.03**	0.12**	0.32†	0.21†	PL ($\gamma = -1.98$)
EV	156	19 ± 18	0.06	0.30	0.07**	0.07**	0.14**	0.26*	0.17†	PL ($\gamma = -1.22$)
LRL	182	26 ± 22	0.07	0.36	0.07**	0.08**	0.16**	0.19**	0.17†	PL ($\gamma = -0.97$)
CAR	237	26 ± 34	0.05	0.19	0.06**	0.06**	0.12†	0.2 ^{NS}	0.15 ^{NS}	PL ($\gamma = -0.65$)

Notes: Abbreviations and their sources, as used in first column: Maspalomas (MAS), Almunia et al. 1999; Benguela (BEN), Yodzis 1998; Coachella (COA), Polis 1991; Chesapeake Bay (CHE), Baird and Ulanowicz 1989; Skipwith Pond (SKI), Warren 1989; St. Martin (STM), Goldwasser and Roughgarden 1993; United Kingdom Grassland (UKG), Martinez et al. 1999; Ythan Estuary (YE), Huxam et al. 1996; Silwood Park (SP), Memmott et al. 2000; El Verde (EV), Reagan and Waide 1996; Little Rock Lake (LRL), Martinez 1991; and Caribbean Coral Reef (CAR), Opitz 1996. Other abbreviations are: S , number of species; k , number of links per species; C , connectance; C_d , connectance of the most dense subweb for the empirical webs; $\langle C_{db} \rangle$, $\langle C_{dc} \rangle$, $\langle C_{dn} \rangle$, $\langle C_{lra} \rangle$, and $\langle C_{dpa} \rangle$, mean connectance of the most dense subweb for 50 replicates of the basic, cascade, niche, local rewiring algorithm, and preferential attachment, respectively. Distribution refers to the best fit of the k subweb frequency distribution (cumulative distribution calculated only for the five largest food webs); PL, power law, with the γ value the scaling exponent (slope). Angle brackets indicate means.

* $P < 0.05$; ** $P < 0.01$; NS, not significant.

† $0.05 < P < 0.1$.

‡ Cumulative distribution not calculated.

the species of the most dense subweb and 44% among these species and the rest of the web). The fraction of interactions in the most dense subweb of El Verde (Fig. 2c), Little Lake Rock (Fig. 2d), and Caribbean Coral Reef (Fig. 2e) (with 27%, 22%, and 31% of species in the web, respectively), represents 78%, 77%, and 89% of the total interactions, respectively (35%, 24%, and 33% among the species of the most dense subweb and 43%, 53%, and 56% among these species and the rest of the web, respectively).

The mean, ± 1 SD, percentage of species in the most dense subweb is $22 \pm 8\%$, and the mean, ± 1 SD, percentage of interactions within the most dense part is $78 \pm 6\%$. This means that a small number of species contain the most interactions. The mean, ± 1 SD, percentage of species in the most dense subweb in the five null models tested is $86 \pm 5\%$ for the basic model, $84 \pm 6\%$ for the cascade model, $43 \pm 10\%$ for the niche model, $37 \pm 15\%$ for the preferential attachment model, and $28 \pm 13\%$ for the local rewiring algorithm model.

Table 1 shows global connectance (C), the connectance of the most dense subweb for real data (C_d) and the mean for each one of the null models tested (the basic, $\langle C_{db} \rangle$; cascade, $\langle C_{dc} \rangle$; niche, $\langle C_{dn} \rangle$; local rewiring algorithm, $\langle C_{lra} \rangle$; and preferential attachment, $\langle C_{dpa} \rangle$; throughout this paper, variables enclosed in angle brackets are means). The values of C_d are significantly higher ($P < 0.01$) in the twelve food webs for the basic and cascade model (see Table 1), with the exception of St. Martin in the cascade model ($0.05 < P < 0.1$). For the Niche model, three of the most resolved food webs (Silwood Park, El Verde, and Little Rock Lake),

departed significantly ($P < 0.01$) and the rest of the most resolved food webs departed marginally ($0.05 < P < 0.1$; with the exception of Ythan, $P = 0.18$). In the local rewiring algorithm, two of the most resolved food webs, El Verde and Little Rock Lake, departed significantly ($P < 0.05$ and $P < 0.01$, respectively), and the rest of the most resolved food webs departed marginally ($0.05 < P < 0.1$), with the exception of the Caribbean food web ($P > 0.1$). Finally, in the preferential attachment model, the most resolved food webs departed marginally ($0.05 < P < 0.1$; see Table 1), with the exception of the Caribbean food web ($P > 0.1$).

While C , $\langle C_{db} \rangle$, $\langle C_{dc} \rangle$, $\langle C_{dn} \rangle$, and $\langle C_{dpa} \rangle$ decay as a power law as the number of species increases ($r^2 = 0.53$, $P < 0.01$; $r^2 = 0.56$, $P < 0.01$; $r^2 = 0.6$, $P < 0.01$; $r^2 = 0.73$, $P < 0.01$; $r^2 = 0.8$, $P < 0.01$, respectively), C_d is independent of species richness ($r^2 \leq 0.16$, $P \geq 0.47$ for all the functions fitted), which suggests a scale-invariant property in the structure of food webs (similarly to the empirical data, the mean value of the C_d in the local rewiring algorithm, $\langle C_{lra} \rangle$ is independent of species richness, $r^2 \leq 0.23$, $P \geq 0.24$ for all the functions fitted).

To further confirm the potential cohesion of the most dense subweb, we removed it and checked whether the remaining web is fragmented, and if so, in how many pieces. The web becomes fragmented in 54 parts in Silwood Park, 37 parts in Ythan Estuary, 29 parts in the Caribbean Coral Reef, 7 parts in El Verde, and did not become fragmented in Little Rock Lake. This multiple fragmentation shows the cohesive role of the most dense subweb.

DISCUSSION

It is well known that (1) connectance has a very narrow range of values (Warren 1990, 1994, Martinez and Lawton 1992), and (2) food webs are not randomly assembled (Cohen 1978, Lawlor 1978, Pimm 1980, Ulanowicz and Wolff 1991, Solow et al. 1999). However, little is known about how different subweb frequency distributions are compatible with a specific connectance value and about implications for dynamic and topologic stability.

In this paper we have studied the statistical properties of the structure in subwebs (k subweb frequency distribution) and the heterogeneous pattern of these subwebs. If this pattern were homogeneous, a single macroscopic description such as connectance would adequately characterize the organization of food webs. But this is not the case. There is a need to move beyond descriptions based on mean field properties such as mean connectance (Cohen 1978, Pimm 1980, Critchlow and Stearns 1982, Yodzis 1982, Sugihara 1983) to consider these other variables characterizing the structural organization of food webs.

Our results indicate both a high level of structure (with well-defined k subwebs) and a cohesive organization (the most dense subweb). While connectance is a scale-variant property (May 1974, Rejmánek and Satory 1979, Yodzis 1980, Jordano 1987, Sugihara et al. 1989, Bersier et al. 1999, Winemiller et al. 2001), the connectance within the most dense subweb in the twelve food webs studied is not correlated to species richness. This is in striking contrast to the null models explored with the exception of the local rewiring algorithm. Although the degree of connectance (see Table 1) and the types of historical and current human disturbances (Baird and Ulanowicz 1993, Raffaelli 1999), as well as other ecological and geographic factors were different in the food webs explored, a similar structural organization was found. This confers a remarkable level of generality to our results.

What type of mechanisms are underlying this cohesive pattern? As we have shown, food web models with increasing heterogeneity in links' distribution do not capture (niche model with the exception of Ythan and Caribbean) or marginally capture (local rewiring algorithm and preferential attachment with the exception of the Caribbean) the internal structure of the most resolved food webs. The biological mechanisms explaining the pattern here reported could be elucidated by comparing the identity and attributes of the species forming the most dense subweb across different food webs. If the species composing the most dense subweb in each food web are taxonomically and phylogenetically different, an ecological explanation should be suggested (Schoener 1989). However, if the species forming the most dense subweb are phylogenetically related, evolutionary mechanisms should be proposed (Williams and Martinez 2000). An intermediate case

would be that in which there are phylogenetic differences but there is correlation with any biological attribute such as body size (Cohen et al. 2003) or other physiological and behavioral feature (Kondoh 2003). In this case, intermediate mechanisms should be suggested.

These results have implications relative to the previously proposed hypothesis about the propagation of perturbations (Pimm and Lawton 1980). The presence of a high number of small subwebs highly connected among themselves through the most dense subweb supports a structured view of the reticulate hypothesis. How do these highly structured and reticulated webs respond to disturbances? On one hand, the significantly larger probability of interactions between highly connected intermediate species may favor the propagation of disturbances (i.e., contaminants) through the web (Melián and Bascompte 2002, Williams et al. 2002). On the other hand, this cohesive structure may decrease the probability of network fragmentation when species are removed (Albert et al. 2000, Solé and Montoya 2001, Dunne et al. 2002). Also, the results presented here may be relevant to studies addressing whether the pattern of subweb structure may affect the likelihood of trophic cascades (Polis 1991, Strong 1992, Berlow 1999, Pace et al. 1999, Yodzis 2000, Shurin et al. 2002).

ACKNOWLEDGMENTS

We thank Sandy Liebhold, Pedro Jordano, George Sugihara, Louis-Félix Bersier, and Miguel A. Fortuna for useful comments on a previous draft, Enric Sala for bringing to our attention Opitz's work, and Enrique Collado for computer assistance. Funding was provided by a grant to J. Bascompte from the Spanish Ministry of Science and Technology (BOS2000-1366-CO2-02) and a Ph.D. fellowship to C. J. Melián (FP2000-6137).

LITERATURE CITED

- Albert, R., H. Jeong, and A.-L. Barabási. 2000. Error and attack tolerance of complex networks. *Nature (London)* **406**:378–382.
- Almunia, J., G. Basterretxea, J. Aristegui, and R. E. Ulanowicz. 1999. Benthic–pelagic switching in a coastal subtropical lagoon. *Estuarine Coastal and Shelf Science* **49**:363–384.
- Baird, D., and R. E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecological Monographs* **59**:329–364.
- Baird, D., and R. E. Ulanowicz. 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. *Marine Ecology Progress Series* **99**:221–237.
- Barabási, A.-L., and R. Albert. 1999. Emergence of scaling in random networks. *Science* **286**:509–512.
- Berlow, E. L. 1999. Strong effects of weak interactions in ecological communities. *Nature (London)* **398**:330–334.
- Bersier, L. F., P. Dixon, and G. Sugihara. 1999. Scale-invariant or scale dependent behavior of the link density property in food webs: a matter of sampling effort? *American Naturalist* **153**:676–682.
- Cohen, J. E. 1978. *Food webs and niche space*. Princeton University Press, Princeton, New Jersey, USA.
- Cohen, J. E., F. Briand, and C. M. Newman. 1990. *Community food webs: data and theory*. Springer-Verlag, Berlin, Germany.

- Cohen, J. E., T. Jonsson, and S. R. Carpenter. 2003. Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences (USA)* **100**:1781–1786.
- Connor, E. F., and D. Simberloff. 1979. The assembly of species communities: chance or competition? *Ecology* **60**:1132–1140.
- Critchlow, R. E., and S. C. Stearns. 1982. The structure of food webs. *American Naturalist* **120**:478–499.
- DeAngelis, D. L. 1975. Stability and connectance in food webs models. *Ecology* **56**:238–243.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Food web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences (USA)* **99**:12917–12922.
- Goldwasser, L., and J. Roughgarden. 1993. Construction and analysis of a large caribbean food web. *Ecology* **74**:1216–1233.
- Gotelli, N. J. 2001. Research frontiers in null model analysis. *Global Ecology and Biogeography* **10**:337–343.
- Hall, S. J., and D. G. Raffaelli. 1993. Food webs: theory and reality. *Advances in Ecological Research* **24**:187–239.
- Huxham, M., S. Beane, and D. Raffaelli. 1996. Do parasites reduce the change of triangulation in a real food web? *Oikos* **76**:284–300.
- Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries and coevolution. *American Naturalist* **129**:657–677.
- Kondoh, M. 2003. Foraging adaptation and the relationship between food web complexity and stability. *Science* **299**:1388–1391.
- Lawlor, L. R. 1978. A comment on randomly constructed model ecosystems. *American Naturalist* **112**:445–447.
- Lawlor, L. R. 1980. Structure and stability in natural and randomly constructed competitive communities. *American Naturalist* **116**:394–408.
- Manly, B. F. J. 1998. *Randomization, bootstrap and monte-carlo methods in biology*. Second edition. Chapman and Hall, London, UK.
- Martinez, N. D. 1991. Artifacts or attributes? effects of resolution on the Little Rock Lake food web. *Ecological Monographs* **61**:367–392.
- Martinez, N. D., B. A. Hawkins, H. A. Dawah, and B. P. Feifarek. 1999. Effects of sampling effort on characterization of food-web structure. *Ecology* **80**:1044–1055.
- Martinez, N. D., and J. H. Lawton. 1992. Constant connectance in community food webs. *American Naturalist* **139**:1208–1218.
- Maslov, S., and K. Sneppen. 2002. Specificity and stability in topology of protein networks. *Science* **296**:910–913.
- May, R. M. 1972. Will a large complex system be stable? *Nature (London)* **238**:413–414.
- May, R. M. 1974. *Stability and complexity in model ecosystems*. Second edition. Princeton University Press, Princeton, New Jersey, USA.
- Melián, C. J., and J. Bascompte. 2002. Complex networks: two ways to be robust? *Ecology Letters* **5**:705–708.
- Memmott, J., N. D. Martinez, and J. E. Cohen. 2000. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *Journal of Animal Ecology* **69**:1–15.
- Montoya, J. M., and R. V. Solé. 2002. Small world pattern in food webs. *Journal of Theoretical Biology* **214**:405–412.
- Opitz, S. 1996. Trophic interactions in Caribbean coral reefs. Technical Report 43. International Centre for Living Aquatic Resource Management (now WorldFish Center), Penang, Malaysia.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* **14**:483–488.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**:667–685.
- Pimm, S. L. 1979. The structure of food webs. *Theoretical Population Biology* **16**:144–158.
- Pimm, S. L. 1980. Properties of food web. *Ecology* **61**:219–225.
- Pimm, S. L. 1982. *Food webs*. Chapman and Hall, London, UK.
- Pimm, S. L., and J. H. Lawton. 1980. Are food webs divided into compartments? *Journal of Animal Ecology* **49**:879–898.
- Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. *American Naturalist* **138**:123–155.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* **147**:813–846.
- Raffaelli, D. 1999. Nutrient enrichment and trophic organization in an estuarine food web. *Acta Oecologica* **20**:449–461.
- Raffaelli, D., and S. Hall. 1992. Compartments and predation in an estuarine food web. *Journal of Animal Ecology* **61**:551–560.
- Ravasz, E., A. L. Somera, D. A. Mongru, Z. N. Oltvai, and A.-L. Barabási. 2002. Hierarchical organization of modularity in metabolic networks. *Science* **297**:1551–1555.
- Reagan, D. P., and R. B. Waide. 1996. *The food web of a tropical rain forest*. University of Chicago Press, Chicago, Illinois, USA.
- Rejmánek, M., and P. Stary. 1979. Connectance in real biotic communities and critical values for stability of model ecosystems. *Nature (London)* **280**:311–315.
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* **37**:317–350.
- Schoener, T. W. 1989. Food webs from the small to the large. *Ecology* **70**:1559–1589.
- Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* **5**:785–791.
- Solé, R. V., and J. M. Montoya. 2001. Complexity and fragility in ecological networks. *Proceedings of the Royal Society of London B* **268**:2039–2045.
- Solow, A. R., and A. R. Beet. 1998. On lumping species in food webs. *Ecology* **79**:2013–2018.
- Solow, A. R., C. Costello, and A. Beet. 1999. On an early result on stability and complexity. *American Naturalist* **154**:587–588.
- Strong, D. R. 1992. Are trophic cascades all wet? differentiation and donor-control in speciose ecosystems. *Ecology* **73**:747–754.
- Sugihara, G. 1983. Holes in niche space: a derived assembly rule and its relation to intervality. Pages 25–35 *in* D. L. DeAngelis, W. Post, and G. Sugihara, editors. *Current trends in food web theory*. Report 5983. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- Sugihara, G., K. Schoenly, and A. Trombla. 1989. Scale invariance in food web properties. *Science* **245**:48–52.
- Ulanowicz, R. E., and W. F. Wolff. 1991. Ecosystem flow networks: loaded dice. *Mathematical Biosciences* **103**:45–68.
- Warren, P. H. 1989. Spatial and temporal variation in the structure of a freshwater food web. *Oikos* **55**:299–311.
- Warren, P. H. 1990. Variation in food-web structure: the determinants of connectance. *American Naturalist* **136**:689–700.
- Warren, P. H. 1994. Making connections in food webs. *Trends in Ecology and Evolution* **9**:136–141.

- Williams, R. J., E. L. Berlow, J. A. Dunne, A.-L. Barabási, and N. D. Martinez. 2002. Two degrees of separation in complex food webs. *Proceedings of the National Academy of Sciences (USA)* **99**:12913–12916.
- Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. *Nature (London)* **404**:180–183.
- Winemiller, K., E. R. Pianka, L. J. Vitt, and A. Joern. 2001. Food web laws or niche theory? six independent empirical tests. *American Naturalist* **158**:193–199.
- Yodzis, P. 1980. The connectance of real ecosystems. *Nature (London)* **284**:544–545.
- Yodzis, P. 1982. The compartmentation of real and assembled ecosystems. *American Naturalist* **120**:551–570.
- Yodzis, P. 1998. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *Journal of Animal Ecology* **67**:635–658.
- Yozdis, P. 2000. Diffuse effects in food webs. *Ecology* **81**:261–266.

2.3 What is New?

The general result of this chapter is that a few highly connected species are connected significantly between them. This pattern shows that food webs are neither randomly assembled nor compartmentalized but highly cohesive, which implies a new feature to test in future better data sets. This pattern has been found in mutualistic networks (Bascompte et al. 2003), which adds more robustness to the previous result. Both concepts studied here, cohesion and connectivity correlation, are not new (see Frank 1995, 1996; Vazquez and Aizen 2004). Cohesion and assortative mixing (see Newman 2002, and Girvan and Newman 2002) could be understood, as a first approximation, as a general property of a certain class of complex networks using cumulative data (assortative mixing is a measure to detect if highly connected nodes are connected among them). However recent work has detected compartments in similar data sets of food webs but using trophic species (Krause et al. 2003). The concepts of compartment and asymmetry, long debated in ecology (Pimm and Lawton 1980; Jordano 1987), are still open, and its relation with the cohesive pattern reported here still needs more accurate empirical and data sets studies.

2.4 Current and Future Work

Results presented in this chapter represent a static pattern using cumulative and qualitative data. What is the interdependence between this pattern and the dynamics of species-rich communities? How is this cumulative pattern related with the temporal fluctuation of interactions? What about persistence? Dynamic null models with temporal variation of links (e.g., effective connectivity instead of total connectivity) alter basic properties of the structure introduced in the analysis (Kondoh 2003a, 2003b; Brose et al. 2003). Defining and controlling properties of the structure introduced (e.g., cohesion among other) could allow to test the distribution of abundances or other property of the system (e.g., persistence, robustness, etc). If abundances are tested, it could be interesting to make an effort to integrate trade-offs (Tilman 1994), and neutral models (Hubbell 2001), which will imply a synthetic approach between the structure of food webs and abundances distribution in a dynamical context.

Another critical point is how are large and qualitative matrices related with the quantitative ones as-

suming fluctuating interactions among species. Recent studies have shown the importance of variance to understand ecological processes (Benedetti-Cecchi 2000; Benedetti-Cecchi 2004) and stability (Kokkoris et al. 2002). It is still very soon to affirm that quantitative matrices contain more information than the qualitative ones, because weak interactions and its variance could be extremely important (Berlow 1999; Berlow et al. 1999).

Regardless of the previous questions concerning the effect of structure and fluctuations on the dynamics of species-rich communities, some basic gaps concerning the structure of small and large systems remain to be explored. Specifically, our current work is focusing on count and compare against a set of null models the relative frequency of four of the most studied subwebs in the most large and resolved food webs. Local and global descriptors of food web structure have been extensively studied in species-rich communities. Two main approaches have been used. First, the study of large data sets exploring combinatorial properties of real niche spaces (*mesoscopic* perspective) (Cohen 1968; Cohen 1978; Sugihara 1982). Second, global properties, as the global connectance (*macroscopic* perspective), the degree of omnivore, vulnerability and generality, etc (Cohen et. al 1990; Ulanowicz and Wolff 1991; Williams and Martinez 2000). A combination of local and global properties in large food webs have been recently explored (e.g., clustering coefficient and small world patterns (Montoya and Solé 2002; Dunne et al. 2002).

On the other hand, field studies, microcosm experiments and theoretical approaches have shown the importance of subweb structure for the dynamics of a few number of species (Paine 1966; Polis and Holt 1992; Bonsall and Hassell 1997; Fussmann and Heber 2002). Recent studies have tested the presence of motifs in food webs and related complex networks (Milo et al. 2002). However, the significant presence of classical studied subwebs (i.e., omnivore, intraguild predation, and related local descriptors (Lawton 1989; Goldwasser and Roughgarden 1993; Post 2002; Williams and Martinez 2004)), the interrelations among subwebs, and the appropriate null models to test their significant presence in species-rich communities remain unclear (Connor and Simberloff 1979; Gotelli 2001; Pimm 2002; Morris et al. 2004; Artzy-Randrup et al. 2004). Basic questions as are there significant presence of subwebs in complex food webs?, and how are subwebs interrelated among themselves to form complex food webs?

are surprisingly unexplored. In the following paragraphs we will try to answer the first question, and speculate on the second.

Table 1 represents the total number of four types of subwebs for both the empirical data and for the five null models (see Table caption). The first three null models are used in the article *Food Web Cohesion*, but the fourth and fifth null models are incorporated in this discussion. I will explain briefly these models and the general results of this analysis.

The fourth null model (based on *Cattin et al.'s* 2004 *Nested Hierarchy model*) preserves the number of prey for each consumer from real data, and similarly to the original model sorted consumers according to their number of interactions (note that the original version of this model determines the number of prey for each consumer following the *Niche model*, before starting to fill the matrix and sorted species according with the niche value in ascending order, see Cattin et al. 2004). The rest of the model is exactly similar to the *Nested Hierarchy model*.

That is, starting with the smallest consumer's niche value, the trophic links are attributed to consumers in a two-stage process. In stage one, prey species of consumer j is randomly chosen among species with rank $< j$. Depending on this randomly chosen prey i , two cases are possible: (1) prey i has no consumer and therefore the next prey of consumer j will again be randomly attributed (with rank of prey $< j$); (2) prey i already has one or more consumers and therefore consumer j joins the group of species i 's consumers, and the next prey of consumer j is then randomly chosen among the set of prey of this group. However, if the number of prey in the group is too small for choosing all remaining preys of consumer j , the remaining preys are again randomly chosen among preys without consumers (with rank $< j$). As commented by Cattin et al. 2004, the second stage is needed if prey still cannot be attributed; remaining preys of consumers for which prey could not be attributed in stage 1 are randomly chosen (prey species can have rank $\geq i$). By creating groups of consumers, stage one (2) expresses the part in food web organization that is determined by phylogenetic constraints. Links attributed to species free of consumers, and links distributed randomly in the second stage, render the adaptation of consumers to new prey (Cattin et al. 2004).

Previous model introduces both, phylogenetic constraints and random adaptation, assuming an homogeneous distribution of consumers and preys. How-

ever, it could be interesting to test the effect of the neighboring or spatial aggregation of consumers that share preys. To test this we introduce our fifth null model (Bascompte and Melián (submitted); Melián and Bascompte (submitted)), as a modification of the previous nested hierarchy model (Cattin et al. 2004). All the rules are equal to the previous model with the following exception: in point (2) of the first stage, prey i already has one or more consumers and therefore consumer j joins the group of species i 's consumers, and the next prey of consumer j is then randomly chosen among the set of prey of this group. However, if the number of prey in the group is too small for choosing all remaining prey of consumer j , the remaining prey are randomly chosen among the set of consumers that share at least one prey with consumer j (instead of randomly chosen among prey without consumers (with rank $< j$)). If the group of consumer that share at least one prey with consumer j is too small for choosing all remaining prey of consumer j , the remaining prey that could not be attributed are randomly chosen (prey species can have rank $\geq i$). Note that this adaptation assumes that consumer j is forced to eat on consumers' species that share prey with consumer j , which implies that individuals of consumer species j use local information to find new resources, which can be interpreted as the increasing probability to interact with other consumer when they share a prey or the spatial neighboring of consumers that share preys.

This modified *Nested Nierarchy model* by introducing *correlation between consumers that share preys*, similarly to the previous model, has the part in food web organization that is determined by phylogenetic constraints. At the same time, links attributed to species free of consumers render the random adaptation of consumers to new prey, and links distributed randomly from the group of consumers that share at least one prey with consumer j in the second stage render the spatial neighboring or spatial aggregation of consumers that share preys.

Results from table 2 are: (1) food webs present structural redundancy to the microscopic level which implies the emergence of more complex, mesoscopic structures (see Fig. 1 and caption), (2) food webs are highly specific to the microscopic level, (3) current static null models of food webs do not reproduce previously studied subwebs. The incorporation of spatial structure or consumer correlations allow us to better capture some features (as omnivore and intraguild predation), but others remain far to be cap-

tured. Preliminary conclusions are: (1) if we examine in detail each food web we can observe that taxonomic groups forming part of the most number of modules are highly specific for each food web, and (2) the introduction of phylogenetic constraint and random adaptation (Cattin et al. 2004) in static models is a simple and elegant way to capture biological principles, and a new step to link and test empirically microscopic and mesoscopic scales.

We could explore dynamically present results: (1) new static null models introducing specific and dynamic rules for each food web, and (2) test against a series of null models the real distribution of subwebs and explore the dynamics of both independent and correlated subwebs. It is interesting to note that most basal, intermediate, and top species are embedded in a small number of modules, but a few number of species are forming part of a very large number of modules. Limits to do this type of simulation remain evident, mainly because the problems with stability (Berlow et al. (2004)), and the high number of parameters when introducing biological information in dynamical models. Finally, my current view concerns the needs of specific static null models with different levels of complexity, and testing simultaneously multiple properties in each food web. This is more related with a Bayesian approach, or an approach where a set of null models could be mixed between them and empirical information could be added to each specific null model.

Literature Cited

- Artzy-Randrup, Y., Fleishman, S. J., Ben-Tal, N., and Stone, L. (2004). Comment on “Network motifs: simple building blocks of complex networks” and “Superfamilies of evolved and designed networks”, *Science*, **305**:1107.
- Bascompte, J., Jordano, P., Melián, C. J., and Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proc. Nat. Acad. Sci. (USA)*, **100**:9383-9387.
- Bascompte, J. and Melián, C. J. (2004). Simple modules for complex food webs. Submitted.
- Berlow, E. L., Navarrete, S. A., Briggs, C. J., Power, M. E., Menge, B. A. (1999). Quantifying variation in the strengths of species interactions. *Ecology*, **80**:2206-2224.
- Berlow, E. L. (1999). Strong effects of weak interactions in ecological communities. *Nature*, **398**:330-334.
- Benedetti-Cecchi, L. (2000). Variance in ecological consumer-resource interactions. *Nature*, **407**:370-374.
- Benedetti-Cecchi, L. (2003). The importance of the variance around the mean effect size of ecological processes. *Ecology*, **84**:2335-2346.
- Bonsall, M. B., and Hassell, M. P. (1997). Apparent competition structures ecological assemblages. *Nature*, **388**:371-373.
- Brose, U., Williams, R. J., and Martinez, N. D. (2003). Comment on *Foraging adaptation and the relationship between food web complexity and stability*. *Science*, **301**:918b.
- Cattin, M-F., Bersier, L-F., Banašek-Ritcher, C., Baltensperger, R., and Gabriel, J-P. (2004). Phylogenetic constraints and adaptation explain food-web structure. *Nature*, **427**:835-839.
- Cohen, J. E., (1968). Interval graphs and food webs: a finding and a problem. RAND Corporation Document D-17696-PR, 30.
- Cohen, J. E. (1978). *Food Web and Niche Space*. Princeton University Press. Princeton. USA.
- Cohen, J. E., Briand, F., and Newman, C. M. (1990). *Community food webs: data and theory*. Springer-Verlag, Berlin, Germany.
- Connor, E. F., and Simberloff, D. (1979). The assembly of species communities: chance or competition? *Ecology*, **60**:1132-1140.
- Dunne, J. A., Williams, R. J., and Martinez, N. D. (2002). Food web structure and network theory: the role of connectance and size. *Proc. Nat. Acad. Sci. (USA)*, **99**:12917-12922.
- Frank, K. (1995). Identifying cohesive subgroups. *Soc. Networks*, **17**:27-56.
- Frank, K. (1996). Mapping interactions within and between cohesive subgroups. *Soc. Networks*, **18**:93-119.
- Fussmann, G. F., and Heber, G. (2002). Food web complexity and chaotic population dynamics. *Ecol. Lett.*, **5**:394-401.
- Girvan, M. and Newman, M. E. J. (2002). Community structure in social and biological networks. *Proc. Nat. Acad. Sci. (USA)*, **99**:8271-8276.
- Goldwasser, L., and Roughgarden, J. (1993). Construction and analysis of a large Caribbean food web. *Ecology*, **74**:1216-1233.
- Gotelli, N. J. (2001). Research frontiers in null model analysis. *Global Ecology and Biogeography* **10**:337-343.
- Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.

sity Press, Princeton, NJ.

Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries and coevolution. *Am. Nat.*, **129**:657-677.

Kondoh, M. (2003a). Foraging adaptation and the relationship between food web complexity and stability. *Science*, **299**:1388-1391.

Kondoh, M. (2003b). Response to Comment on *Foraging adaptation and the relationship between food web complexity and stability*. *Science*, **301**:918c.

Kokkoris, G. D., Jansen, V. A. A., Loreau, M., and Troumbis, A. Y. (2002). Variability in interaction strength and implications for biodiversity. *J. Anim. Ecol.*, **71**:362-371.

Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E., and Taylor, W. W. (2003). Compartments revealed in food-web structure. *Nature*, **426**:282-285.

Lawton, J. H. (1989). Food Webs. In *Ecological concepts*, J. M. Cherrett ed. Blackwell Scientific, Oxford.

Melián, C. J., and Bascompte, J. (2005). Are subwebs relevant to complex food web structure? Submitted.

Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., and Alon, U. (2002). Network motifs: simple building blocks of complex networks. *Science*, **298**:824-827.

Montoya, J. M., and Solé, R. V. (2002). Small world pattern in food webs. *J. Theor. Biol.*, **214**:405-412.

Morris, R. J., Lewis, O. T., and Godfray, C. J. (2004). Experimental evidence for apparent competition in a tropical forest food web. *Nature*, **428**:310-313.

Newman, M. E. J. (2002). Assortative mixing in networks. *cond-mat/0205405*.

Paine, R. T. (1966). Food web complexity and species diversity. *Am. Nat.*, **100**:850-860.

Pimm, S. L., and Lawton, J. H. (1980). Are food webs divided into compartments? *J. Anim. Ecol.*, **49**:879-898.

Pimm, S. L. (2002). Food Webs. The University of Chicago Press. *2nd edition*.

Polis, G. and Holt, R. D. (1992). Intraguild predation: The dynamics of complex trophic interactions. *TREE*, **7**:151-154.

Post, D. M. (2002). The long and short of food-chain length. *TREE*, **17**:269-277.

Sugihara, G. (1982). *Niche Hierarchy: Structure, Organization and Assembly in Natural Communities*. Ph.D. thesis, Princeton University, Princeton.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, **75**:2-16.

Ulanowicz, R. E., and Wolff, W. F. (1991). Ecosystem flow networks: loaded dice?. *Math. Biosci.*, **103**:45-68.

Vázquez, D. P., and Aizen, M. A. (2004). Asymmetric specialization: a pervasive feature of plant-pollinator interactions. *Ecology*, **85**:1251-1257.

Williams, R. J., and Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, **404**:180-183.

Williams, R. J., and Martinez, N. D. (2004). Limits to trophic levels and omnivory in complex food webs: theory and data. *Am. Nat.*, **163**:458-468.

	STC D.	STC C.	P	STC N.	P	STC L.	P	STC Nh	P	STC Nc	P
Ythan Est.	3284	1815(85)	P<0,0001	1776(170)	P<0,0001	2929(103)	P<0,0001	1653(87)	P<0,0001	1558(118)	P<0,0001
Silwood P.	885	611(48)	P<0,0001	591(70)	P<0,0001	818(52)	P=0,13	651(41)	P<0,0001	515(33)	P<0,0001
El Verde	11655	9730(232)	P<0,0001	10188(695)	P<0,01	13576(359)	P=1	9388(514)	P<0,0001	9567(1069)	P<0,05
LRL	22256	21412(395)	P<0,05	22493(1358)	P=0,58	22560(478)	P=0,72	18638(1404)	P<0,05	23098(1738)	P=0,58
Caribbean	28181	29649(673)	P=0,995	30738(1841)	P=0,91	25739(598)	P<0,0001	25189(841)	P<0,0001	20620(1766)	P<0,0001
OMN D.	OMN D.	OMN C.	P	OMN N.	P	OMN L.	P	OMN Nh	P	OMN Nc	P
Ythan Est.	487	115(11)	P<0,0001	215(59)	P<0,0001	470(39)	P=0,34	144(31)	P<0,0001	588(72)	P=0,95
Silwood P.	358	19(4)	P<0,0001	51(26)	P<0,0001	238(28)	P<0,0001	14(6)	P<0,0001	164(31)	P<0,0001
El Verde	2817	1206(38)	P<0,0001	2101(306)	P<0,0001	3077(154)	P=0,95	1757(209)	P<0,001	3726(393)	P=1
LRL	9654	3150(79)	P<0,0001	5344(618)	P<0,0001	8082(240)	P<0,0001	5818(659)	P<0,001	10763(1348)	P=0,84
Caribbean	9063	3201(107)	P<0,0001	5637(715)	P<0,0001	11512(274)	P=1	8624(719)	P=0,26	10487(690)	P=1
APC D.	APC D.	APC C.	P	APC N.	P	APC L.	P	APC Nh	P	APC Nc	P
Ythan Est.	2683	238(26)	P<0,0001	238(26)	P<0,0001	677(90)	P<0,0001	540(71)	P<0,0001	854(158)	P<0,0001
Silwood P.	266	20(6)	P<0,0001	20(6)	P<0,0001	190(67)	P=0,14	240(28)	P=0,17	234(29)	P=0,14
El Verde	21431	5099(225)	P<0,0001	5099(225)	P<0,0001	6043(485)	P<0,0001	8133(1452)	P<0,0001	10417(2204)	P<0,0001
LRL	77538	17497(493)	P<0,0001	17497(493)	P<0,0001	30025(1462)	P<0,0001	23314(2823)	P<0,0001	24739(9912)	P<0,0001
Caribbean	168095	18545(555)	P<0,0001	18545(555)	P<0,0001	97861(2739)	P<0,0001	45505(4535)	P<0,0001	58808(6489)	P<0,0001
IGP D.	IGP D.	IGP C.	P	IGP N.	P	IGP L.	P	IGP Nh	P	IGP Nc	P
Ythan Est.	603	16(6)	P<0,0001	45(43)	P<0,0001	330(81)	P<0,01	22(15)	P<0,0001	381(147)	P=0,1
Silwood P.	976	1(1)	P<0,0001	12(16)	P<0,0001	207(68)	P<0,0001	1(1)	P<0,0001	50(25)	P<0,0001
El Verde	6594	716(61)	P<0,0001	2014(825)	P<0,0001	5180(692)	P<0,05	1420(423)	P<0,0001	6905(2119)	P=0,5
LRL	40554	3004(160)	P<0,0001	8537(2055)	P<0,0001	16375(1486)	P<0,0001	8289(2707)	P<0,0001	39967(12617)	P=0,54
Caribbean	25269	2231(125)	P<0,0001	6446(2143)	P<0,0001	22857(1854)	P=0,1	14890(2971)	P<0,0001	16087(4382)	P<0,05

Table 1 represents the subwebs explored in Bascompte and Melián, *Simple modules for complex food webs*, (Submitted), and in Melián and Bascompte, *Are subwebs relevant to Complex Food Web Structure?* (Submitted). These modules are: Simple trophic chain (*STC*), Omnivory (*OMN*), Apparent competition (*APC*), and intraguild predation (*IGP*). *D*, represents empirical data, *C* Cascade model, *N* Niche model, *L*, Local rewiring algorithm, *Nh* Nested hierarchy model, and *Nc* Nested hierarchy with correlation between consumers that share prey. *P* is the probability that a random replicate has a number of modules equal or higher than the observed value.

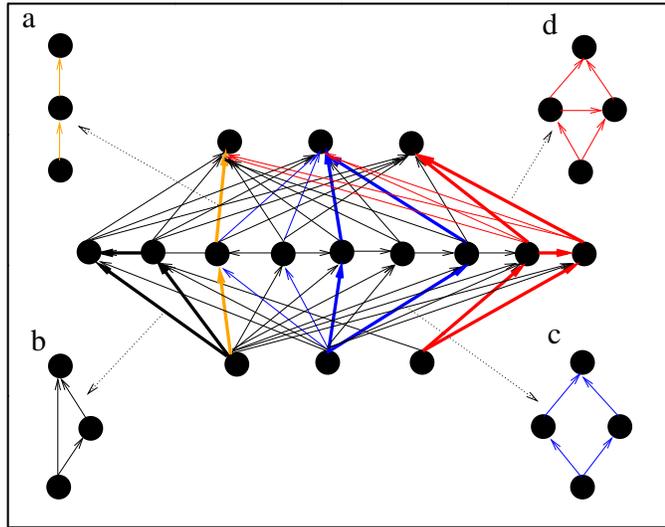


Figure 1: A hypothetical food web graph. The four types of subwebs explored are shown (a, simple trophic chain (*STC*); b, omnivory (*OMN*); c, apparent competition (*APC*) and d, intraguild predation (*IGP*)). This graph has 121 simple trophic chains. A graph from the Niche model with equal S and C reproduces this structure ($P > 0.05$ with mean 96 ± 20 from 100 replicates). However, Niche model does not reproduce apparent competition ($P < 0.0001$ with 142 modules in this graph and a mean of 30 ± 18 from the Niche model) and intraguild predation ($P < 0.05$ with 61 modules in this graph and 23 ± 17 from the Niche model). *blue* and *red* links represent the structural redundance of apparent competition (6 *APC* subwebs), and intraguild predation (3 *IGP* subwebs).

Chapter 3

From Quantitative Food Web Structure to Dynamics

Until now I have tried to understand ecological networks from a qualitative and static view. From the previous chapter we have learnt that food webs are neither randomly assembled nor compartmentalized but highly cohesive. In the present chapter we explore the structure and dynamics of simple modules in the largest quantitative food web to date. The general result is that strongly interacting chains and chains with omnivory are not distributed randomly in the food web, which implies a different response to overfishing.

3.1 Interaction Strength Motifs and the Overfishing of Ma- rine Food Webs

Interaction strength motifs and the overfishing of marine food-webs

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Abstract

The strengths of species interactions are structured non-randomly in a large Caribbean marine food-web. The co-occurrence of strong interactions on two consecutive levels of food chains occurs less frequently than expected by chance. Even when they do occur, these strongly interacting chains are accompanied by strong omnivory more often than expected by chance. These interaction strength combinations or motifs reduce the likelihood of trophic cascades after the overfishing of top predators. However, fishing selectively removes predators that are over-represented in strongly interacting chains. Hence, the potential for strong community-wide effects remains a threat.

1 Introduction

Quantification of the strength of interactions between species is essential for understanding how ecological communities are organized and how they respond to human exploitation. Food-webs are characterized by many weak interactions and a few strong interactions (1-5), which appears to promote community persistence and stability (6-8). However, little is known about how interaction strengths are combined to form the basic construction blocks of food-webs (9, 10). Here we analyze a real, large food web to describe how interaction strengths are combined, and the implications for food web dynamics.

We compiled from published studies (11, 12) the largest quantitative food-web to date: 249 species/trophic groups and 3,313 interactions. It depicts the trophic interactions of a Caribbean marine ecosystem covering approximately 1,000 km^2 , and comprises all benthic and pelagic communities from the surface to 100 m depth, including detritus, 4 primary producer groups, 35 invertebrate taxa, 208 fish species, sea turtles, and sea birds (11, 12) (see Supporting Information for the strengths and limitations of data). To investigate the structure of the food-web we calculated a per capita, standardized measure of the strength of the interaction of predators on their prey (1, 4).

2 Materials and Methods

2.1 Estimation of Per Capita Interaction Strength

The strength of the interaction between predators and their prey was estimated as the proportion of prey biomass consumed per capita (per unit biomass of predator), per day, i.e.,

$$\frac{(Q/B)_j \times DC_{ij}}{B_i}$$

where $(Q/B)_j$ is the number of times an age-structured population of predator j consumes its own weight per day (13), DC_{ij} is the proportion of prey i in the diet of predator j , and B_i is biomass of prey i (see Supporting Information for the detailed derivation of the above expression). Parameter values were obtained from many individual studies compiled by Opitz (see ref. 12). DC_{ij} values were obtained primarily from fish stomach contents in the US Virgin Islands (11). The biomass (gm^{-2}) of the species used here are average estimates for the US Virgin Islands - Puerto Rico region (12).

Per capita interaction strengths (pcis) were classified in four quartile classes: (1) $pcis < 10^{-7}$; (2) $10^{-7} \leq pcis < 10^{-5}$; (3) $10^{-5} \leq pcis < 10^{-3}$, (4) $pcis \geq 10^{-3}$. We defined (4) as strong interactions. We looked at combinations of interaction strength values within class (4) in tri-trophic food chains and food chains with omnivory. Other classifications did not qualitatively change the results here presented.

To assess the statistical significance of the co-occurrence of strong interaction strengths within tri-trophic food chains and chains with omnivory, we randomised the original food-web by randomly exchanging predator-prey pairs of interaction strengths. These pairs were kept as such intact to preserve the topological structure of the matrix (9). We generated a total of 50,000 replicate food-webs. For each replicate food-web, we classified interaction strengths in the previous four classes and measured the number of food chains with two strong interactions. We then used the distribution of the number of food chains with two strong interactions to determine the probability that a random food web has a smaller or larger number of such food chains than that in the real food-web. Since not all interaction strength values necessarily form a TFC, we have used a second null model in which only the interaction strengths which do belong to at least a TFC are randomized. Results are qualitatively similar.

2.2 The Food Web Model

We used a bioenergetic model of a simple tri-trophic food chain and a food chain with omnivory (7, 14, 15). Although the model describes independent trophic modules, the motifs studied in this paper are embedded within the entire food-web. A first step into addressing this is by adding allochthonous inputs A to the model, which captures the fact that resources and consumers feed on other species. Thus, our modules are not completely isolated from the food-web (see Supporting Information for more details). The model can be written as:

$$\begin{aligned} \frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - \\ - \frac{(1 - \Omega_{Ac})X_{RC}Y_C R^n C}{(1 - \Omega_{Ac})R^n + \Omega_{Ac}A_c^n + (1 + c_C C)R_0^n} - \\ - \frac{\Omega_{RP}X_{RP}Y_P R^n P}{\Omega_{RP}R^n + \Omega_{Ap}A_p^n + \Omega_{CP}C^n + (1 + c_P P)R_{02}^n} \end{aligned} \quad (1)$$

$$\begin{aligned} \frac{dC}{dt} = -X_C C + \\ + \frac{(1 - \Omega_{Ac})X_{RC}Y_C R^n C}{(1 - \Omega_{Ac})R^n + \Omega_{Ac}A_c^n + (1 + c_C C)R_0^n} + \\ + \frac{\Omega_{Ac}X_{AC}Y_C A_c^n C}{(1 - \Omega_{Ac})R^n + \Omega_{Ac}A_c^n} - \\ - \frac{\Omega_{CP}X_{CP}Y_P C^n P}{\Omega_{RP}R^n + \Omega_{Ap}A_p^n + \Omega_{CP}C^n + (1 + c_P P)C_0^n} \end{aligned} \quad (2)$$

$$\begin{aligned} \frac{dP}{dt} = -X_P P - FP + \\ + \frac{\Omega_{RP}X_{RP}Y_P R^n P}{\Omega_{RP}R^n + \Omega_{Ap}A_p^n + \Omega_{CP}C^n + (1 + c_P P)R_{02}^n} + \\ + \frac{\Omega_{CP}X_{CP}Y_P C^n P}{\Omega_{RP}R^n + \Omega_{Ap}A_p^n + \Omega_{CP}C^n + (1 + c_P P)C_0^n} + \\ + \frac{\Omega_{Ap}X_{AP}Y_P A_p^n P}{\Omega_{RP}R^n + \Omega_{Ap}A_p^n + \Omega_{CP}C^n} \end{aligned} \quad (3)$$

where R is the resource biomass, C is the consumer biomass, and P is the top predator biomass. r is the resource intrinsic growth rate (its

production-to-biomass ratio (15). K is the resource carrying capacity, R_0 , R_{02} , and C_0 are the half saturation densities of the resource when consumed by C , by P , and of the consumer itself when consumed by P , respectively. X_{ij} is the mass-specific metabolic rate of species j estimated using the i -to- j body mass ratio, and Y_j is the ingestion rate per unit metabolic rate (15) of species j . F is the fishing rate of the top predator.

Ω_{ij} represents the species j preference for species i . Thus, model (1-3) represents a simple tri-trophic food chain when $\Omega_{RP} = 0$, and an omnivory food-web when $\Omega_{RP} > 0$.

Parameter values for X_{ij} were chosen so that body mass ratios between prey and predator were the median values for the fish species on each trophic level of the Caribbean food-web (see Supporting Information). Metabolic parameters (Y_j) are the equivalent for vertebrate ectotherms (15).

We have tested Holling type II (15, 16) ($n = 1$, $c_i = 0$), Holling type III (15, 16) ($n = 2$, $c_i = 0$), and predation interference (17) ($n = 1$, $c_i > 0$) functional responses. All three functional responses and a range of realistic parameter combinations showing stable dynamics have given similar qualitative results (except for predator interference for certain parameter combinations, see Supporting Information in pp. 47). The specific parameter combination used in Fig. 3 is: Functional response is Holling type II, $\Omega_{AC} = 0.6$, $\Omega_{CP} = 0.4$, $\Omega_{AP} = 0.6$ (Fig. 3a and b), $\Omega_{AP} = 0.2$, $\Omega_{RP} = 0.4$ (Fig. 3c). $X_{ij} = 0.1$ and $Y_i = 3$, corresponding to weak interactions as depicted in the inset (Fig. 3a). $X_{ij} = 0.2$ and $Y_i = 4$ corresponding to strong interactions (Fig. 3b and c). Other parameter values are: $r = 1$, $K = 1$, $R_0 = R_{02} = C_0 = 0.75$, $n = 1$, $c_C = 0.005$, $c_P = 0.35$, and $A_C = A_P = 0.01$.

3 Results

Fig. 1a shows a random fraction of the whole food-web for representation purposes. A few strong interactions are distributed within a matrix of weak interactions, confirming previous results (1-5). The frequency distribution of per capita interaction strengths (interaction strengths hereafter) fits a lognormal distribution with marginal significance ($P = 0.06$, Lilliefors' test; Fig. 1b). It spans seven orders of magnitude, highlighting the extreme variability of predator-prey interaction strengths.

The frequency distribution of interaction strengths is an adequate way to explore some

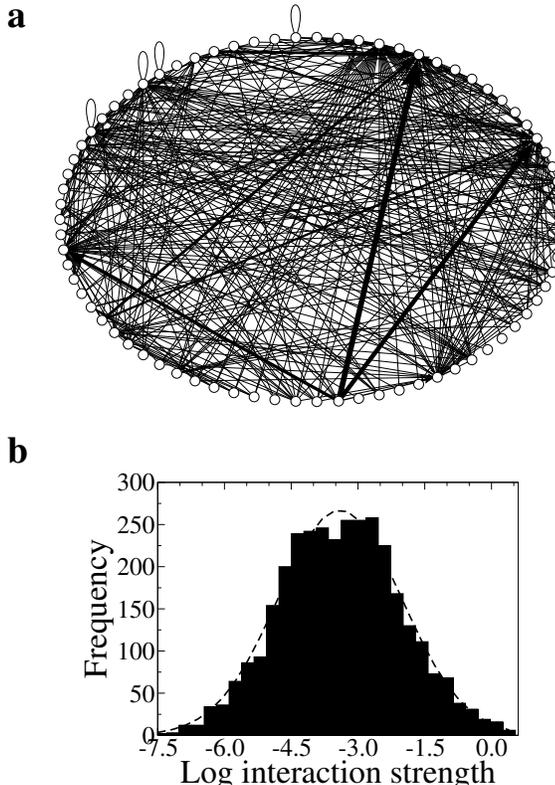


Figure 1: (a) Random sample of the Caribbean food-web containing 30% of the species and 11% of the interactions. Each node represents a species or taxon. Arrows represent trophic interactions between predators and their prey. Arrow thickness is proportional to the interaction strength. Loops represent cannibalism. (b) Frequency distribution of interaction strengths ($n=3,313$), spanning seven orders of magnitude. The line represents the best fit to a lognormal distribution.

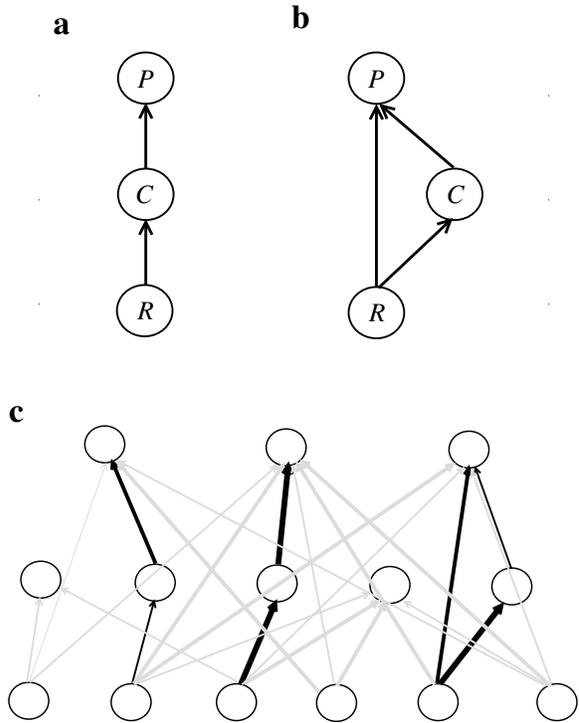


Figure 2: (a) Tri-trophic food chain. (b) Tri-trophic food chain with omnivory. Nodes from top to bottom represent the top predator (P), the consumer (C), and the resource (R). Arrows represent trophic links. (c) Schematic representation of a food-web highlighting three tri-trophic food chains (one of them with omnivory). The central food chain shows co-occurrence of two strong interaction strengths, the combination explored in this paper.

fundamental properties of food-webs. However, it is only a first step towards understanding the structure of complex communities (6, 9). Here, we move beyond this statistical distribution by studying how interaction strength values are combined to form the basic construction blocks of this food-web. We describe how interaction strengths are distributed in tri-trophic food chains (TFCs) in which a top predator P eats a consumer C , which in turn eats a resource R (Fig. 2a). This basic chain can be viewed as the building block of complex food-webs (10) (Fig. 2c), or the simplest representation of multitrophic relationships frequently used in theoretical studies (7, 18, 19). We were interested in determining how strong interactions are structured within TFCs, since the co-occurrence of strong interactions on two consecutive levels of a trophic chain has the potential to modify the structure and dynamics of whole food-webs through trophic cascades (20-24). Trophic cascades are predator-prey effects that alter biomass or abundance of a species across more than one trophic link (20, 24). Specifically, reductions in the abundance of a predator through fishing would propagate through the food chain resulting in increased consumer abundance and fewer resources (21).

To investigate interaction strength motifs or combinations that may induce trophic cascades, we first classified interactions into four categories on the basis of the order of magnitude of interaction strength. We counted the number of TFCs with co-occurrence of two strong interaction strengths (those belonging to the upper quartile of the log per capita interaction strength distribution, $n = 3,086$; see Fig. 2c). The fish species involved in most strongly interacting TFCs were sharks as top predators, groupers (family Serranidae) as consumers, and herbivorous fishes of the Blenniidae, Clupeidae, Engraulidae, Pomacentridae, and Scaridae families as base of the TFC. To determine whether co-occurrence of two strong interactions was significant, we built a null model using randomized networks (see Materials and Methods). Omnivory (the top predator also feeds on the resource; Fig. 2b) has been shown to stabilize the dynamics of food-webs (14, 25), although it is unclear whether it can compensate trophic cascades when top predators and consumers are strong interactors (26). Consequently, we assessed the likelihood of strong omnivory accompanying strong tri-trophic interactions in the Caribbean food-web.

Our analysis showed that co-occurrence of two strong interactions in TFCs is less frequent than ex-

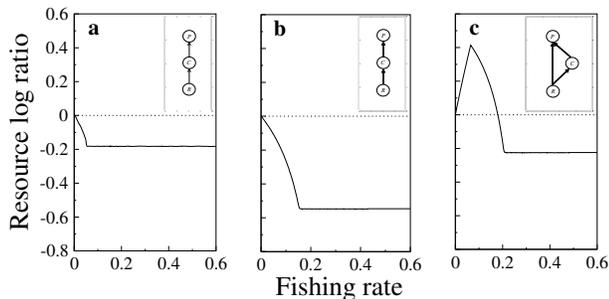


Figure 3: Response of the resource as a function of the fraction of predators fished in tri-trophic food chains with two weak interactions (*a*), two strong interactions (*b*), and food chains with omnivory and three strong interactions (*c*). Based on a bioenergetic model (see Materials and Methods). The magnitude of the trophic cascade (measured as the resource log ratio) is greater for food chains with two strong interactions (compare *a* with *b*), and it is reduced when there is a similarly strong omnivory link (compare *b* with *c*). The dotted line is used as a reference. Parameter combinations are specified on Materials and Methods.

pected by chance ($P = 0.0018$). When two strong interactions co-occur, strong TFCs have a strong omnivory link more often than expected by chance ($n = 585, P = 0.0001$). To assess the implications of these non-random combinations (i.e., motifs) of interaction strength on trophic cascades, we used a food-web model for simple tri-trophic chains and tri-trophic chains with omnivory (7, 14, 15, see Materials and Methods). Because overfishing tends to eliminate the species in the higher levels of food chains (27, 28), we simulated the fishing of top predators and explored the subsequent change in resource biomass. As in related studies, the magnitude of the trophic cascade was measured as the log ratio of resource biomass without fishing of the top predator to resource biomass with fishing of the top predator (23).

The co-occurrence of two strong interactions in the basic TFC increases the magnitude of the trophic cascade (Fig. 3, compare *a* with *b*). However, the magnitude of the trophic cascade is reduced in the presence of strong omnivory (Fig. 3, compare *b* with *c*). In addition, omnivory changes qualitatively the response of the resource, which may first increase with moderate fishing of the top predator (Fig. 3, compare *b* with *c*). These results indicate that the interaction strength motifs in the web reduce the likelihood of trophic cascades,

with important implications for food-web dynamics. However, our model describes isolated modules (although coupled to some extent through the allochthonous inputs, see Materials and Methods and Supporting Information). Future work is needed to explore how results are affected by the use of modules more explicitly embedded within the whole food-web. This remains a challenge since more complex models become increasingly unstable for biologically realistic parameter combinations.

4 Discussion

The global reduced tendency for trophic cascades resulting from the reported interaction strength combinations, however, does not imply that this community is buffered from the effects of exploitation. Fishing selectively targets a biased sample of species belonging to upper trophic levels (27, 28). These species, which include top predators, are over-represented in the relatively rare strongly interacting TFCs. For example, ten heavily fished top predators (sharks from seven families) account for 48 % of the strongly interacting TFCs in the Caribbean food-web. The likelihood of trophic cascades after the depletion of these strong interactors will thus depend on the relative fraction of strong omnivory. 31% of these strongly interacting TFCs have the buffering effect of strong omnivory, still leaving roughly two out of three strongly interacting TFCs susceptible to trophic cascades.

The dynamic consequences of the structural patterns here reported provide a framework to assess the community-level impacts of overfishing. Strongly interacting TFCs include species at the base such as parrotfishes (Scaridae) and other herbivores which are important grazers of macroalgae (11). The removal of herbivores by fishing may have been partly responsible for the shift of Caribbean reefs from coral- to algal-dominated (29). Our results suggest that overfishing of sharks may have also contributed to the depletion of herbivorous fishes through trophic cascades, thus enhancing the degradation of Caribbean reefs. The community-wide impacts of fishing are stronger than expected because fishing preferentially targets species whose removal can destabilize the food-web.

We thank J. Alroy, F. Ballantyne, P. Buston, J. Jackson, P. Jordano, N. Knowlton, A.G. Sáez, S. Sandin, E. Seabloom, G. Sugihara, and D. Vázquez

for interesting discussions. Funding was provided by the Spanish Ministry of Science and Technology (Grant to JB and Ph.D. Fellowship to CJM), and the History of Marine Animal Populations Program of the Census of Marine Life, sponsored by the Alfred P. Sloan Foundation (Grant to ES and J. Jackson). JB and CJM thank the faculty at Scripps for their hospitality during a three month visit in 2002. Part of this work was conducted at the National Center for Ecological Analysis and Synthesis while JB was a visiting scientist. This paper is dedicated to the memory of Ramon Margalef (1919-2004).

5 References

1. Paine, R.T. (1992) *Nature* **355**, 73-75.
2. Fagan, W.F. & Hurd, L.E. (1994) *Ecology* **75**, 2022-2032.
3. Raffaelli, D. & Hall, S.(1995) in *Food Webs, Integration of Patterns and Dynamics*, eds. Polis, G. & Winemiller, K. (Chapman & Hall, New York), pp. 185-191.
4. Wootton, J.T. (1997) *Ecol. Monogr.* **67**, 45-64.
5. Goldwasser, L. & Roughgarden, J. (1997) *Ecology* **78**, 41-54.
6. May, R.M. (1973) *Stability and Complexity in Model Ecosystems* (Princeton University Press, Princeton).
7. McCann, K., Hastings, A. & Huxel, G.R. (1998) *Nature* **395**, 794-798.
8. Kokkoris, G.D., Troumbis, A.Y. & Lawton, J.H. (1999) *Ecol. Lett.* **2**, 70-74.
9. Neutel, A., Heesterbeek, J.A.P. & Ruiters, P.C. (2002) *Science* **296**, 1120-1123.
10. Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D. & Alton, U. (2002) *Science* **298**, 824-827.
11. Randall, J.E. (1967) *Studies in Tropical Oceanography* **5**, 665-847.
12. Opitz, S. (1996) *Trophic Interactions in Caribbean Coral Reefs* (ICLARM Technical Reports 43 Makati City, Philippines).
13. Pauly, D.A. (1986) *Fishery Bulletin* **84**, 827-840.
14. McCann, K. & Hastings, A. (1997) *Proc. R. Soc. Lond. B* **264**, 1249-1254.
15. Yodzis, P. & Innes, S. (1992) *Am. Nat.* **139**, 1151-1175.
16. Real, L. A. (1997) *Am. Nat.* **111**, 289-300.
17. Beddington, J. R. (1975) *J. Anim. Ecol.* **51**, 331-340.
18. Pimm, S.L. & Lawton, J.H. (1997) *Nature* **268**, 329-331.
19. Holt, R.D. (1996) in *Multitrophic interactions*, eds. Begon, M., Gange, A. & Brown, V. (Chapman & Hall, London), pp. 333-350.
20. Carpenter, S.R. & Kitchell, J.F. (1993) *The Trophic Cascade in Lake Ecosystems* (Cambridge University Press, New York).
21. Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999) *Trends Ecol. Evol.* **14**, 483-488.
22. Paine, R.T. (1980) *J. Anim. Ecol.* **49**, 667-685.
23. Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D. & Halpern, B.S. (2002) *Ecol. Lett.* **5**, 785-791.
24. Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M.-L., Hereu, B., Milazzo, M., Zabala, M., D'Anna, G. & Pipitone, C. (2000) *Env. Cons.* **27**, 179-200.
25. Fagan, W.F. (1997) *Am. Nat.* **150**, 554-567.
26. Polis, G.A. & Holt, R.D. (1992) *Trends Ecol. Evol.* **7**, 151-154.
27. Myers, R.A. & Worm, B. (2003) *Nature* **423**, 280-283.
28. Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres Jr, F. (1998) *Science* **279**, 860-863.
29. Hughes, T.P. (1994) *Science* **265**, 1547-1551.

SUPPORTING INFORMATION

1 Materials and methods

1.1 Data: strengths and limitations

Our food-web represents the largest, best resolved quantitative food web to date. First, while the bulk of previous studies use food webs with a number of species ranging from 25 to 94 (only one food web has as much as 181 species), our food web has 249 species. Second, in the previously published food webs the level of aggregation is really high (nodes of the web correspond to trophic species, not taxonomic species). In contrast, the bulk of species in our food web correspond to taxonomic species (but see below). Third, almost all previously studied food webs are qualitative, while we present quantitative information. However, our data have still weaknesses. While these weaknesses do not prevent the calculations conducted in the paper, they need to be acknowledged to put our conclusions in perspective. There are two potential limitations: the variability in diet and biomass estimates and the unequal level of resolution.

First, calculations of interaction strength are based on estimates of diet preferences, biomass (calculated as the average number of individuals per square meter times their average body mass), and the number of times an age-structured population of predator j consumes its own weight per day $(Q/B)_j$ (see Methods). From these parameters, $(Q/B)_j$ is probably the most reliable. It is estimated as the metabolic efficiency of an average individual during its growth (Pauly 1986). Information on this metabolic efficiency comes from experimental studies for almost all fish species considered in this food web (Opitz 1996). One has to make some simplifying inferences, however, when estimating body mass and densities.

The first is estimated as the average body mass of adults (a well-known amount) multiplied by a correction factor describing the age-structure of the population (the average body mass is reduced, assuming that the bulk of individuals are juveniles; see Opitz 1996 for details). This is, however, a common correction factor for all species, and could be improved by considering species-specific age-structure data. Density estimates were made by Opitz synthesizing several sources. She quantified previously qualitative mea-

asures of density. The only exception are fire corals, for which no information was available. We thus obtained the relative surface of fire corals from McField (1998). Multiplying this last ratio by the biomass of total corals we obtained an estimate of fire coral biomass.

Diet is estimated mainly from stomach contents of a total of 5,526 specimens of 212 fish species (Randall 1967, Opitz 1996). The average number of individuals per species is 27.1. The variance, however is quite high (842.9). 54 species are represented by 10 or less individuals. Variability of estimates for these species has to be considered high, and future studies should focus on these less represented species. Two species of Carcharhinidae (*Galleocerdo cuvier*, and *Negaprion brevirostris*) are represented by only two individuals, and Opitz complements this information based on accounts in Fisher (1978).

Despite the limitations of diet data, they stand as the best resolved studies for fish feeding habits in the Caribbean, and for some species *may be regarded as definitive expression of their food habits* (Randall 1967). Randall's study is extremely detailed, which helps in reducing the weakness of this approach. Specifically, it addresses the fact that some species may feed in different habitats. As an example, one can read on page 671 of Randall (1967): *Many species of reef fishes occur in diverse habitats, and their food habits may differ profoundly from area to area ... For this reason an effort was made in the present study to collect in all environments in the Virgin Islands and Puerto Rico in which the fishes were encountered.*

Randall's study also overcomes the possible diet bias when studying intestine contents: *One source of error ... is the result of the varying rate of digestion of the different food organisms... The inevitable result is a bias in the data towards the less digestible organisms. Such a bias is greater if working with intestinal contents than with stomach contents; for this reason, only stomach-content analysis were made except for a few fishes such as the diodontids and Lachnolaimus maximus which feed almost exclusively on invertebrates with shells or exoskeletons* (Randall 1967, pp 671).

But variability is, probably, still high. This variability may affect the calculations of interaction strength, but it is quite unlikely that is the responsible for the 7 orders of magnitude of observed variability. Data errors are likely going to represent white, unbiased noise, with a variance increasingly reduced because of the aggregate nature of these

measures. Before most detailed data is available, the results have to be look in the perspective of these weaknesses, but we do not expect this variability is going to bias in any qualitative way the results shown in the paper. Future work should look at smaller sets of species with higher levels of resolution.

Second, the level of resolution is not homogeneous through all ecological groups. Fishes are resolved at the species level, but other species are still highly aggregated: zooplankton, microfauna, sponges, stonycorals, octopuses, echiuroids, amphipods, tanaisids, isopods, shrimps, spiny lobster, scyllarid lobsters, hermit crabs, crabs, and echinoids. To what extent results may be affected by this biased level of resolution? This is a difficult question to answer (e.g., Martinez 1991; Bersier et. al 1999), and future studies are needed to be able to understand how aggregation may affect results on food webs. In our case, the aggregated groups are basal species in 56% of the strongly interacting tri-trophic chains (intermediate species in 20.5%, and top species in 1%), but they are basal species in only 23% of the strong omnivory chains (intermediate species in 10%, and top species in 1%). Thus, if we make the extreme assumption that all aggregated species have similar resources and predators, body mass, and abundances, the number of simple trophic chains with two strong interactions would increase approximately two times more than the number of omnivory food chains.

However, even in this case we would need to look at all the universe of possible combinations to see whether this is a relative increase or decrease (we look at the number of motifs in relation to the number observed in a randomly built network). The alternative scenario is suggested by the observation that individual species in the aggregates present high variation in body mass and densities, all of which affect the calculation of interaction strength. Thus, one could assume a random variation of interaction strength values and frequencies of motifs around the average represented by the aggregated values, with no seriously biased differences in results. These would be the two extremes. Knowing where the reality lies between these two extremes requires more resolved data and specific calculations. This is beyond the scope of the present paper, but it would be interesting to explore in the future. Aggregation problems occur in all previous food web studies, and the present study, in fact, reduces this problem for a significant part of the community.

1.2 Measure of per capita interaction strength

This supporting information describes the derivation of the measure of per capita interaction strength used in the paper. Pauly (1986) defined $(Q/B)_j$ as the number of times an age-structured population of species j consumes its own biomass per day. B_j is the biomass of this age-structured population, calculated as the average number of individuals per square meter times their average body mass (see Randall 1967 and Opitz 1996 for details).

The product of the above two terms $((Q/B)_j \times B_j)$ defines the biomass that an age-structured population would require per day to persist. DC_{ij} is the percentage in volume of prey i in the diet of predator j (Randall 1967). The product of the previous three terms $((Q/B)_j \times B_j \times DC_{ij})$ is thus the biomass of prey i consumed daily by an age-structured population of species j . To make this last expression per capita, we divide by the biomass of predator:

$$\frac{(Q/B)_j \times B_j \times DC_{ij}}{B_j} = (Q/B)_j \times DC_{ij}$$

Dividing the last expression by prey biomass B_i we obtained our measure of per capita interaction strength, as the proportion of prey population consumed daily by a predator biomass unit:

$$\frac{(Q/B)_j \times DC_{ij}}{B_i}$$

1.3 Linking Structural and Dynamical Measures of Interaction Strength

There are two main approaches to calculate interaction strength. First, Paine’s (1992) seminal paper was based on a dynamical assessment of the “absolute prey response standardized by some measure of prey abundance.” This measure is empirically calculated for a few species. On the other hand, observational, indirect (static) information has been used to estimate interaction strength for larger communities (e.g. Wootton 1997). Our measure of interaction strength used to describe the structure of this food web builds from the last one, which unfortunately precludes any inference about dynamical implications. For this reason, we bridge between static and dynamics measures when relating the results on structure to the dynamical model, a model built in a way that maximizes

the use of observational information. This facilitates comparisons. As a first step, we have parametrized a bioenergetic model with biologically realistic values (see section 2.4). Motifs defined by the structural interaction strength are incorporated in the dynamical model by combining preference, non-linear functional response, metabolic parameters, and body mass ratios. The above static and dynamic measures of interaction strength have the following similarities and differences: Similarities:

1. They represent a property of each individual link (Berlow et al 2004).
2. They provide a top-down measure of consumption intensity (Berlow et al 2004).
3. They do not measure prey response (Berlow et al. 2004).
4. Prey preference is used in both measures: Ω in the model, and DC_{ij} (i.e., relative fraction of prey i in the diet of predator j) in the static measure of interaction strength.
5. (Q/B) is essentially identical to the maximum ingestion rate Y , although the first is per unit biomass and the second is per unit metabolic rate.

Differences:

1. Our static measure ignores functional responses (it is based on fixed biomass of prey). On the other hand, our model considers functional responses which captures the fact that interaction strength varies with prey and predator density. The first measure can be calculated for lots of species, while the latter can only be calculated for a small subset of species (the real form of the functional response is unknown for the bulk of species).

Unifying structural and theoretical measures of interaction strength and using biologically realistic parameter values is still an open problem. Acknowledging the similarities and differences in different measures will provide a way to bridge between independent ways to understand the relationship between structure and dynamics in food webs.

1.4 Food-web model

Here we provide additional information on the parameter fit of the food-web model described in the paper (see Materials and Methods; McCann et al. 1998, McCann and Hastings 1997, Yodzis and Innes 1992) and assess the robustness of the dynamic results presented in the paper by exploring other biologically realistic parameter combinations. As commented in Box 1, the average body mass ratio between basal and intermediate species ($R : C$) was 0.135, a value obtained by averaging the body mass of basal and intermediate species present in all the food chains in the food-web. Specifically, the median body mass was 10g. and 188g. for basal and intermediate species, respectively.

The average body mass ratio between consumers and predators ($C : P$) was 0.06, with a body mass' median for top predators of 27090g. The most frequent top predators were ten species of sharks of the Carcharhinidae and Sphyrnidae families, which are included in 48% of all the strongly interacting tri-trophic food chains and 80% of all strongly interacting tri-trophic food chains with strong omnivory (see species names in Supplementary Methods 1). The average body mass ratio between resources and predators ($R : P$) is 0.009.

The mass-specific metabolic rate X_{ij} was estimated using the above body mass ratios following the equation by Yodzis and Innes (1992):

$$X_{ij} = \frac{a_T}{a_i f_i} \left(\frac{M_i}{M_j} \right)^{0.25}$$

where M_i and M_j are the average body mass of prey and predator, respectively. a_T is the respiration rate, set in this case for ectothermic vertebrates to $2.30 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$ (Brett and Groves 1979). a_i is the maximum possible production-to-biomass ratio for ectothermic vertebrates (see Yodzis and Innes 1992) and is equal to $a_i = a_J - a_T$, where a_J is the maximal ingestion rate of ectothermic vertebrates or the limit to the amount of energy that can be consumed, processed, and converted into either production or respiration and is equal to $8.9 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$.

Therefore, $a_i = 6.6 \text{ kg}(\text{kg yr})^{-1} \text{ kg}^{0.25}$ in ectothermic vertebrates (Yodzis and Innes 1992). f_i is the fraction of total time allocated to absorbing and processing food. For example, $f_i = 1$ means that there are no interferences in metabolising food, and so that physiology limits the capacity of the population to

metabolise food. Running away from predators, for example, would decrease f_i . In here, f_i has been set to 0.7, a conservative value for resources and consumers (see Yodzis and Innes 1992; Peters 1983). Using above values, $X_{RC} = 0.27$, $X_{CP} = 0.21$ and $X_{RP} = 0.15$.

Similarly, Y_i ($i = C, P$) has been estimated using the equation by Yodzis and Innes (1992):

$$Y_i = \frac{f_J a_J}{a_T},$$

where f_J is defined as f_r and is set to 1, that is, physiology and no other ecological factors limit the capacity of population i to metabolise food. a_J and a_T are as defined above. $Y_i = 3.87$ with values defined above.

Here we explore three possible functional responses: Holling type II ($n = 1, c_i = 0$, Fig. SI-1a), Holling type III ($n = 2, c_i = 0$, Fig. SI-1b), and predation interference ($n = 1, c_i > 0$, specifically $c_C = 0.005$ and $c_P = 0.35$, Fig. SI-1c). For each functional response, we compare the magnitude of the trophic cascade as top predators are fished for strong tri-trophic food chains (continuous line) and strong omnivory chains (broken line). Four values are explored for each module and each functional response, illustrating a range of strong interaction strength values. Each combination corresponds to a line in Fig. SI-1 and is obtained by combining the following parameter values: $Y_i = Y_C = Y_P$ is either 3.7 or 3.9; $X_{CP} = X_{RP}$ is either 0.1 or 0.2. Other parameter values are $X_{RC} = 0.2$, $X_{AC} = X_{AP} = 0.05$, $r = 1$, $K = 1$, R_o, R_{o2} , and $C_o = 0.75$.

The magnitude of the trophic cascade (measured as

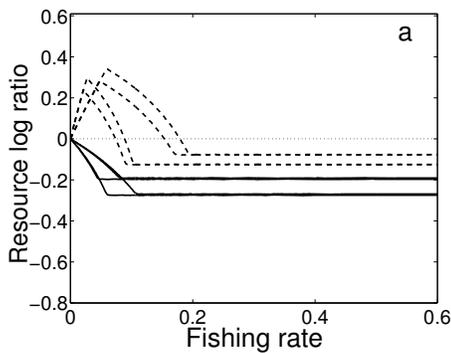


Figure 1: a-SI

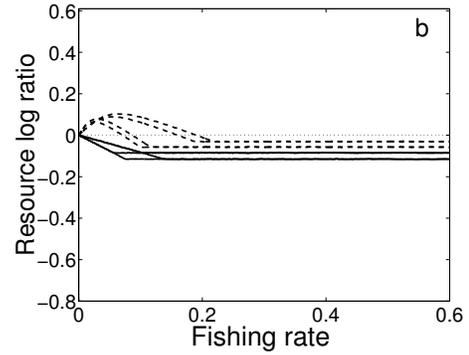


Figure 2: b-SI

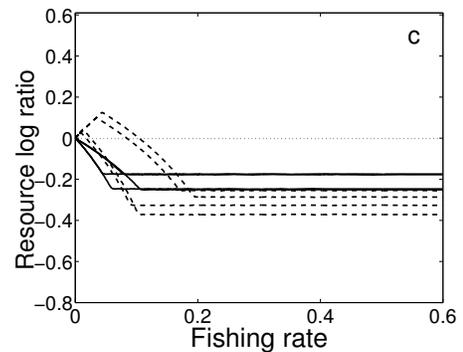


Figure 3: c-SI

the resource log ratio) is always greater for strongly interacting tri-trophic food chains without omnivory (continuous line) with the exception of predation interference (Fig. SI-1c). Thus, the results presented in Fig. 3 of the paper are robust to changes in interaction strength value and functional response with a single exception.

Although the model describes independent trophic modules, the motifs studied in this paper are embedded within the entire food-web. A first step into addressing this is by adding allochthonous inputs A to the model, which captures the fact that resources and consumers feed on other species. Thus, our modules are not completely isolated from the food-web.

Assuming these inputs come from a large number of species whose fluctuations are asynchronous and cancel out, it is reasonable to describe them as a fixed amount A . It would be very convenient to extend this modeling exercise by considering larger trophic modules. However, a modeling approach using much more species is complicated. As reviewed by Berlow et al (2004), *most published dynamic food web models were limited to relatively few species... Persistent dynamics for systems beyond six species are difficult to generate without using biologically unrealistic species and interaction parameter values*. These problems should be sorted out in order to make progress in this direction.

2 References

Beddington, J.R. (1975). Mutual interference between parasites and predators and its effects on searching efficiency. *J. Anim. Ecol.*, **51**: 331-340.

Berlow, E.L. Neutel, A-M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M., Fox, J.W., Jansen, V.A.A., Jones, J.I., Kokkoris, G.D., Logofet, D.O., McKane, A.J., Montoya, J.M., and Petchey, O. (2004). Interaction strengths in food webs: issues and opportunities. *J. Anim. Ecol.*, **73**: 585-598.

Bersier, L.F., Dixon, P., and Sugihara, G. (1999). Scale-invariant or scale dependent behavior of the link density property in food webs: a matter of sampling effort? *Am. Nat.*, **153**: 676-682.

Brett, J. R., and Groves, T. D. D. (1979). Physiological energetics. In W. S. Hoar, D. J. Randall, and J. R. Brett, eds. *Fish physiology, Vol. 8. Bioenergetics and Growth*. Academic Press. New York.

Fisher, W., editor. (1978). *FAO Species Identification Sheets for Fishery Purposes. Western Cen-*

tral Atlantic (Fishing Area 31). Volume I-VII. Food and Agriculture Organization of the United Nations, Rome.

Martinez, N.D. (1991). Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecol. Monogr.*, **61**: 367-392.

McField, M. (1998). *The Influence of Disturbance and Management on Coral Reef Communities in Belize*. Ph.D. Thesis. University of Newcastle, U.K.

Opitz, S. (1996). *Trophic Interactions in Caribbean Coral Reefs* (ICLARM Technical Reports 43 Makati City, Philippines).

Paine, R.T. (1992). Food-web dynamics through field measurement of per capita interaction strength. *Nature* **355**: 73-75.

Pauly, D.A. (1986). A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments. *Fishery Bulletin*, **84**: 827-840.

Peters, R. H. (1983). *The Ecological Implications of Body Size*. Cambridge University Press, New York.

Randall, J. E. (1967). Food habits of reef fishes of the west Indies. *Studies in Tropical Oceanography*, **5**: 665-847.

Real, L.A. (1977). The kinetics of functional response. *Am. Nat.* **111**: 289-300.

Yodzis, P. and Innes, S. (1992). Body size and consumer-resource dynamics. *Am. Nat.* **139**: 1151-1175.

Wootton, J.T. (1997). Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. *Ecol. Monogr.* **67**: 45-64.

3.2 What is New?

Few works have attempted to study together the structural properties of a large quantitative food web, and its dynamical implications to conservation. This work tries to link these aspects. The main point of this work is not the well known frequency distribution of interaction strengths, but how these interaction strengths are combined to form the basic building blocks. Many weak and a few strong interactions are not telling us how are connected between species strong interactions (the case is similar to questions asked in chapter two: the degree distribution using qualitative matrices can be assortative and disortative, and only a more depth measure could uncover the structure of the matrix). Strongly interacting chains and chains with omnivore are not distributed randomly in the food web, which implies a different response to overfishing. This is the first time that such a description has been made for a real and large food web.

3.3 Current and Future Work

Natural extensions and complementary works are: (1) the improvement and comparison of the interaction strengths measures, (2) the understanding of the dynamics from a few number of species to more complex quantitative subwebs, and (3) the development of models and metrics including fluxes or interaction strength from basic metabolic principles. A great advance is now taking place in these three points. First, a recent synthetic work has detected gaps and problems with measures of interaction strength (Berlow et al. 2004), and new and more accurate descriptors (Peacor and Werner 2004) are now being introduced in the ecological literature.

Second, the devious strategies to get more stable complex food webs are starting to be discovered, although problems remain (Kondoh 2003a,b; Brose et al 2003). Third, both static and dynamic quantitative food web matrices are being better described (Ulanowicz and Wolff 1991; Cohen et al. 2003; Emmerson and Raffaelli 2004), and parallelly the field of complex networks is developing very fast new methods and metrics to detect properties in weighted networks (Dorogovtsev and Mendes 2004). Specifically, the introduction of new measures of quantitative matrices (Bersier et al. 2002; Zorach and Ulanowicz 2003), null models with metabolic considerations (Reuman and Cohen in press), and new ways to detect

empirically interaction strengths in large species communities (Emmerson and Raffaelli 2004) are starting to uncover the linking between empirical data, the quantitative structure and the dynamic stability of large food webs.

After uncover the cohesive pattern in qualitative food webs, a natural extension of that pattern in quantitative food webs is to ask how are species with strong interactions related among them?, i.e., is the modular view presented in this chapter capturing the structural properties of a real complex food web? In order to answer this question I present a preliminary analysis based on the same quantitative food web studied here (based on Melián and Cohen (in prep)). I will use the same definition of subweb as in the paper *Food web cohesion* presented in the chapter 2. But now considering only strong links defined as in the paper presented in this chapter ($IS_{ij} \geq 0.001$). The connectance of the quantitative densest subweb ($C_{qds w}$, where strong links $IS_{ij} \geq 0.001$), the average number of species of the $C_{qds w}$, and the body mass ratio within the densest subweb ($M_{r_{ij}} = M_j - M_i / M_j$, where M_i and M_j are the adult average body size of prey and predator respectively) were calculated for the empirical data.

Models to generate the position of links using the empirical distribution of body size and interaction strength were created. The connectance of the quantitative densest subweb ($C_{qds w}$), the average number of species of the $C_{qds w}$, and the body mass ratio within the densest subweb ($M_{r_{ij}}$) were investigated by two null models. The models were the Cascade model (Cohen et al. 1990), and an adaptation of the Niche model (Williams and Martinez 2000; Reuman and Cohen 2004).

The Cascade model, with the species index interpreted as a rank ordering of the empirical body mass, was used to model the selection of links from the set of pairs of species. When predator had a higher species index, that is, a higher body mass than the prey, one link is randomly and uniformly chosen from the empirical interaction strength distribution.

The second model is an adapted version of the Niche model by Williams and Martinez (2000). This model assigns a randomly drawn *niche value* to each species, similarly to the Cascade model. The adapted version used here re-normalized the log body masses of the empirical data to create the niche value (Reuman and Cohen 2004). That is, each species was chosen uniformly on the interval generated by the re-normalization. Species are then constrained

to consume all prey species within one range of values whose randomly chosen center is less than the consumer's niche value. Each link for each species within the range is randomly and uniformly chosen from the empirical interaction strength distribution. In the Niche model cannibalism and smaller species eating on bigger ones is allowed (this type of interactions represent approximately the 5% of links in the Caribbean Coral Reef). We excluded this links from all analysis involving body mass ratio. In the original Niche model, Williams and Martinez eliminated isolated species and replaced them until there were no isolated species. The adapted model removed simulated food webs that contained isolated species because the niche values were determined in advance by the Caribbean Coral Reef body mass distribution, which could not be changed (Reuman and Cohen 2004).

The models were tested against empirical data using each to generate 100 food webs, computing the Kolmogorov-Smirnov statistics of the body mass ratio distribution of each, and comparing the resulting distribution of 100 statistics to the Kolmogorov-Smirnov statistic of the Caribbean Coral Reef body mass ratio distribution. The statistic to test the C_{qds_w} , and the average number of species of the C_{qds_w} , (P) is the probability that a random replicate has a C_{qds_w} or a number of species value equal or higher than the observed value. Figure 1 represents the graph of the quantitative densest subweb of the Caribbean Coral Reef.

First, body mass ratio distribution from both Cascade and Niche model differ significantly from the Caribbean Coral Reef body mass ratio distribution ($P < 0.01$ in both cases). The average body mass ratio for real data is 0.97, and 0.65 and 0.58 after 100 replicates for the Cascade and Niche model respectively. Second, the value of C_{qds_w} is 0.18 for real data and the average value for the Cascade and Niche model is 0.08 and 0.10 respectively, differing significantly in both cases from the value of the real data ($P < 0.01$). Third, The number of species within the densest subweb is 76 for real data and the average value for Cascade and Niche model is 105 and 91 respectively (with $P < 0.01$ for the Cascade and $P < 0.05$ for the Niche model).

What type of preliminary conclusions could be obtained from these results? How introduce these results in the current framework of quantitative interactions? If we make a detailed scrutiny of species composition of the quantitative densest subweb in the

Caribbean Coral Reef we observe:

- (1) Most species under 100 g. form schooling (approximately 80% of species).
- (2) The average body size ratio is close to one in the real data (0.97), which suggest that the differences in adult body size between each pair of species tend to be maximized (there is a strong verticality as shown in Fig. 1).
- (3) Data from the Caribbean does not support correlation between body mass ratio and the strength of the interaction. Both weak and strong interactions occur between extremes body mass ratios. However, current results have shown that there is a strong positive correlation between the ratio of body mass (measured as (M_j/M_i)), and the strength of the interaction (Emmerson and Raffaelli 2004; Montoya et al. (in press)).

How could be related this mesoscopic structural pattern with the dynamics of a large complex food web? It could be interesting to speculate on this difference of the body mass ratio between strong interactors within the densest subweb. Species forming schools tend to be highly productive, in the sense that they have a high intrinsic growth rate (I have not check this for each specific species from literature). On the other hand, the 13 species in the top part of the subweb (species above 1000 g.) have a small intrinsic growth rate and form complex social groups. What could be the dynamics and the stability properties of this food web if we introduce this feature?

Literature Cited

- Bersier, L-F., Banasek-Richter, C., and Cattin, M. F. (2002). Quantitative descriptors of food web matrices. *Ecology*, **83**:2394-2407.
- Berlow, E. L., Neutel, A-M., Cohen, J. E., DeRuiter, P. C., et al. (2004). Interaction strengths in food webs: issues and opportunities. *J. Anim. Ecol.* **73**:585-598.
- Brose, U., Williams, R. J., and Martinez, N. D. (2003). Comment on *Foraging adaptation and the relationship between food web complexity and stability*. *Science*, **301**:918b.
- Cohen, J. E., Briand, F., and Newman, C. M. (1990). *Community food webs: data and theory*. Springer-Verlag, Berlin, Germany.
- Cohen, J. E., Jonsson, T., and Carpenter, S. R. (2003). Ecological community description using the food web, species abundances, and body size. *Proc.*

- Nat. Acad. Sci. (USA), **100**:1781-1786.
- Dorogovtsev, S. N., and Mendes, J. F. F. (2004). Minimal models of weighted scale-free networks. *cond-mat/0408343*.
- Emmerson, M. C., and Raffaelli, D. (2004). Predator-prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.*, **73**:399-409.
- Kondoh, M. (2003a). Foraging adaptation and the relationship between food web complexity and stability. *Science*, **299**:1388-1391.
- Kondoh, M. (2003b). Response to Comment on *Foraging adaptation and the relationship between food web complexity and stability*. *Science*, **301**:918c.
- Melián, C. J., and Cohen, J. E. Body mass ratio and the structure of interaction strength in a complex food web. (in prep).
- Montoya, J. M^a., Emmerson, M., Woodward, G. Body size, interaction strength and food web dynamics. In *Dynamics food webs: multispecies assemblages, ecosystem development and environmental change*. Eds, P. C. DeRuiter, V. Wolters, and J. C. Moore. Academic Press. (in press)
- Peacor, S. D., and Werner, E. E. (2004). How dependent are species-pair interaction strengths on other species in the food web? *Ecology*, **85**:2754-2763.
- Reuman, D. C., and Cohen, J. E. (2004). Trophic links' length and slope in the Tuesday Lake food web with species body mass and numerical abundance. *J. Anim. Ecol.* (in press).
- Reuman, D. C., and Cohen, J. E. Estimating relative energy fluxes using the food web, species abundance, and body size. *Adv. Ecol. Res.* (in press)
- Ulanowicz, R. E., and Wolff, W. F. (1991). Ecosystem flow networks: loaded dice?. *Math. Biosci.*, **103**:45-68.
- Williams, R. J., and Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, **404**:180-183.
- Zorach, A. C., and Ulanowicz, R. E. (2003). Quantifying the complexity of flow networks: how many roles are there? *Complexity*, **8**:68-76.

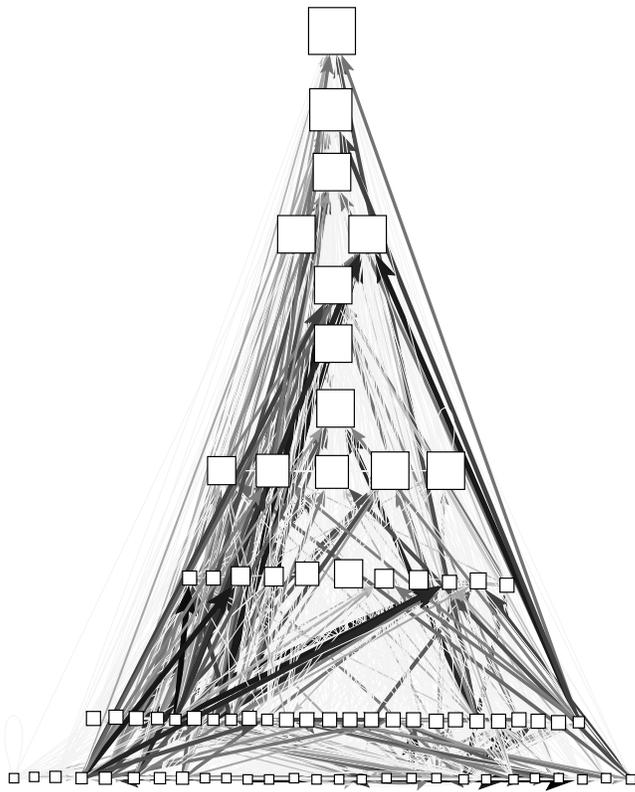


Figure 1: The empirical quantitative densest subweb of the Caribbean Coral Reef showing the strength of the interactions according with the level of grey in links (from white to black represent the magnitude of IS , from $IS_{ij}=0.001$ (white lines) to $IS_{ij}=5$ (black lines). The interaction strength is defined following the definition of the paper presented in this chapter. The size of the square shows the \log_{10} average adult body mass (kg).

Chapter 4

The Spatial Dimension of Food Webs

Up to now we have shown that, (1) complex food webs have a significative presence of subwebs, (2) these subwebs are arranged in a way that are neither randomly assembled nor compartmentalized but highly cohesive, and (3) strongly interacting chains and chains with omnivory are not distributed randomly in the Caribbean coral reef food web, which implies a different response to overfishing. However we have been working within a local community and with only one interaction type (i.e., antagonism). How we can introduce the spatial dimension of ecological networks? This chapter tries to integrate different types of subwebs in the spatial context. In the first paper we theoretically study the set of subwebs explored in chapter two in relation with habitat loss (*Food web structure and habitat loss*). In the second study we combine the synthesis of data between five different habitats of the Caribbean food web, introduce a null model to test the spatial structure of subwebs composition, and extend a metacommunity model by incorporating trophic modules (*Spatial structure and dynamics in a marine food web*).

4.1 Food Web Structure and Habitat Loss

REPORT

Food web structure and habitat loss

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Abstract

In this paper we explore simple food web models to study how metacommunity structure affects species response to habitat loss. We find that patch abundances and extinction thresholds vary according to the kind of food web. Second, for intermediate species, a slight decrease in the exploration cost of the better competitor has a strong effect on the extinction threshold of the poorer competitor. When predicting extinction risk one should consider not only the amount of habitat destroyed, but also the structure of the food web in which species are embedded. Both direct and indirect interactions are critical for predicting the consequences of habitat destruction.

Keywords

Metacommunity, habitat destruction, omnivory, apparent competition, intraguild predation, indirect interactions.

Ecology Letters (2002) 5: 37–46

INTRODUCTION

Ongoing habitat destruction is the primary cause of biodiversity loss (Pimm & Raven 2000). Little is still known about how biodiversity is reduced in complex ecological webs. The goal of this paper is to explore how metacommunity structure affects the response of food webs to habitat loss.

Previous theoretical studies of habitat loss have investigated single-species (Lande 1987; Bascompte & Solé 1996), two-species (Nee & May 1992; May 1994; Holt 1997; Nee *et al.* 1997; Bascompte & Solé 1998a,b; Namba *et al.* 1999; Swihart *et al.* 2001) and *n*-competing species models (Hastings 1980; Tilman 1994; Tilman *et al.* 1994; Kareiva & Wennergren 1995). These studies emphasize two important findings. First, the existence of a correlation between trophic rank and extinction threshold, whereby specialist predators are driven extinct before their prey (Kareiva 1987; Kruess & Tscharntke 1994; Bascompte & Solé 1998a; Gilbert *et al.* 1998; Holt *et al.* 1999; Steffan-Dewenter & Tscharntke 2000). This is in agreement with empirical observations in host-parasitoid (Kruess & Tscharntke 1994) and butterfly–plant communities (Steffan-Dewenter & Tscharntke 2000). Consequently, prey species outbreaks may be more common once their natural enemies have been driven extinct by destruction of habitat (Kruess & Tscharntke 1994). Second, habitat loss has a more severe effect on species that are better competitors but poorer dispersers (Hanski 1983; Nee & May 1992). Thus, the species most prone to extinction are the highly successful

competitor species which we might never guess are at risk (Tilman *et al.* 1994; Kareiva & Wennergren 1995).

Few studies have considered the effects of habitat loss in food webs with more than two trophic levels (but see Holt 1993 and Holt 1997 for a related study of metacommunity dynamics of food webs in heterogeneous landscapes). However, habitat destruction may yield qualitatively new consequences when considering species that are embedded in an intricate web of ecological relationships (Nee *et al.* 1997). A few empirical and experimental papers seem to confirm the context-dependence of the response of food webs to perturbations. Patterson (1984) pointed out that for small mammals in boreal forest fragments, the proportion of predators declined with habitat loss, but the proportion of insectivores remained constant and the proportion of herbivores increased. Similarly, Fox & Olsen (2000) studied the propagation of indirect effects through food webs having different degrees of complexity. They found that in reticular webs the top predator exhibited more sensitivity to perturbations on basal species than in simpler linear webs. This occurs because indirect effects (i.e. competition between both prey species; Wootton 1994) become increasingly important in complex, reticulate food webs (Fox & Olsen 2000).

Omnivory, defined broadly as feeding on more than one trophic level, occupies a prominent position in discussions about food web structure and dynamics. According to classical results from food web theory, omnivory destabilizes ecological communities (Pimm & Lawton 1978), whereas more recent conceptual syntheses

suggest that it should be a strongly stabilizing factor in food webs (Polis & Strong 1996; Fagan 1997; McCann & Hastings 1997; Holyoak & Sachdev 1998; McCann *et al.* 1998). This paper complements this perspective by investigating spatial persistence after human-induced habitat loss.

INTEGRATING METAPOPOPULATION MODELS

Through this paper we will integrate several basic models derived as extensions of the metapopulation model by Levins (1969). The Levins' model, which has become the centrepiece of the metapopulation paradigm in conservation biology (Hanski 1998), can be written as:

$$\frac{dR}{dt} = cR(1 - R) - eR, \quad (1)$$

where R is the proportion of patches occupied, c is the colonization rate, and e is the local extinction rate. The rate of newly colonized sites is given by the product of propagule production by the occupied sites, cR , and the proportion of sites that are not yet occupied, $1 - R$. Similarly, the rate at which occupied sites become vacant is given by the product of the extinction rate e , and the proportion of occupied sites R . This equation has a globally stable non-trivial equilibrium, given by $R^* = 1 - e/c$.

Building on the Levins' framework, Lande (1987) allowed only a fraction b of the habitat (i.e. territories) to be available. His results emphasize that we do not have to destroy all patches to extinguish a metapopulation that persists by virtue of a balance between local extinctions and recolonizations in a mosaic environment. Similarly, habitat destruction (Tilman 1994; Tilman *et al.* 1994; Kareiva & Wennergren 1995) has been represented as $d = 1 - b$ in a model derived from Eq. (1).

But how do interactions among species change patch abundances and extinction thresholds? Nee & May (1992) and Tilman *et al.* (1994) expanded the Levins' metapopulation model to two and n -competing species assuming a trade-off between competition and colonization (Tilman 1994; Tilman *et al.* 1994). Hence, Tilman (1994) considers two competing species whose interactions are structured to give a competitive hierarchy. This leads to the following equations:

$$\frac{dR_1}{dt} = c_1 R_1 (1 - R_1) - e_1 R_1, \quad (2)$$

$$\frac{dR_2}{dt} = c_2 R_2 (1 - R_1 - R_2) - e_2 R_2 - c_1 R_1 R_2 \quad (3)$$

The superior competitor, R_1 , is described by the same equation as would a species living by itself (identical to Levins' metapopulation model in Eq. (1)), and thus it is totally unaffected by the inferior competitor. The superior

competitor always displaces the inferior competitor when both species co-occur in a site, but the inferior competitor can neither invade nor displace the superior competitor from a site. The inferior competitor, R_2 , can colonize only sites in which both it and species R_1 are absent (the term $(1 - R_1 - R_2)$ in Eq. (3)). This represents interference or direct competition between both competitors. Furthermore, species R_1 can invade and displace species R_2 (the term $-c_1 R_1 R_2$ in Eq. (3)). A fraction d of patches destroyed can be incorporated as $(1 - R_1 - d)$ in Eq. (2) and $(1 - R_1 - R_2 - d)$ in Eq. (3). Tilman assumed a trade-off between colonization and competition and showed that habitat loss induces the selective extinction of the best competitors (Tilman *et al.* 1994). Habitat destruction lowers effective colonization rates of all species, but most has the greatest impact on species with lower colonization rates, the better competitors in Tilman's model.

The third model considered here is a specialist predator-prey metapopulation model (May 1994; Bascompte & Solé 1998a). The model can be expressed as follows:

$$\frac{dR}{dt} = c_1 R(1 - R) - e_1 R - \mu C, \quad (4)$$

$$\frac{dC}{dt} = e_2 C(R - C) - e_2 C \quad (5)$$

where R is the patch occupancy of a resource or prey, and C is the patch occupancy of a consumer or predator. This model assumes that predators need prey in order to survive in a patch, that is, C is a subset of R (this is the reason for the term $R - C$ in Eq. (5)). This model further incorporates the effect of varying levels of predator control on prey populations via the parameter μ . In this model, specialist predators are driven extinct by habitat loss before their prey (Bascompte & Solé 1998a).

Finally, we introduce Swihart *et al.*'s (2001) model (an expansion of Bascompte & Solé's 1998a model) constructed to understand the effect of habitat destruction on a generalist predator. The novelty is that the predator colonization of a patch occurs independently of patch occupation by the preferred prey. Therefore, in patches without prey, predators pay an added cost (ψ) in terms of an increase in the rate of local extinction for mistakenly colonizing an inferior resource patch. The model is written as:

$$\frac{dR}{dt} = c_1 R(1 - R) - e_1 R - \mu RC, \quad (6)$$

$$\frac{dC}{dt} = e_2 C(1 - C) - e_2 C - \psi C(1 - R) \quad (7)$$

In contrast to specialist predators, Swihart *et al.* (2001) found that habitat destruction is not as detrimental for generalist predators. Thus, habitat loss does not necessarily reduce the length of food chains as showed for specialist predators (Bascompte & Solé 1998a).

suggest that it should be a strongly stabilizing factor in food webs (Polis & Strong 1996; Fagan 1997; McCann & Hastings 1997; Holyoak & Sachdev 1998; McCann *et al.* 1998). This paper complements this perspective by investigating spatial persistence after human-induced habitat loss.

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In contrast to specialist predators, Swihart *et al.* (2001) found that habitat destruction is not as detrimental for generalist predators. Thus, habitat loss does not necessarily reduce the length of food chains as showed for specialist predators (Bascompte & Solé 1998a).

In summary, much of the theory about how habitat loss affects the dynamics of multi-species interactions deals only with simple two-species interactions or n competing species. The question that we address in the remainder of this paper is “how do these results change when we consider increasing food web complexity and indirect effects?”

METACOMMUNITY MODELS

Over the past decade, the view that food webs are highly interconnected assemblages characterized by recurrent structures has overcome the former concept of ecosystems as linear food chains. Because combinations of competition and predation can represent these common food web structures, the use of simple food web modules has been advocated to explore the repercussions of these ubiquitous interactions (McCann 2000, and references therein). We synthesize trophic and competitive interactions using models assuming that all the species have a similar population structure and habitat requirements; they are influenced by habitat loss in exactly the same way. We consider four types of food web illustrated in Fig. 1: a simple food chain, an omnivorous food web (e.g. Fagan 1997), a food web with apparent competition (e.g. Holt & Lawton 1994; Bonsall & Hassell 1997), and finally a food web with intraguild predation (e.g. Polis & Holt 1992). The model for the simple food chain (Fig. 1) can be described as:

$$\frac{dR}{dt} = c_1R(1 - R - d) - e_1R - \mu_1RC, \quad (8)$$

$$\frac{dC}{dt} = e_2C(1 - C - d) - e_2C - \psi_1C(1 - R) - \mu_2CP, \quad (9)$$

$$\frac{dP}{dt} = e_3P(1 - P - d) - e_3P - \psi_2P(1 - C). \quad (10)$$

Here R is the basal species patch density, C is the patch density of the intermediate species, and P is the patch

density of the top species. d is the fraction of sites destroyed. c_i and e_i represent colonization and extinction rates of species i . As noted above, we assume that colonization of a patch by the predator occurs independently of patch occupancy by its main prey. Therefore, in patches without prey, intermediate and top species pay an added cost (ψ_1 and ψ_2 in Eqs (9) and (10)) in terms of an increase in the rate of local extinction for mistakenly colonizing an inferior resource patch. That is, extreme specialist predators go immediately extinct in patches without their prey. When C and P are extreme generalists, ψ_1 and ψ_2 are equal to 0 (Swihart *et al.* 2001). Finally, μ_i represents the increase in mortality due to predation. Our model extends the basic ignorant predator model by Swihart *et al.* (2001) by adding an additional trophic level, with new direct and indirect interactions.

In the omnivorous food web (Fig. 1), vertical complexity is now increased relative to the simple food chain, via feeding links between the top species and the two lower trophic levels. The model can be written as:

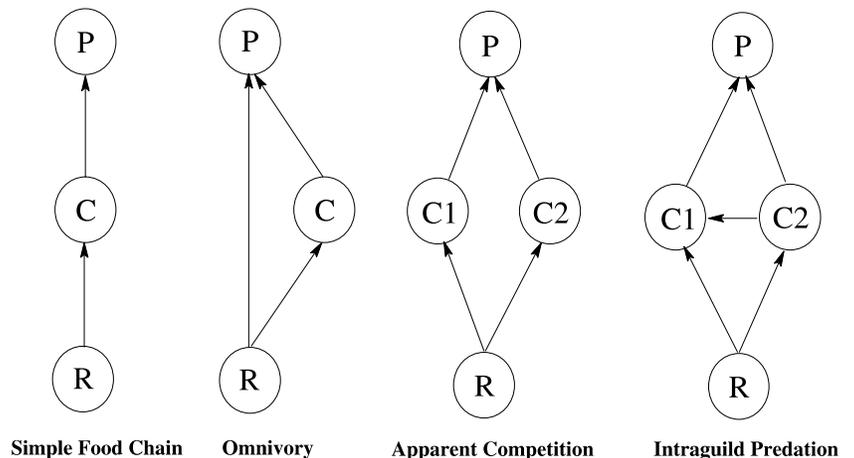
$$\frac{dR}{dt} = c_1R(1 - R - d) - e_1R - \mu_1RC - \mu_2RP, \quad (11)$$

$$\frac{dC}{dt} = e_2C(1 - C - d) - e_2C - \psi_1C(1 - R) - \mu_3CP, \quad (12)$$

$$\frac{dP}{dt} = e_3P(1 - P - d) - e_3P - \frac{\psi_2}{2}P(1 - R) - \frac{\psi_3}{2}P(1 - C), \quad (13)$$

where all parameters are defined as above (Eqs (8)–(10)). We consider omnivory in a restrictive sense, that is, top species’ persistence is maximum when both prey species are present in the same patch. We assume that an omnivorous top species needs species from two trophic levels in each patch to minimize the foraging cost (Ball 1994; Sih

Figure 1 The four types of food-web studied are, from left to right, a simple food chain, a food web including omnivory, a food web with the top species feeding on two intermediate consumers (apparent competition), and a food web with consumer 1, C_1 , feeding on the basal species and on the second consumer C_2 (intraguild predation). R denotes the basal species; C_1 and C_2 denote intermediate species; P denotes the top species. Note that in this paper we introduce a spatial component, and the food web may be incomplete in some patches.



& Christensen 2001). Thus, if ψ_2 is the cost for a top predator in a simple food web, then the cost associated in the omnivorous food web when one of the prey species is absent would be $\psi_2/2$ or $\psi_3/2$ (Eq. (13)). As a result, when omnivorous top species colonize a new patch and none of the prey species are present, the total cost, ψ_t , is:

$$\psi_t = \frac{\psi_2}{2} + \frac{\psi_3}{2}, \quad (14)$$

and the extinction rate in such an empty patch is $e_3 + \psi_2/2 + \psi_3/2$. In a similar way, when only one of the two prey species (i.e. basal or intermediate) is absent in a patch, the extinction rate is $e_3 + \psi_i/2$.

The extinction term for the top species when there is apparent competition (Fig. 1) or intraguild predation (Fig. 1) is defined similarly to that for the omnivorous top species. We assume that the top species needs the two prey species in each patch to minimize the foraging cost. In both cases, the top species feeds on two intermediate species, C_1 and C_2 . Thus, species C_1 and C_2 are engaged in apparent competition by sharing the same predator (see Fig. 1). They are also engaged in indirect competition because they share the same resource (the basal species). We assume a trade-off between competition and colonization: C_1 is a better competitor but C_2 is a better disperser. The asymmetry in colonization rates allows the coexistence of C_1 and C_2 . C_2 can not occupy patches already occupied by C_1 (this is described by the term $1 - C_1 - C_2 - d$ in Eqs (17) and (21)), and C_1 can occupy either empty patches or patches occupied by C_2 . Here, we do not assume that C_1 displaces species C_2 from patches occupied by both C_1 and C_2 as assumed by Tilman (1994). These are a less severe assumptions than that made for a purely competitive system (e.g. Tilman 1994; see Eq. (3)), and represents a less intensive competition between C_1 and C_2 . This can be translated into the following model (Fig. 1):

$$\frac{dR}{dt} = c_1R(1 - R - d) - e_1R - \mu_1RC_1 - \mu_2RC_2, \quad (15)$$

$$\frac{dC_1}{dt} = e_2C_1(1 - C_1 - d) - e_2C_1 - \psi_1C_1(1 - R) - \mu_3C_1P, \quad (16)$$

$$\frac{dC_2}{dt} = e_3C_2(1 - C_1 - C_2 - d) - e_3C_2 - \psi_2C_2(1 - R) - \mu_4C_2P, \quad (17)$$

$$\frac{dP}{dt} = c_4P(1 - P - d) - e_4P - \frac{\psi_3}{2}P(1 - C_1) - \frac{\psi_4}{2}P(1 - C_2). \quad (18)$$

Finally, when allowing C_1 to also feed on C_2 (with a similar extinction term as for the top species), we can write the following model for the food web with intraguild predation (Fig. 1):

$$\frac{dR}{dt} = c_1R(1 - R - d) - e_1R - \mu_1RC_1 - \mu_2RC_2, \quad (19)$$

$$\frac{dC_1}{dt} = e_2C_1(1 - C_1 - d) - e_2C_1 - \frac{\psi_1}{2}C_1(1 - R) - \frac{\psi_2}{2}C_1(1 - C_2) - \mu_3C_1P, \quad (20)$$

$$\frac{dC_2}{dt} = e_3C_2(1 - C_1 - C_2 - d) - e_3C_2 - \psi_3C_2(1 - R) - \mu_4C_2P - \mu_5C_2C_1, \quad (21)$$

$$\frac{dP}{dt} = c_4P(1 - P - d) - e_4P - \frac{\psi_4}{2}P(1 - C_1) - \frac{\psi_5}{2}P(1 - C_2). \quad (22)$$

We will focus on the extinction thresholds, that is, the critical values of habitat destruction, d_c , at which a given species goes extinct. The inverse of such an extinction threshold could be considered as a measure of vulnerability to extinction due to habitat loss. In addition to the extinction threshold, the dependence of patch occupancy on habitat destruction is also important to understand the effects of habitat loss on metacommunity persistence, and we will also consider this as a benchmark for comparison. As we will show, both extinction thresholds and the decline of patch occupancy can be difficult to predict when indirect interactions are at work.

RESULTS

Our goal is to consider how food web structure alters the top species' (P) response to habitat loss for two different ecological scenarios, namely donor control and top-down control. To explore this question we analyse the metacommunity models developed in the previous section. Through this paper we explore a broad range of biologically realistic parameter combinations. The results presented here are qualitatively robust for all parameter combinations examined. Specifically, we have used numerical methods to derive the non-trivial solutions for symmetrical parameter combinations, that is, all species have the same parameter values, ranging from donor control $\mu_i = 0$ to top-down control $\mu_i = 0.7$; colonization/extinction from $c_i = 0.4$, $e_i = 0.1$ to $c_i = 0.7$, $e_i = 0.3$; and exploration cost from $\psi_i = 0.3$ to $\psi_i = 0.7$. This range of parameter combinations meets our criteria of (i) biological realism, and (ii) existence of stable non-trivial solutions.

To begin with, let us start with a donor control scenario (i.e. prey dynamics constrain the distribution of the predator, without reciprocal effects by the predator on its prey, $\mu_i = 0$). We consider intermediate (C_1 and C_2) and top (P) species as specialists, but not extreme specialists, that is, they have a high degree of selective searching behaviour.

They have an increased rate of local extinction for mistakenly colonizing an inferior resource patch ($\psi_i > 0$). We start with symmetric demographic rates, in which basal, intermediate and top species have the same colonization/extinction rates. Note that the top species' persistence is maximum when both prey species are present in the same patch. We also explored a less restrictive assumption and qualitative results remained.

For the above parameter values, a positive numerical equilibrium exists. We plot this equilibrium patch occupancy as a function of habitat destruction in Fig. 2(a). We find that:

1 The extinction threshold for the top species in an omnivorous web occurs at a higher level of habitat destruction ($d_c = 0.32$) than for webs with apparent competition ($d_c = 0.26$) and simple linear chains ($d_c = 0.26$). The top species goes extinct sooner in webs with intraguild predation ($d_c = 0.19$).

2 The top species decreases linearly but with different slopes for each type of food web. The steepest decline is for the simple and apparent competition food web, followed by the omnivory food web. The decline is less steep for intraguild predation.

Let us now consider an example of top-down control. We find that the pattern is qualitatively similar to donor control.

All else being equal, patch abundances are lower for top-down control, and the top species' extinction threshold occurs at a lower fraction of sites destroyed (compare Figs 2a and b).

Until now, we have only considered the response of the top species. What happens with the rest of the community? We plot the decline in the number of species for each food web as more habitat is destroyed in Fig. 3. Each step corresponds to the extinction of one of the species. The first species going extinct is the top species (P), and the last is the basal species (R). We find that the basal species has a similar response in each configuration (that is, its extinction threshold is the same for each configuration). This is not a surprise because after the rest of species have gone extinct, we have the same single Levins' species model. For the intermediate species (C_1 and C_2), the extinction threshold is the same for both the simple (Fig. 3a) and the omnivorous (Fig. 3b) food web. On the other hand, the extinction thresholds for the intermediate species depend on whether they are embedded in the web with apparent competition or intraguild predation. With apparent competition, C_1 and C_2 have similar extinction thresholds (Fig. 3c), whereas C_1 goes extinct before C_2 for intraguild predation (Fig. 3d). Top-down control exacerbates these differences. In general, all species go extinct sooner when control is top-down as opposed to donor (see Fig. 3).

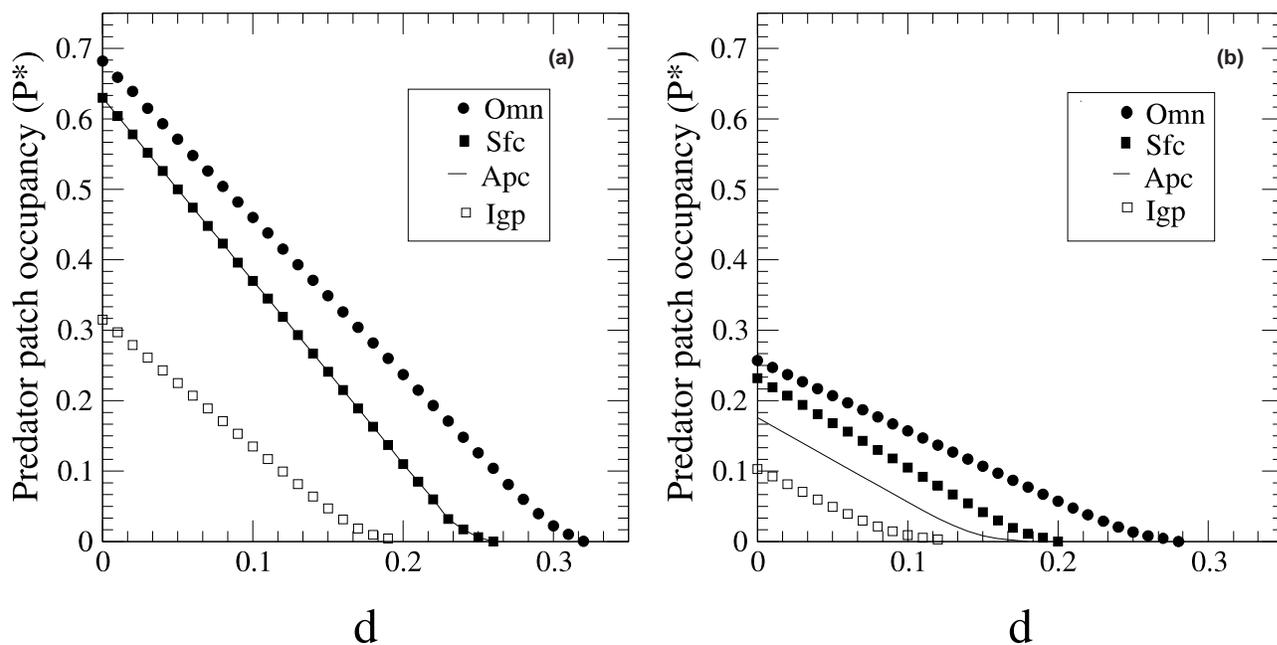


Figure 2 The patch occupancy of the top species (P) is plotted as a function of the fraction of habitat destroyed (d). As we explicitly point out in the figure, the different lines represent an omnivorous food web (●), a simple food chain (■), a food web with apparent competition (—), and a food web with intraguild predation (□). (a) represents donor control ($\mu_i = 0$), and (b) represents top-down control ($\mu_i = 0.7$). A high exploration cost or selective searching behaviour ($\psi_i = 0.6$) is assumed. Other parameters are: $c_i = 0.7$ and $e_i = 0.1$.

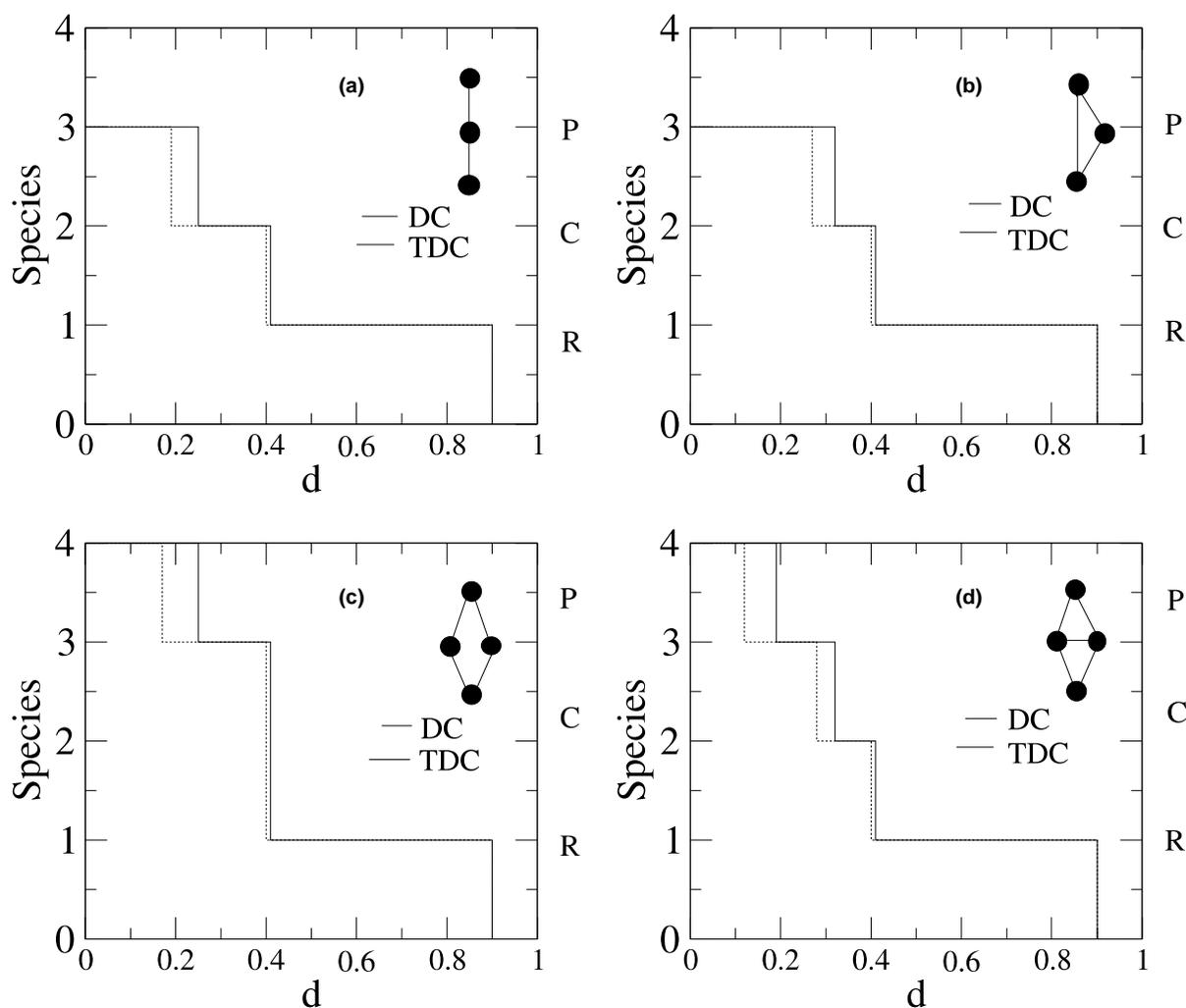


Figure 3 The fraction of extant species relative to the initial number of species is plotted as a function of the fraction of habitat destroyed. Continuous line represents donor control ($\mu_i = 0$), and dotted line represents top-down control ($\mu_i = 0.7$). The simple food chain (a) and the omnivorous web (b) have three species, whereas the food web with apparent competition (c) and intraguild predation (d), have four species. This explains the difference in the y -axis scale. Parameter values are similar to those in Fig. 2(a) (for donor control) and 2(b) (for top-down control). Each step represents the extinction of one species. From left to right, the order of extinction is for the top species (P), the intermediate species (C) and the basal species (R).

Finally, we may ask how indirect effects and non-linearities in the interactions affect the predictability of metapopulation responses to habitat loss. We explore this response in (i) an intraguild predation web, and (ii) an apparent competition web where intermediate species (C_1 and C_2) engage in direct competition. We study asymmetric demographic and exploration cost rates. Again, we have studied a broad range of biologically realistic parameter values corresponding to stable non-trivial solutions. Specifically, the range of parameter values explored here is as follows: $\mu_i = 0$ (donor control) to $\mu_i = 0.7$ (top-down control); $c_i = 0.4$, $e_i = 0.1$ to $c_i = 0.7$, $e_i = 0.3$; $c_2 = 0.3$ to $c_2 = 0.5$; $\psi_i = 0.4$ to $\psi_i = 0.7$ with ψ_1 (i.e. the exploration cost of the better competitor) from

$\psi_1 = 0$ to $\psi_1 = 1$. Our results are robust for this entire suite of asymmetric parameter combinations.

For the case of apparent competition, we observe in Fig. 4(a) that the better competitor (C_1 , dotted line) has a higher patch occupancy and a lower extinction threshold than the better colonizer, poorer competitor (C_2 , continuous line). We observe in Fig. 4(b) that a small reduction in the exploration cost of the better competitor C_1 (from $\psi_1 = 0.3$ to $\psi_1 = 0.1$) has a non-linear indirect effect on the extinction threshold of the less abundant, poorer competitor species (C_2).

Figure 5(a) shows the extinction threshold of both the better (C_1) and poorer (C_2) competitors for different values

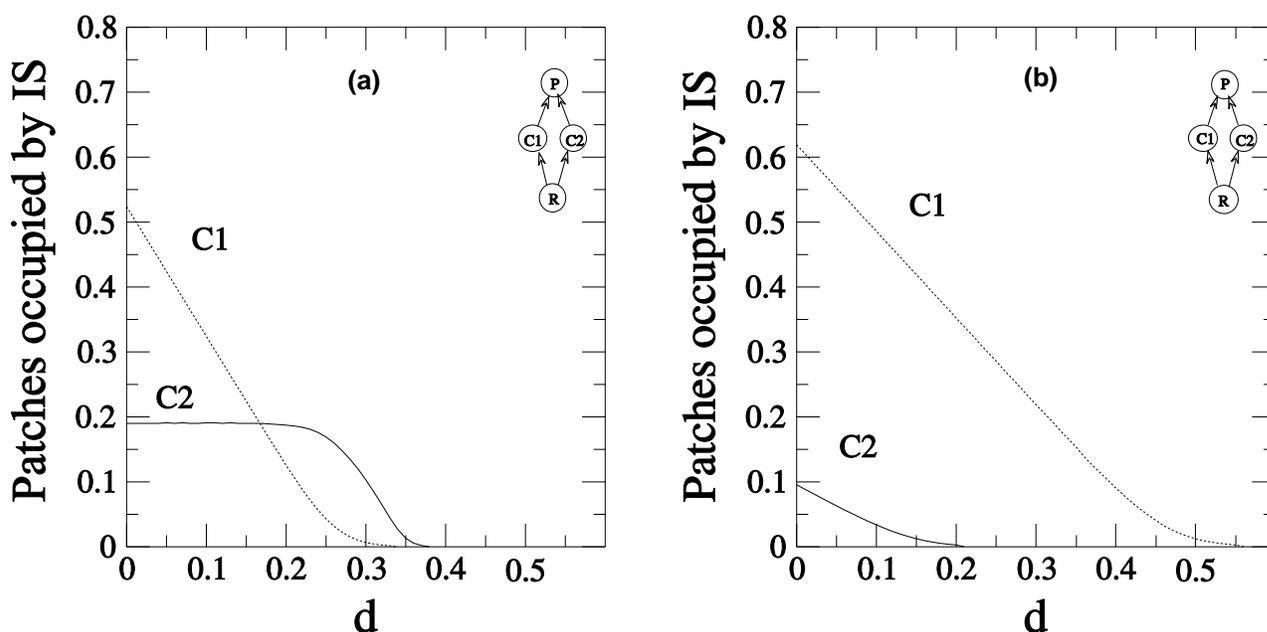


Figure 4 The patch occupancy of the two competing species (C_1 and C_2) in the food web with apparent competition are plotted as a function of the fraction of habitat destroyed (d). Continuous and discontinuous lines represent intermediate species (IS), that is, the poorer (C_2) and the better competitor (C_1), respectively. The colonization rate of the better competitor is $c_2 = 0.3$ in both cases. The other parameter values are $\mu_i = 0$, $e_i = 0.1$, $c_i = 0.7$ and $\psi_i = 0.7$. As noted, a slight decrease in the exploration cost of C_1 implies a big change in the extinction threshold for both competing species.

of the exploration cost for the better competitor. Figure 5(b) shows how the extinction threshold for the poorer competitor depends on the colonization rates of the better competitor. Evolutionary changes in the demographic parameters of one species can cascade through the food web with unanticipated consequences for the other species.

SUMMARY AND DISCUSSION

The following remarks emphasize some of our conclusions:

- 1 Food web structure alters the top species response to habitat loss.
- 2 Direct and indirect interactions between two intermediate prey decrease the patch occupancy of top predators.
- 3 Omnivory confers higher persistence for the top species for a specific value of habitat loss.
- 4 The extinction threshold of the top species is lower for top-down control than for donor control, but the difference attenuates with decreasing trophic level.
- 5 Although the top species' regional abundance is lower for top-down control, its rate of decrease as habitat is destroyed is also lower. That is, all else being equal, donor control would lead to situations with high abundance but low resistance to habitat destruction, whereas the opposite would happen for top-down control.

6 In apparent competition and intraguild predation with direct and indirect competition between intermediate species, a slight decrease in the exploration cost of the better competitor (C_1) results in a strong effect on the extinction threshold of the poorer competitor (C_2).

The present results confirm the finding that predators with high selective searching behaviour are driven extinct for lower destruction values than their prey; however, many natural communities are dominated by non-specialized consumers (Polis & Strong 1996). In the latter scenario, habitat destruction will favour generalist predators with low exploration cost (Mikkelsen 1993; Swihart *et al.* 2001). In both cases, patch abundance and extinction thresholds depend on the food web structure in which the top species are embedded.

Trophic generalization can lead to a wide range of indirect interactions in food webs such as exploitative competition, apparent competition and intraguild predation (Holt *et al.* 1999). Additionally, there is a surprising number of cases in which the removal of a predator leads to a decrease in the abundance of the focal prey (Sih *et al.* 1985). Many of these cases seem to involve indirect interactions in multispecies assemblages (e.g. competitive interactions among prey held in check by a generalist predator, Holt 1997). In this paper we have first explored the relative effect

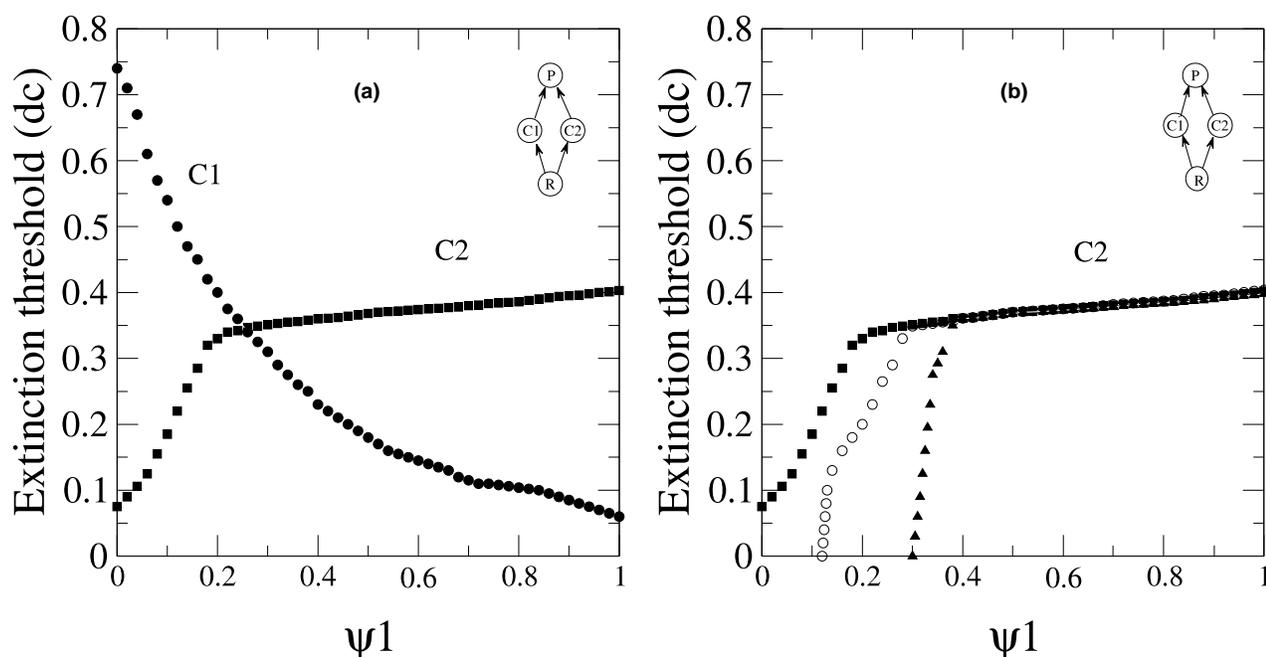


Figure 5 (a) The extinction thresholds for both competitors (C_1 and C_2) in the food web with apparent competition are plotted as a function of the exploration cost of the better competitor (ψ_1). ● corresponds to C_1 and ■ corresponds to C_2 . Parameter values are as in Fig. 4. (b) Represents the extinction thresholds for C_2 as a function of the exploration cost of the better competitor for three colonization rates of the better competitor (C_1). Colonization rates of C_1 are plotted as $\eta_2 = 0.3$ (■), $\eta_2 = 0.4$ (○) and $\eta_2 = 0.5$ (▲). Other parameter values are as in Fig. 4. As noted, there is a strong interaction between the exploration cost of the better competitor and the extinction threshold of the poorer competitor. Similar results remain for intraguild predation and top down-control for all the range of parameter values explored.

of direct and indirect interactions (Stone & Roberts 1991) in the context of habitat loss.

We have shown that indirect interactions from apparent competition and intraguild predation depress the extinction threshold for the top species. That is, direct and indirect interactions reduce the fraction of habitat destroyed at which the top species is driven extinct. This has been demonstrated empirically by Fox & Olsen (2000). By using microcosms, these authors showed that perturbations had a larger impact on predators embedded in reticulated food webs.

Our results add a complementary perspective to the empirical evidence pointing towards higher stability for multichannel omnivory food webs (Polis & Strong 1996; Fagan 1997; Holyoak & Sachdev 1998; McCann *et al.* 1998). In this paper, we provide evidence showing how top species may persist at higher values of habitat destruction when embedded in a food web with high levels of omnivory.

Fagan (1997) observed that the return to equilibrium after a range of disturbances in a multipatch scale was faster in omnivorous structures, although there is still a lack of theoretical interpretation (Fagan 1997). The present paper represents a first step in this direction. Note that we use stability in the sense of spatial persistence in response to

habitat loss, rather than return to the equilibrium after a local perturbation such as a reduction in abundance (Pimm & Lawton 1978; Fagan 1997).

The extinction threshold is lower for the better competitor (C_1) than for the poorer competitor (C_2) for a broad range of parameter values. This result is in agreement with previous results from single trophic-level models (Tilman 1994; Tilman *et al.* 1994, 1997), according to which the initially most abundant species in undisturbed habitat fragments can be the most susceptible to eventual extinction. However, as shown in this paper, the order of extinction can change dramatically depending on the exploration cost of the best competitor.

Species are typically enmeshed in an entangled web of direct and indirect interactions. Our results suggest that the response of the metacommunity to disturbances can be a complex interaction of different trends. These results call for extreme caution when the goal is the management of endangered species in fragmented habitats. Also, minor changes in the exploration cost of better competitors can have a large influence on the regional abundance of poorer competitors. This emphasizes how evolutionary changes at the level of generalization of one species may cascade through the rest of the community (Schmitz 1998).

In summary, patch abundances and extinction thresholds are not only determined by demographic rates (Levins 1969), behavioural and life history traits (Lande 1987), competitive-colonization abilities (Tilman 1994) and landscape properties (Bascompte & Solé 1996), but also by the structure of the food web in which the species are embedded.

ACKNOWLEDGEMENTS

We thank Bill Fagan, Shane Richards, John Sabo and Pedro Jordano for useful comments on a previous draft. Funding was provided by a Grant from the Spanish Ministry of Science and Technology (BOS2000-1366-C02-02) and a Ph.D. fellowship to C.J.M. (FP2000-6137).

REFERENCES

- Ball, J.P. (1994). Prey choice of omnivorous canvasbacks: imperfectly optimal ducks? *Oikos*, 70, 233–244.
- Bascompte, J. & Solé, R.V. (1996). Habitat fragmentation and extinction thresholds in spatially explicit models. *J. Anim. Ecol.*, 65, 465–473.
- Bascompte, J. & Solé, R.V. (1998a). Effects of habitat destruction in a prey-predator metapopulation model. *J. Theoret. Biol.*, 195, 383–393.
- Bascompte, J. & Solé, R.V. (1998b). Models of habitat fragmentation. In: *Modeling Spatiotemporal Dynamics in Ecology* (eds Bascompte, J. & Solé, R.V.). Springer-Verlag, Berlin, pp. 127–149.
- Bonsall, M.B. & Hassell, M.P. (1997). Apparent competition structures ecological assemblages. *Nature*, 388, 371–373.
- Fagan, W. (1997). Omnivory as a stabilizing feature of natural communities. *Am. Naturalist*, 150, 554–567.
- Fox, J.W. & Olsen, E. (2000). Food web structure and the strength of transient indirect effects. *Oikos*, 90, 219–226.
- Gilbert, F.A., Gonzalez, A. & Evans-Freke, I. (1998). Corridors maintain species richness in the fragmented landscapes of a microecosystem. *Proc. Roy. Soc. Lond. B*, 265, 577–582.
- Hanski, I. (1983). Coexistence of competitors in a patchy environment. *Ecology*, 64, 493–500.
- Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396, 41–49.
- Hastings, A. (1980). Disturbance, coexistence, history and the competition for space. *Theoret. Population Biol.*, 18, 363–373.
- Holt, R.D. (1993). Ecology at the mesoscale: The influence of regional processes on local communities. In: *Species Diversity in Ecological Communities* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, pp. 77–88.
- Holt, R.D. (1997). From metapopulation dynamics to community structure. In: *Metapopulation Biology. Ecology, Genetics and Evolution* (eds Hanski, I. & Gilpin, M.). Academic Press, San Diego, pp. 149–164.
- Holt, R.D. & Lawton, J.H. (1994). The ecological consequences of shared natural enemies. *Annu. Rev. Ecol. Syst.*, 25, 495–520.
- Holt, R.D., Lawton, J.H., Polis, G.A. & Martinez, N.D. (1999). Trophic rank and the species-area relationship. *Ecology*, 80, 1495–1504.
- Holyoak, M. & Sachdev, S. (1998). Omnivory and the stability of simple food webs. *Oecologia*, 117, 413–419.
- Kareiva, P. (1987). Habitat fragmentation and the stability of predator-prey interactions. *Nature*, 326, 388–390.
- Kareiva, P. & Wennergren, U. (1995). Connecting landscape patterns to ecosystem and population processes. *Nature*, 373, 299–302.
- Kruess, A. & Tscharntke, T. (1994). Habitat fragmentation, species loss, and biological control. *Science*, 264, 1581–1584.
- Lande, R. (1987). Extinction thresholds in demographic models of territorial populations. *Am. Naturalist*, 130, 624–635.
- Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.*, 15, 237–240.
- May, R.M. (1994). The effect of spatial scale on ecological questions and answers. In: *Large-Scale Ecology and Conservation Biology* (eds Edwards, P.J., May, R.M. & Webb, N.R.). Blackwell Scientific Publications, Oxford, pp. 1–17.
- McCann, K. (2000). The diversity-stability debate. *Nature*, 405, 228–233.
- McCann, K. & Hastings, A. (1997). Re-evaluating the omnivory-stability relationship in food webs. *Proc. Roy. Soc. Lond. B*, 264, 1249–1254.
- McCann, K., Hastings, A. & Huxel, G.R. (1998). Weak trophic interactions and the balance of nature. *Nature*, 395, 794–798.
- Mikkelsen, G.M. (1993). How do food webs fall apart? A study of changes in trophic structures during relaxation on habitat fragments. *Oikos*, 67, 539–547.
- Namba, T., Umemoto, A. & Minami, E. (1999). The effects of habitat fragmentation on persistence of source-sink metapopulations in systems with predator and prey or apparent competitors. *Theoret. Population Biol.*, 56, 123–137.
- Nee, S. & May, R.M. (1992). Dynamics of metapopulation: habitat destruction and competitive coexistence. *J. Anim. Ecol.*, 61, 37–40.
- Nee, S., May, R.M. & Hassell, M.P. (1997). Two species metapopulation models. In: *Metapopulation Biology. Ecology, Genetics and Evolution* (eds Hanski, I. & Gilpin, M.). Academic Press, San Diego, pp. 123–147.
- Patterson, B.D. (1984). Mammalian extinction and biogeography in the Southern Rocky Mountains. In: *Extinctions* (ed. Nitecki, M.). University of Chicago Press, Chicago, pp. 247–293.
- Pimm, S.L. & Lawton, J.H. (1978). On feeding on more than one trophic level. *Nature*, 275, 542–544.
- Pimm, S.L. & Raven, P. (2000). Extinction by numbers. *Nature*, 403, 843–845.
- Polis, G.A. & Holt, R.D. (1992). Intraguild predation: the dynamics of complex trophic interactions. *Trends Ecol. Evol.*, 7, 151–154.
- Polis, G.A. & Strong, D.R. (1996). Food web complexity and community dynamics. *Am. Naturalist*, 147, 813–846.
- Schmitz, O.J. (1998). Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am. Naturalist*, 151, 327–342.
- Sih, A. & Christensen, B. (2001). Optimal diet theory: when does it work, and when and why does it fail? *Anim. Behav.*, 61, 379–390.
- Sih, A., Crowley, P., McPeck, M., Petranka, J. & Strohmeier, K. (1985). Predation, competition, and prey communities: a review of field experiments. *Annu. Rev. Ecol. Syst.*, 16, 269–312.
- Steffan-Dewenter, I. & Tscharntke, T. (2000). Butterfly community structure in fragmented habitats. *Ecol. Lett.*, 3, 449–456.
- Stone, L. & Roberts, A. (1991). Conditions for a species to gain advantage from the presence of competitors. *Ecology*, 72, 1964–1972.

- Swihart, R., Feng, Z., Slade, N.A., Mason, D.M. & Gehring, T.M. (2001). Effects of habitat destruction and resource supplementation in a predator-prey metapopulation model. *J. Theoret. Biol.*, 210, 287–303.
- Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2–16.
- Tilman, D., Lehman, C.L. & Yin, C. (1997). Habitat destruction, dispersal, and deterministic extinction in competitive communities. *Am. Naturalist*, 149, 407–435.
- Tilman, D., May, R., Lehman, C.L. & Nowak, M.A. (1994). Habitat destruction and the extinction debt. *Nature*, 371, 65–66.
- Wootton, J.T. (1994). The nature and consequences of indirect effects in ecological communities. *Annu. Rev. Ecol. Syst.*, 25, 443–466.

Editor, M. Hochberg

Manuscript received 4 May 2001

First decision made 15 June 2001

Second decision made 30 August 2001

Manuscript accepted 13 September 2001

4.2 Spatial Structure and Dynamics in a Marine Food Web

Spatial structure and dynamics in a marine food web

Carlos J. Melián, Jordi Bascompte, and Pedro Jordano

Introduction

The role of space in population and community dynamics has been recently emphasized (e.g. Hanski and Gilpin 1997; Tilman and Kareiva 1997; Bascompte and Solé 1998). Several models for the coexistence of interacting species in heterogeneous environments have been formulated. These include the energy and material transfer across ecosystem boundaries and its implication for succession and diversity (Margalef 1963; Polis et al. 1997), the geographic mosaic of coevolution (Thompson 1994), the regional coexistence of competitors via a competition–colonization trade-off (Tilman 1994), the random assembly of communities via recruitment limitation (Hubbell 2001), and metacommunities (Wilson 1992). As a general conclusion of these approaches, succession, dispersal, local interactions, and spatial heterogeneity have appeared strongly linked to the persistence of diversity. However, the underlying pattern of ecological interactions in a spatially structured ecosystem and its implications for the persistence of biodiversity remains elusive by the lack of synthetic data (Loreau et al. 2003).

Introducing space and multiple species in a single framework is a complicated task. As Caswell and Cohen (1993) argued, it is difficult to analyze patch-occupancy models with a large number of species because the number of possible patch states increases exponentially with species richness. Therefore, most spatial studies have dealt with a few number of species (Hanski 1983), predator–prey systems (Kareiva 1987), or n -competing species (Caswell and Cohen 1993; Tilman 1994; Mouquet and Loreau 2003). On the other hand, the bulk of

studies in food-web structure and dynamics have dealt with either large (but see Hori and Noda 2001) or small (but see Caldarelli et al. 1998) number of species, but make no explicit reference to space (Caswell and Cohen 1993; Holt 1996, 1997). Only a few studies have explored the role of space on a small subset of trophic interacting species (Holt 1997; Melián and Bascompte 2002).

The present study is an attempt to link structure and dynamics in a spatially structured large marine food web. We use data on the diet of 5526 specimens belonging to 208 fish species (Randall 1967) in a Caribbean community in five different habitats (Opitz 1996; Bascompte et al., submitted). First, we analyze structure by addressing how simple trophic modules (i.e. tri-trophic food chains (FCs) and chains with omnivory (OMN) with the same set of species are shared among the five habitats. Second, we extend a previous metacommunity model (Mouquet and Loreau 2002) by incorporating the dynamics of trophic modules in a set of connected communities. Specifically, the following questions are addressed:

1. How are simple trophic modules composed by the same set of species represented among habitats?
2. How does the interplay between dispersal and food-web structure affect species dynamics at both local and regional scales?

Data collection: peculiarities and limitations

The Caribbean fish community here studied covers the geographic area of Puerto Rico–Virgin Islands.

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Data were obtained in an area over more than 1000 km² covering the US Virgin Islands of St Thomas, St John, and St Croix (200 km²), the British Virgin Islands (343 km²), and Puerto Rico (554 km²). The fish species analyzed and associated data were obtained mainly from the study by Randall (1967), synthesized by Opitz (1996).

Spatially explicit presence/absence community matrices were created by considering the presence of each species in a specific habitat only when that particular species was recorded foraging or breeding in that area (Opitz 1996; Froese and Pauly 2003). Community matrices include both the trophic links and the spatial distribution of 208 fish taxa identified to the species level. Randall's list of shark species was completed by Opitz (1996), which included more sharks with affinities to coral reefs of the Puerto Rico–Virgin islands area, based on accounts in Fischer (1978). Note that our trophic modules are composed only by fishes, and that all fish taxa is identified to the species level, which implies that results presented here are not affected by trophic aggregation.

The final spatially explicit community matrix includes 3,138 interactions, representing five food webs in five habitat types. Specifically, the habitat types here studied are mangrove/estuaries (m hereafter; 40 species and 94 interactions), coral reefs (c hereafter; 170 species and 1,569 interactions), seagrass beds/algal mats (a hereafter; 98 species and 651 interactions), sand (s hereafter; 89 species and 750 interactions), and offshore reefs (r hereafter; 22 species and 74 interactions). To a single habitat 85 species are restricted while 46, 63, 12, and 2 species occupy 2, 3, 4, and 5 habitats, respectively. Global connectivity values (C) within each habitat are similar to previously reported values for food webs (Dunne et al. 2002). Specifically, $C_m = 0.06$, $C_c = 0.054$, $C_a = 0.07$, $C_s = 0.095$, and $C_r = 0.15$.

Food-web structure and null model

We consider tri-trophic FCs (Figure 2.1(a)) and FCs with OMN (Figure 2.1(c)). We count the number and species composition of such trophic modules within the food web at each community. We then make pair-wise comparisons among communities ($n = 10$ pair-wise comparisons) and count the

number of chains (with identical species at all trophic levels) shared by each pair of communities. To assess whether this shared number is higher or lower than expected by chance we develop a null model. This algorithm randomizes the empirical data at each community, yet strictly preserves the ingoing and outgoing links for each species. In this algorithm, a pair of directed links A–B and C–D are randomly selected. They are rewired in such a way that A becomes connected to D, and C to B, provided that none of these links already existed in the network, in which case the rewiring stops, and a new pair of links is selected.

We randomized each food web habitat 200 times. For each pair of habitats we compare each successive pair of replicates and count the shared number of simple tri-trophic FCs and chains with OMN containing exactly the same set of species. Then we estimated the probability that a pair-wise comparison of a random replicate has a shared number of such modules equal or higher than the observed value. Recent algorithm analysis suggest that this null model represents a conservative test for presence–absence matrices (Miklós and Podani 2004).

We calculated the number of tri-trophic FCs, and OMN chains common to all pairs of communities, and compared this number with that predicted by our null model (Figure 2.1(b) and (d)). The coral reef habitat shares with all other habitats a number of FCs and OMN larger than expected by chance ($P < 0.0001$ in all pair-wise comparisons except for the mangrove comparison, where $P < 0.002$ and $P < 0.01$ for FCs and OMN, respectively). Similarly, seagrass beds/algal mats and sand (a/s contrasts) share a significant number of FCs and OMN ($P < 0.0001$). Globally, from the 10 possible intercommunity comparisons, five share a number of modules higher than expected by chance (Figure 2.1(a) and (c) where arrows are thick when the pair-wise comparison is statistically significant, and thin otherwise). This suggests that habitats sharing a significant proportion of trophic modules are mainly composed by a regional pool of individuals.

The average fraction of shared FCs and OMN between habitat pairs is $38\% \pm 24.5\%$ and $41\% \pm 25\%$, respectively, which still leaves more than 50% of

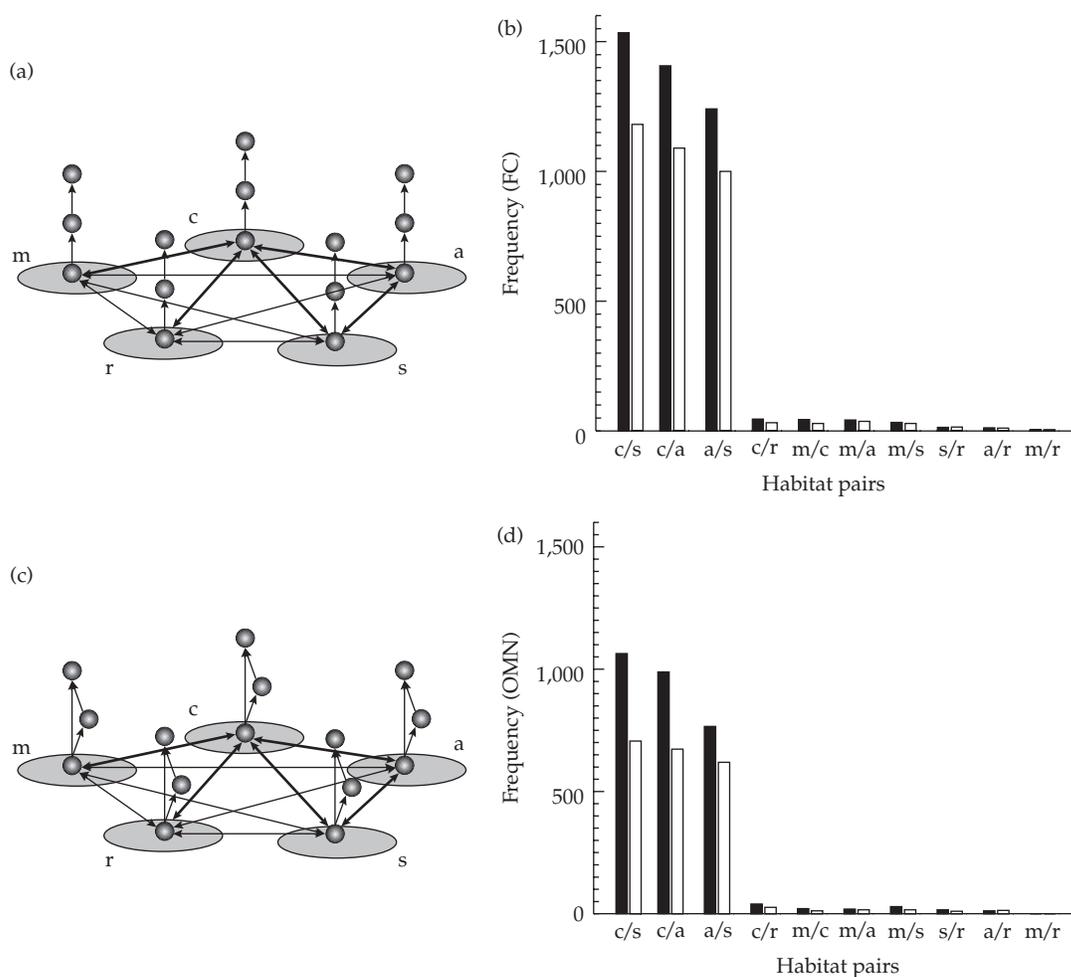


Figure 2.1 The food-web modules studied here are (a) tri-trophic FCs, and (c) OMN chains. Circles represent the five different habitat types. For each habitat pair, the link connecting the two habitats is thick if the number of shared trophic modules is significant, and thin otherwise; (b) and (d) represent the frequency of shared tri-trophic FCs and OMN chains, respectively in all pair-wise community comparisons. Black and white histograms represent the observed and the average expected value, respectively. Habitat types are mangrove/estuaries (m), coral reefs (c), seagrass beds/algal mats (a), sand (s), and offshore reefs (r). As noted, coral reefs (c), share with the rest of the habitats a number of FCs and OMN larger than expected by chance, which suggest a high degree of connectance promoted by dispersal.

different species composition trophic modules between habitats. However, it is interesting to note that 15 species (specifically, herbivorous species from *Blenniidae* and *Scaridae* families, and top species from *Carcharhinidae* and *Sphyrnidae* families) are embedded in more than 75% of trophic modules, which suggests that a small number of species are playing an important role in connecting through dispersal local community dynamics. Note that these highly connected species link

trophic modules across space in larger structures, which suggest a cohesive spatial structure (Melián and Bascompte 2004).

Dynamic metacommunity model

In order to assess the local and regional dynamics of the structure studied, we extend a previous metacommunity model (Mouquet and Loreau 2002, 2003) by incorporating trophic modules

(tri-trophic FCs and FCs with OMN) in a set of interacting communities. The model follows the formalism of previous metapopulation models (Levins 1969) applied to the scale of the individual (Hastings 1980; Tilman 1994). At the local scale (within communities), we consider a collection of identical discrete sites given that no site is ever occupied by more than one individual. The regional dynamics is modeled as in mainland–island models with immigration (Gotelli 1991), but with an explicit origin of immigration that is a function of emigration from other communities in the meta-community (Mouquet and Loreau 2003). Therefore, the model includes three hierarchical levels (individual, community, and metacommunity). The model reads as follows:

$$\frac{dP_{ik}}{dt} = \theta I_{ik} V_k + (1 - d) c_{ik} P_{ik} V_k - m_{ik} P_{ik} + R_{ik} P_{ik} - C_{ik} P_{ik}. \quad (2.1)$$

At the local scale, P_{ik} is the proportion of sites occupied by species i in community k . Each community consists of S species that indirectly compete within each trophic level for a limited proportion of vacant sites, V_k , defined as:

$$V_k = 1 - \sum_{j=1}^S P_{jk}, \quad (2.2)$$

where P_{jk} represents the proportion of sites occupied by species j within the same trophic level in community k . The metacommunity is constituted by N communities. d is the fraction of individuals dispersing to other habitats, and dispersal success, θ , is the probability that a migrant will find a new community, c_{ik} is the local reproductive rate of species i in community k , and m_{ik} is the mortality rate of species i in community k .

For each species in the community, we considered an explicit immigration function I_{ik} . Emigrants were combined in a regional pool of dispersers that was equally redistributed to all other communities, except that no individual returned to the community it came from (Mouquet and Loreau 2003). After immigration, individuals were associated to the parameters corresponding to the community they immigrated to. I_{ik} reads as:

$$I_{ik} = \frac{d}{N-1} \sum_{l \neq k}^N c_{il} P_{il}, \quad (2.3)$$

where the sum stands for all the other communities l . R_{ik} represents the amount of resources available to species i in community k

$$R_{ik} = \sum_{j=1}^S a_{ijk} P_{jk}, \quad (2.4)$$

where a_{ijk} is the predation rate of species i on species j in community k , and the sum is for all prey species. Similarly, C_{ik} represents the amount of consumption exerted on species i by all its predators in community k , and can be written as follows:

$$C_{ik} = \sum_{j=1}^S a_{jik} P_{jk}, \quad (2.5)$$

where a_{jik} is the predation rate of species j on species i in community k , and the sum is for all predator species.

We have numerically simulated a metacommunity consisting of six species in six communities. In each community, either two simple tri-trophic FCs, or two OMN chains are assembled with the six species. The two trophic modules within each community are linked only by indirect competition between species within the same trophic level. We assumed a species was locally extinct when its proportion of occupied sites was lower than 0.01. Mortality rates (m_{ik}) are constant and equal for all species. Dispersal success (θ) was set to 1.

We considered potential reproductive rates to fit the constraint of strict regional similarity, SRS (Mouquet and Loreau 2003). That is, species within each trophic level have the same regional basic reproductive rates, but these change locally among communities. Under SRS, each species within each trophic level is the best competitor in one community. Similarly, we introduce the constraint of strict regional trophic similarity (SRTS). That is, each consumer has the same set of local energy requirements but distributed differently among communities. Additionally, we assumed a direct relationship between the resource's local reproductive rate and the intensity it is predated with (Jennings and Mackinson 2003).

Under the SRS and SRTS scenarios, regional species abundance and intercommunity variance are equal for each of the two species within the same trophic level. Regional abundance in OMN is

higher, equal, and lower for top, intermediate, and basal species, respectively. Local abundances differ significantly between the two modules explored. Specifically, when there is no dispersal ($d=0$) there is local exclusion by the competitively superior species (Mouquet and Loreau 2002). This occurs for the basal and top species in the simple trophic chain. The variance in the abundance of the basal and top species between local communities is thus higher without dispersal for tri-trophic FCs (Figure 2.2(a)).

However, the situation is completely different for OMN. Now, intercommunity variance is very low for both the basal and top species in the absence of dispersal, and dramatically increases with d in the case of the top species. When the communities are extremely interconnected, the top species disappears from the two communities ($P_{ik} < 0.01$), and is extremely abundant in the remaining communities. For intermediate species, increasing dispersal frequency decreases the intercommunity variance, except when d ranges between 0 and 0.1 in FCs (Figures 2.2(a) and (b)).

Finally, we can see in Figure 2.2(b) (as compared with Figure 2.2(a)) that intercommunity variance for high d -values is higher in a metacommunity with OMN. Thus, the interplay between dispersal among spatially structured communities and food-web structure greatly affects local species abundances. The results presented here were obtained with a single set of species parameters. Under the SRS and SRTS scenarios, results are qualitatively robust to deviations from these parameter values.

Summary and discussion

It is well known that local communities can be structured by both local and regional interactions (Ricklefs 1987). However, it still remains unknown what trophic structures are shared by a set of interacting communities and its dynamical implications for the persistence of biodiversity. The present study is an attempt to link local and regional food-web structure and dynamics in a spatially structured marine food web.

Communities in five habitats of the Caribbean have shown significantly similar trophic structures which suggest that these communities are open to

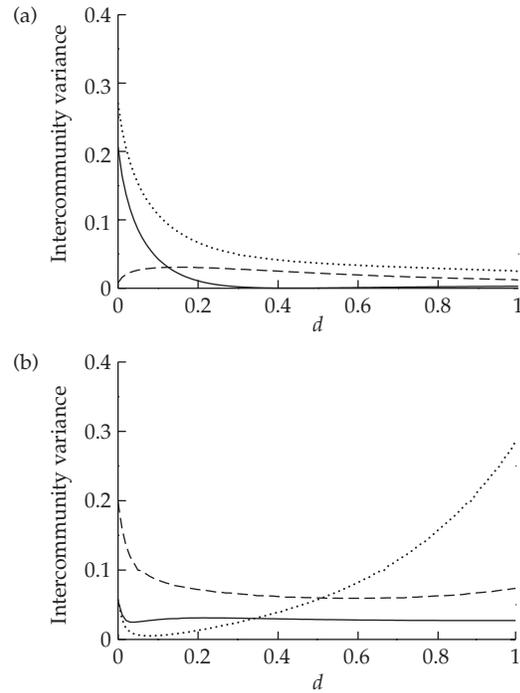


Figure 2.2 Intercommunity variance in local species abundance for the basal (continuous line), intermediate (dotted line), and top (circles) species as a function of the proportion of dispersal between communities (d). (a) Represents tri-trophic FCs and (b) OMN chains. Parameter values are $m_{ik}=0.2$, c_{ik} for basal species is 3, 2.8, 2.6, 2.4, 2.2, and 2 from the first to the sixth community, respectively. For intermediate species c_{ik} is 1.5, 1.4, 1.3, 1.2, 1.1, and 1, respectively from the first to the sixth community. Top species reproductive values are 0.8, 0.75, 0.7, 0.65, 0.6, and 0.55, respectively. Predation rates of intermediate and top species j on species i in community k are 0.6, 0.5, 0.4, 0.3, 0.2, and 0.1, respectively. The initial proportion of sites occupied by species i in community k , (P_{ik}) is set to 0.05. As noted, in closed metacommunities, tri-trophic FCs show an extreme variation in local abundances for both the basal and top species ($P_{ik} < 0.01$) in two and three communities, respectively, and the reverse happens in extreme interconnected communities with OMN. The top species becomes unstable, and goes extinct in two local communities ($P_{ik} < 0.01$).

immigration (Karlson and Cornell 2002). It has been recently shown that mangroves in the Caribbean strongly influence the local community structure of fish on neighboring coral reefs (Mumby et al. 2004). Additionally, empirical studies have shown that dispersal among habitats and local species interactions are key factors for

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metacommunity structure (Shurin 2001; Cottenie et al. 2003; Kneitel and Miller 2003; Cottenie and De Meester 2004), and the persistence of local and regional diversity (Mouquet and Loreau 2003). However, it still remains unclear how the interplay between dispersal and more complex trophic structures affects species persistence in local communities (Carr et al. 2002; Kneitel and Miller 2003).

In the present work, closed communities ($d=0$) with tri-trophic FCs showed an extreme variation in local abundances for both the basal and top species (Figure 2.2(a)). However, the reverse happens in closed communities with OMN ($d=1$). The top species becomes unstable, and goes extinct in two local communities (Figure 2.2(b)). Recent empirical studies have shown that increasing dispersal frequency in intermediate species decreases the variance among local communities (Kneitel and Miller 2003), a pattern consistent with theoretical results presented here (see dotted line in Figure 2.2(a) and (b)). Further data synthesis and theoretical work is needed here to integrate the functional links between habitats and the local dynamics of species embedded in food webs.

In summary, the similarity in the trophic modules reported here suggests a strong link among the spatially structured communities. The level of connectivity among these local communities and the type of trophic modules alter local abundance of species and promote local changes in diversity. It still remains unexplored how the results here presented change by the introduction of a larger number of interacting modules in a set of spatially structured communities. Our results predict a relative stability in the composition of basal species, and a dramatic influence in the abundance of top species depending on the connectivity (i.e. dispersal) among distinct habitats.

Acknowledgments

We thank the editors of this book for inviting us to contribute this chapter. We thank Miguel A. Fortuna and Mayte Valenciano for their useful comments on a previous draft. Funding was provided by the Spanish Ministry of Science and Technology (Grants REN2003-04774 to JB and REN2003-00273 to PJ, and Ph.D. Fellowship FP2000-6137 to CJM).

- Urabe, J., and R. W. Sterner. 1996. Regulation of herbivore growth by the balance of light and nutrients. *Proceedings of the National Academy of Sciences, USA* **93**: 8465–8469.
- Urabe, J., J. J. Elser, M. Kyle, T. Sekino, and Z. Kawabata. 2002a. Herbivorous animals can mitigate unfavorable ratios of energy and material supplies by enhancing nutrient recycling. *Ecology Letters* **5**: 177–185.
- Urabe, J., M. Kyle, W. Makino, T. Yoshida, T. Andersen, and J. J. Elser. 2002b. Reduced light increases herbivore production due to stoichiometric effects of light: nutrient balance. *Ecology* **83**: 619–627.
- Vadstein, O., B. O. Harkjerr, A. Jensen, Y. Olsen, and H. Reinertsen. 1989. Cycling of organic carbon in the photic zone of a eutrophic lake with special reference to the heterotrophic bacteria. *Limnology and Oceanography* **34**: 840–855.
- Varma, A., and B. O. Palsson. 1994. Metabolic flux balancing: basic concepts, scientific and practical use. *BioTechnology* **12**: 994–998.
- Vrede, T., J. Persson, and G. Aronsen. 2002. The influence of food quality (P:C ratio) on RNA:DNA ratio and somatic growth rate of *Daphnia*. *Limnology and Oceanography* **47**: 487–494.
- * Weider, L. J., K. L. Glenn, M. Kyle, and J. J. Elser. 2004. Associations among ribosomal (r)DNA intergenic spacer length, growth rate, and C:N:P stoichiometry in the genus *Daphnia*. *Limnology and Oceanography* (in press).
- Wildermuth, M. C. 2000. Metabolic control analysis: biological applications and insights. *Genome Biology* **1**: (Reviews): 1031–1035.
- Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussmann, and J. Hairston, N. G. 2003. Rapid evolution drives ecological dynamics in a predator–prey system. *Nature* **424**: 303–306.
- Caswell, H., and J. E. Cohen. 1993. Local and regional regulation of species–area relations: a patch–occupancy model. In: R. E. Ricklefs and D. Schluter (eds), *Species Diversity in Ecological Communities*. The University of Chicago Press. Chicago, IL.
- Cottenie, K., E. Michelis, N. Nuytten, and L. De Meester. 2003. Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. *Ecology* **84**: 991–1000.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Food web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences, USA* **99**: 12917–12922.
- Fisher, W.(ed). 1978. *FAO Species Identification Sheets for Fishery Purposes. Western Central Atlantic (Fishing area 31)*. Vol I–VII. Food and Agriculture Organization of the United Nations, Rome.
- Froese, R., and D. Pauly. 2003. FishBase World Wide Web electronic publication. <http://fishbase.org>, version 24 September 2003.
- Gotelli, N. J. 1991. Metapopulation models: the rescue effect, the propagule rain, and the core–satellite hypothesis. *American Naturalist* **138**: 768–776.
- Hanski, I. 1983. Coexistence of competitors in a patchy environment. *Ecology* **64**: 493–500.
- Hanski, I., and M. E. Gilpin. (ed). 1997. *Metapopulation Biology: Genetics, and Evolution*. Academic Press, San Diego.
- Hastings, A. 1980. Disturbance, coexistence, history and the competition for space. *Theoretical Population Biology* **18**: 363–373.
- Holt, R. D. 1996. Food webs in space: an island biogeographic perspective. In: G. A. Polis, and K. O. Winemiller (eds), *Food Webs: Integration of Patterns and Dynamics*. Chapman and Hall, London.
- Holt, R. D. 1997. From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. In: I. Hanski, and M. Gilpin (eds), *Metapopulation Biology*. Academic Press, San Diego, pp. 149–164.
- Hori, M., and T. Noda. 2001. Spatio-temporal variation of avian foraging in the rocky intertidal food web. *Journal of Animal Ecology* **70**: 122–137.
- Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Jennings, S., and S. Mackinson. 2003. Abundance–body mass relationships in size-structured food webs. *Ecology Letters* **6**: 971–974.
- Kareiva, P. 1987. Habitat fragmentation and the stability of predator–prey interactions. *Nature* **326**: 388–390.

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Chapter 2

Bascompte, J., and R. V. Solé. (eds). 1998. *Modeling Spatiotemporal Dynamics in Ecology*. Springer, Berlin.

- * Bascompte, J., C. J. Melián, and E. Sala. 2004. Interaction strength motifs and the overfishing of marine food webs. (submitted).

Caldarelli, G., P. G. Higgs, and A. J. McKane. 1998. Modelling coevolution in multispecies communities. *Journal of Theoretical Biology* **193**: 345–358.

Carr, M. H., T. W. Anderson, and M. A. Hixon. 2002. Biodiversity, population regulation, and the stability of coral-reef fish communities. *Proceedings of the National Academy of Sciences, USA*, **99**: 11241–11245.

AQ: Please provide journal name for Bascompte, Melián and Sala (2004).

- Karlson, R. H., and H. V. Cornell. 2002. Species richness of coral assemblages: detecting regional influences at local spatial scales. *Ecology* **83**: 452–463.
- Kneitel, J. M., and T. E. Miller. 2003. Dispersal rates affect species composition in metacommunities of *Sarraceniapurpurea* inquilines. *American Naturalist* **162**: 165–171.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**: 237–240.
- Loreau, M., Mouquet, N., and R. D. Holt. 2003. Metacommunities: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters* **6**: 673–679.
- Margalef, R. 1963. On certain unifying principles in ecology. *American Naturalist* **97**: 357–374.
- Melián, C. J., and J. Bascompte, 2002. Food web structure and habitat loss. *Ecology Letters* **5**: 37–46.
- Melián, C. J., and J. Bascompte, 2004. Food web cohesion. *Ecology* **85**: 352–358.
- Miklós, I., and J. Podani. 2004. Randomization of presence–absence matrices: comments and new algorithms. *Ecology* **85**: 86–92.
- Mouquet, N., and M. Loreau. 2002. Coexistence in metacommunities: the regional similarity hypothesis. *American Naturalist* **159**: 420–426.
- Mouquet, N., and M. Loreau. 2003. Community patterns in source–sink metacommunities. *American Naturalist* **162**: 544–557.
- Mumby, P. J., A. J. Edwards, J. E. Arias-González, K. C. Lindeman, P. G. Blackwell, et al. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* **427**: 533–536.
- Opitz, S. 1996. Trophic Interactions In Caribbean Coral Reefs. Technical Report 43. International Centre for Living Aquatic Resource Management (now World-Fish Center), Penang, Malaysia.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* **28**: 289–316.
- Randall, J. E. 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* **5**: 665–847.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**: 167–171.
- Shurin, J. B. 2001. Interactive effects of predation and dispersal on zooplankton communities. *Ecology* **82**: 3404–3416.
- Thompson, J. N. 1999. Specific hypotheses on the geographic mosaic of coevolution. *American Naturalist* **153**: S1–S14.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**: 2–16.
- Tilman, D., and P. Kareiva (ed) 1997. *Spatial Ecology. The Role of Space in Population Dynamics and interspecific Interactions*. Princeton University Press, Princeton, NJ.
- Wilson, D. S. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology* **73**: 1984–2000.

Chapter 3

- Almunia, J., G. Basterretxea, J. Aristegui, and R. E. Ulanowicz. 1999. Benthic–pelagic switching in a coastal subtropical lagoon. *Estuarine, Coastal and Shelf Science* **49**: 363–384.
- Baird, D. 1998. Orientors and ecosystem properties in coastal zones. In: F. Muller and M. Leupelt (eds), *Ecotargets, Goal Functions, and Orientors*. Springer-Verlag, Heidelberg. pp. 232–242.
- Baird, D. and J. J. Heymans. 1996. Assessment of the ecosystem changes in response to freshwater inflow of the Kromme River Estuary, St Francis Bay, South Africa: a network analysis approach. *Water SA* **22**: 307–318.
- Baird, D., J. M. Mcglade, and R. E. Ulanowicz. 1991. The comparative ecology of six marine ecosystems. *Philosophical Transactions of the Royal Society London B* **333**: 15–29.
- Baird, D., and R. E. Ulanowicz. 1989. Seasonal dynamics of the Chesapeake Bay ecosystem. *Ecological Monographs* **59**: 329–364.
- Baird, D. and R. E. Ulanowicz. 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. *Marine Ecology Progress Series* **991**: 221–237.
- Baird, D., R. E. Ulanowicz, and W. R. Boynton. 1995. Seasonal nitrogen dynamics in the Chesapeake Bay: a Network Approach. *Estuarine, Coastal and Shelf Science* **41**: 137–162.
- Baird, D., J. Luczkovich, and R. R. Christian. 1998. Assessment of spatial and temporal variability in ecosystem attributes of the St Marks National Wildlife Refuge, Apalachee Bay, Florida. *Estuarine, Coastal and Shelf Science* **47**: 329–349.
- Baird, D., R. R. Christian, C. H. Peterson, and G. Johnson. 2004. Consequences of hypoxia on estuarine ecosystem function: energy diversion from consumers to microbes. *Ecological Applications* **14**: 805–822.
- Batagelj, V., and A. Mrvar. 2002. Pajek 0.85 Network Software. Available at: <http://vlado.fmf.uni-lj.si/pub/networks/pajek/>.

4.3 What is New?

Most studies incorporating species interactions in space have focused on one, two, or n-species within the same trophic level. On the other hand, most studies on food webs have obviated space. The present chapter introduces trophic modules in a spatial context. The most important result in the first paper is that the extinction threshold depends on the food web structure in which species are embedded. Second, dramatical changes in the extinction threshold of poorer competitors after adaptive behaviour or decreasing exploration the cost of better competitor in the context of apparent competition and intraguild predation suggest non-linear dynamics in complex food webs. Third, the second paper links local and regional food web structure and dynamics in a spatially structured marine food web, and uncovers how the level of connectivity among local communities and the type of trophic modules alter species local abundances and promote local changes in diversity. Both studies are potentially extensible to more complex subwebs in space.

4.4 Current and Future Work

Space is undoubtedly the missing ingredient in food web approaches. Although previous studies suggested conceptually the need to integrate food webs in space (Margalef 1963; Holling 1992; Holt 1997; Polis et al. 1997), only recently different approaches have introduced data and modelling to link habitat area, species diversity and trophic interactions (Leibold et al. 2004; Brose et al. 2004). Cellular automata has been used to explore explicitly the structure of metapopulations and metacommunities using n-individuals with fixed (Keitt 1997) and changing strategies (Nowak and Sigmund 2004), and n-species within neutral communities (Solé et al. 2004) but the introduction of multiple interacting species within the framework of homogeneous or explicit space using different trophic levels remains far from being understood (Leibold et al. 2004). It is interesting to note that the introduction of subwebs in space with two types of ecological interactions alter dramatically species abundances. How could the introduction of multiple interaction types alters the structure and dynamics of communities? Next chapter will try to answer this question.

How could we introduce more complex ecological networks in the spatial context? New data syn-

thesis, methods and comparative studies are now being developed using different spatial approaches (Roughgarden et al. 1989; Dieckmann et al. 2000; Gastner and Newman 2004). What remains unclear is to explore the structural and dynamical differences between few and many interacting species in the spatial context (see Solé et al. 2003). The two studies presented here are extensible to n-species within multiple trophic levels in an heterogeneous space, which implies the introduction of different large matrices in a set of habitats using different types of ecological interactions.

Literature Cited

Brose, U., Ostling, A., Harrison, K., and Martinez, N. (2004). Unified spatial scaling of species and their trophic interactions. *Nature*, **428**:167-171.

Dieckmann, U., Law, R., and Metz, J. A. J. (eds.) (2000). *The Geometry of Ecological Interactions: Simplifying the Spatial Complexity*, Cambridge Univ. Press. Cambridge.

Gastner, M., and Newman, M. E. J. (2004). The spatial structure of networks. *cond-mat/0407680*.

Holling, C. S. (1992). Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol. Monogr.*, **62**:447-502.

Keitt, T. H. (1997). Stability and complexity on a lattice: coexistence of species in an individual-based food web model. *Ecol. Model.*, **102**:243-258.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., and Gonzalez, A. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.*, **7**:601-613.

Margalef, R. (1963). On Certain Unifying Principles in Ecology. *Am. Nat.*, **97**:357-374.

Nowak, M. A., and Sigmund, K. (2004). Evolutionary Dynamics of Biological Games. *Science*, **303**:793-799.

Polis, G. A., Anderson, W. B., and Holt, R. D. (1997). Toward an integration of landscape and food web ecology. *Annu. Rev. Ecol. Syst.*, **28**:289-316.

Roughgarden, J., May, R. M., and Levin, S. A. (eds.) (1989). *Perspectives in Ecological Theory*, Princeton University Press, Princeton, NJ.

Solé, R. V., Alonso, D., and Saldanya, J. (2004). Habitat fragmentation and biodiversity collapse in neutral communities. *Ecological Complexity*, **1**:65-75.

Chapter 5

Linking Different Types of Ecological Interactions

The study presented in this chapter is a draft. Our concern to introduce this chapter is related with the idea that future data on ecological networks will introduce multiple interaction types. Previous results suggest (from chapter 4 and present chapter) that central questions in ecology as the structure, assembly, and dynamics of communities could be greatly affected if multiple interaction types were introduced. Specifically, the draft presented here is a first step toward a more detailed integration between historical and current data, and static and dynamic null models in the framework of multiple types of ecological interactions in a species-rich community.

5.1 The Structure and Dynamics of the Antagonistic-Mutualistic Doñana Ecological Network

The Structure and Dynamics of the Antagonistic-Mutualistic Doñana Ecological Network.

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Abstract

Most studies in community ecology have focused on single interaction types (i.e., antagonistic, mutualistic or competitive). Works focusing on subsets of plant-animal interactions have shown how different types of interactions (e.g., antagonistic versus mutualistic) can act in a non-additive way to alter the structure and dynamics of subwebs. However, it still remains unknown the structural integration between antagonistic and mutualistic communities, and its dynamical implications to species persistence. In the present study we have synthesized and analyzed plant-antagonistic-mutualistic community from the Doñana ecological network. Specifically, (1) we have characterized the structure by comparing the frequency of a simple module with the two interaction types with a static null model, and (2) we have simulated the dynamics of the antagonistic-mutualistic community for both real data and data from the null model, and compared the resulting frequency distribution of extinct species. First, the number of simple modules is higher in empirical data than data from the null model. Second, the frequency of plant species involved in n -modules is highly skewed with most plants embedded in a few number of modules and a few number of plants in 67% of the modules. Third, the frequency distribution of extinct species in the real network is highly skewed with most events of extinctions smaller than the random network, but with rare and extremely large events of extinctions. Our results suggest that plant community exposed to pollinators are visited significantly by herbivores and this structure alters the dynamics and persistence of the community. Because general results about stability of real communities come from independent interaction types, our results suggest that we must take carefully such conclusions.

1 Introduction

Early studies on plant-mutualistic-antagonistic interactions suggested the introduction of different types of interactions (i.e., higher order interactions) to understand local traits of species and community assembly (Janzen 1969; Levins 1975; Herrera 1982; Jordano 1987). However, the bulk of studies on plant-mutualistic, and plant-herbivore interactions have been developed almost in complete isolation of one another (Armbruster 1997; Herrera 2000; Thompson 2002). Empirical studies focusing mainly on a small subset of interacting species have shown that interaction types (i.e., considering together mutualistic and antagonistic interactions) can act synergistically or antagonistically to alter ecological and evolutionary outcomes (Armbruster et al 1997; Strauss 1997; Herrera 2000; Strauss and Irwin 2004). However, despite its potential importance for community structure and stability (Thompson 2002; Berlow et al. 2004), the relevance of these results have not been tested at the community level.

The present study is an attempt to characterize the structure and dynamics of a community with antagonistic and mutualistic interactions. We synthesized data from a plant (170 species), antagonistic (16 *herbivores*), and mutualistic (181 *pollinizers* and 27 *seeds dispersers*) community in Doñana National Park, Southern Spain (see sources of empirical data in Appendix, Table 1, and Table 2).

Specifically, we address the following questions: (1) Are plant-herbivores, and plant-mutualistic communities independently organized?, that is, are communities with different interaction types randomly assembled? (2) Is there any relation between structure and dynamics in a community with multiple interaction types? In order to answer these questions we introduce (1) a static null model to test the significant presence of a simple module with antagonistic and mutualistic interactions, and (2) a dynamic null model for n -species to test the effect of the structure with antagonistic and mutualistic interactions on the dynamics of the ecological network.

2 Methods: Static and Dynamic Null Model

2.1 Static Null Model

A null model was compared with the total number of simple modules (i.e., a plant sharing an antagonistic and a mutualistic interaction) in the empirical data (Fig 1a). We generated 1000 replicates of the model with the same number of species (S) and connectance C than in the real data (where $C = L/P * A$, with L the total number of links, and P and A the total number of plant and animal species respectively). Note that in this study $C = L_a + L_m / P * A$, where L_a is the number of links in the plant-antagonistic community, and L_m is the number of links in the plant-mutualistic community. Our statistic (P) is the probability that a random replicate has a number of modules equal or higher than the observed value.

The random model maintains, (1) the total number of links ($L^r = L$, where L^r is the number of links in the randomized matrix), (2) the total number of each type of link ($L_a^r = L_a$ and $L_m^r = L_m$, where L_a^r and L_m^r are the number of links in the randomized plant-antagonistic and plant-mutualistic community respectively) for both the antagonistic and the mutualistic community, assuming that each herbivore, pollinator, and seed disperser has an equal number of links as in the empirical data, but (3) assigning the number of plant species for each herbivore with equal probability among the set of plant species that have antagonistic or antagonistic-mutualistic links as in real data (the total number of plant species with antagonistic links are 93, and with antagonistic-mutualistic links are 39). Similarly for each pollinator and seed disperser (the number of plant species with mutualistic links are 38). The biological meaning of this model is that each herbivore, pollinator or seed disperser can interact with equal probability with all plant species that have in real data antagonistic or antagonistic-mutualistic links, and mutualistic or mutualistic-antagonistic links respectively. Therefore, shuffling takes place only among plants which are pollinated or dispersed in the real data, thus avoiding unrealistic scenarios such as a non-flowering plant being artificially assigned a pollinator (the same occur in plants with only herbivores species).

2.2 Dynamic Null Model

In order to assess the effect of the structure on the dynamics of the networks resulting from both the real data and the static null model, we introduce a dynamic model for n -species with antagonistic and mutualistic interactions. Few studies have attempt to introduce different types of ecological interactions in a dynamical model (Ringel et al. 1996; Chen and Cohen 2001). The basic building block of this model is represented in Fig. 1a,



Figure 1: a) The simple module studied represented by a plant species (*center*), a pollinator or seed disperser (*right*), and an herbivore (*left*), and b) Doñana Ecological Network showing plants, pollinators-seed dispersers, and herbivores in the center, right and left column, respectively.

and the model with n-species and two types of ecological interactions reads as follows:

$$\frac{dP_i}{dt} = r_i P_i - c_i P_i^2 + M_{iS_j} - A_{iS_k}, \quad (1)$$

$$\frac{dI_j}{dt} = r_j I_j - c_j I_j^2 + M_{jS_i}, \quad (2)$$

$$\frac{dH_k}{dt} = r_k H_k - c_k H_k^2 + A_{kS_i}, \quad (3)$$

where P_i , I_j , and H_k are the densities of plant species i , pollinator or seed disperser j , and herbivores species k respectively. r_i , r_j , and r_k are the intrinsic growth rates of plant i , pollinator or disperser j , and herbivore k . c_i , c_j , and c_k are the intraspecific competition coefficient between plant species i , pollinator or disperser j , and herbivore k . M_{iS_j} , represents the total effect of pollinators and seed dispersers on plant species i , and can be defined as:

$$M_{iS_j} = \sum_{j=1}^{S_j} m_{ij} P_i I_j, \quad (4)$$

where S_j is the number of pollinators or seed dispersers that interact with plant species i , with m_{ij} as the per capita effect of the pollinator or disperser j on plant species i . M_{jS_i} is defined similarly to M_{iS_j} , but now m_{ji} represents the per capita effect of the plant species i on the pollinator or seed disperser species j . Finally A_{iS_k} is the total effect of herbivores on plant species i , and can be defined as:

$$A_{iS_k} = \sum_{k=1}^{S_k} a_{ik} P_i H_k, \quad (5)$$

where S_k represents the number of herbivores species that interact with plant species i . a_{ik} is the per capita effect of the herbivore species k on plant species i . A_{kS_i} is defined similarly to A_{iS_k} , but now a_{ki} represents the per capita effect of the plant species i on the herbivore species k .

We have numerically simulated the dynamics of the model 1–3 for both, the structure observed in real data, and using randomizations from the static null model. Specifically we generated 500 replicates from each of the two structures and observed the resulting species' dynamics after 100 time steps for each replicate.

The values of intrinsic growth rates (r_i , r_j , and r_k), intra-specific competition coefficient (c_i , c_j , and c_k), and the per capita interaction strength (m_{ij} , m_{ji} , a_{ik} , and a_{ki}) for each species and replicate are chosen randomly from a uniform distribution over the open interval (0.85,1.15), (0.1,0.9), and (0.001,0.03) respectively. After assigning randomly the parameter values in the starting point of each replicate, the rest of the numerical simulation is completely deterministic. The number of iterations in each replicate, 100 was found to be sufficient for the system to reach its asymptotic state. We

consider extinct the species with densities lower than 1, and recorded the number of species with densities lower than 1 for each replicate.

To study the persistence of the real and randomized communities we (1) normalized the distribution of extinction size by the highest number of extinct species, and (2) partitioned the interval (0,1) of possible values of extinct species per replica into ten subintervals of equal width (0–0.1], (0.1–0.2], (0.2–0.3], (0.3–0.4], and so on until (0.9–1). We compared both distributions using the two-sample *Kolmogorov–Smirnov-test* to observe if independent random samples from real and randomized networks are drawn from the same underlying continuous distribution.

3 Results

The final network analyzed here has 394 species and 798 interactions (578 mutualistic links and 220 antagonistic links) (see Fig. 1b), which implies a low global connectivity ($C = 0.02$, with $C_m = 0.016$ as the connectivity considering only mutualistic interactions, and $C_a = 0.086$ when considering only antagonistic interactions). The average number of links per pollinator-seed disperser and herbivore is 2.8, and 13.75 respectively. The distribution of links per species is highly skewed for both pollinators-dispersers (most species of lepidoptera 1 link and a few species more than 14 links (i.e., three bird species of *Sylvia* genera, the honey bee *Apis mellifera*, and the turtle *Testuda graeca*)), and herbivores (most species with less than 10 links, and *Dama dama*, and *Cervus elaphus* with 54 and 50 links respectively).

We calculated the total number of simple modules with a plant sharing one mutualistic and antagonistic interaction (Fig. 1a), and compared this number with the predicted by our static null model. The number of modules in the real data is 670, and after 1000 replicates of our null model the average number of modules is 491 ± 59 . The number of plants sharing both types of interactions is larger than expected by chance ($P < 0.0001$). Thus, if a plant has an antagonistic interaction it tends also to have a mutualistic interaction more often than expected by chance.

Thirty nine plant species have mutualistic and antagonistic interactions. Eight plant species are embedded in 1 module (*Typha sp.*, *Ranunculus sp.*, *Vulpia sp.*, *Polypogon maritimus*, *Paspalum sp.*, *Onionis sp.*, *Cytisus grandiflorus*, and *Malcolmia lacera*). Three families of plants summing 9 plant species (3 in each family) form part of 67% of the total number of modules. Specifically, *Cistaceae* family with *Cistus salvifolius*, 54 modules, *Halimium halimifolium*, 76, and *Halimium calycinum* 12, *Lamiaceae*, with *Rosmarinus officinalis*, 84, *Thymus mastichina*, 22, and *Lavandula stoechas*, 17, and *Rosaceae*, with *Rubus ulmifolius* 180, *Crataegus monogyna* 4, and *Pyrus bourgaeana* 4. The frequency

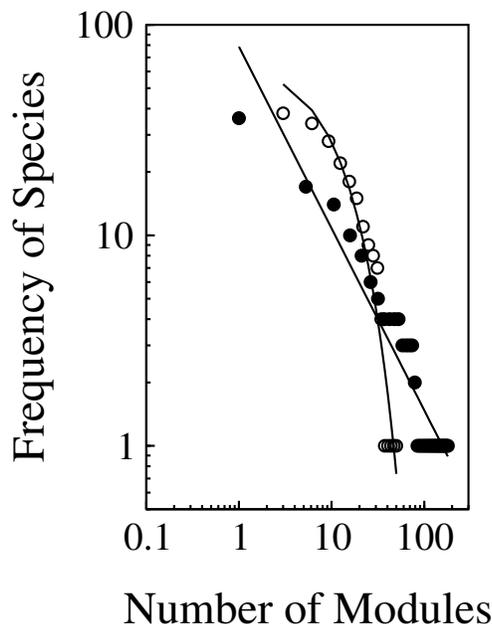


Figure 2: Frequency distribution of modules per plant, that is, the number of plant species embedded in a given number of modules. The distribution is highly skewed, decaying as a power law ($R^2 = 0.9$, $P = 0.05$, *black circles*). The distribution for the randomized networks decays exponentially ($R^2 = 0.96$, $P < 0.01$, *white circles* represent the average of 100 replicates).

distribution of modules per plant (i.e., how many plants are in 1,2,...,n modules) is highly skewed, decaying as a power law ($R^2 = 0.9$, $P = 0.05$) (*black circles* in Fig. 2). However, the distribution for the randomized networks decays exponentially ($R^2 = 0.96$, $P < 0.01$) (Fig. 2, *white circles* represent the average on 100 replicates).

It is interesting to note that 39 out 170 plant species share antagonistic and mutualistic interactions in the real data, which implies that the rest of plant species have only one type of interaction (i.e., highly connected plant species with only mutualistic interactions are *Daphne gnidium* with 93 pollinators and seed dispersers, *Asparagus aphyllus*, with 21, *Smilax aspera* with 21, and *Armeria velutina* with 19).

Is there any relation between structure and dynamics in a community with antagonistic and mutualistic interactions? The distribution of extinct species for real data after 500 replicates differ significantly from the randomized network (*KS-test*, $P < 0.001$). The distribution is highly skewed for the real data (Fig. 3), with 63% of local extinctions smaller than 15 species, and 1% of events bigger than 50 species (1 event with 59 and other with 79 extinct species). The contrary happens in the randomized networks. 50% of extinctions are smaller than 15 species, and the reminder 50% are mainly between 25-30 species without events bigger than 50 extinctions.

4 Summary and Discussion

Most studies detecting structure and persistence in community ecology have generally focused on either single-interaction perspectives with a large number of species (i.e., antagonistic, competitive, mutualistic, etc) (Lawlor and Maynard Smith 1976; Kokkoris et al. 1999; Berlow et al. 2004), or in different interaction types in a small subset of species (Herrera 1982; Jordano 1987; Armbruster 1997; Strauss 1997) (although see Hori 1987 and Yuma 1993). Both perspectives agree that higher order interactions could improve our understanding of community structure and persistence. But the analysis of multiple interaction types still remains a challenge in community ecology (Hori 1987; Yuma 1993; Thompson 2002; Berlow et al. 2004).

The present study is an attempt to bridge the structure and dynamics of a large community with antagonistic and mutualistic interactions. We introduce a static null model to characterize its structure and the effects of this structure on the dynamics of the network. We have found three main features in the community analyzed: (1) plant exposed to pollinators are visited significantly by herbivores, (2) a highly skewed frequency distribution of modules per plant with few species of plants accounting for almost 70% of the modules, and (3) under that structure, small extinction events are more frequent in the real data than in the randomized

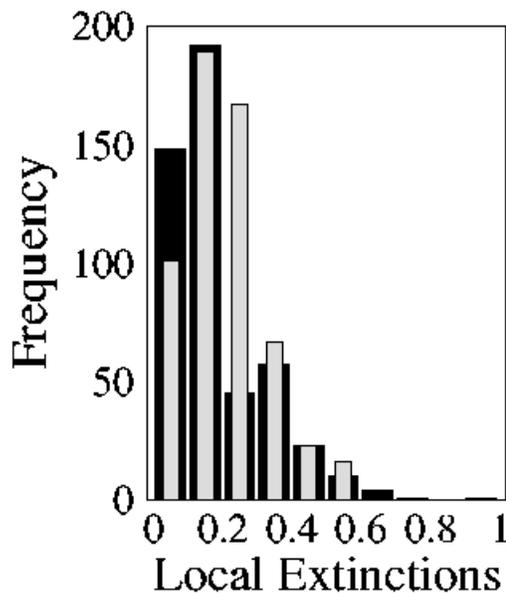


Figure 3: The frequency of extinctions for both the real data (*black bars*, following the power law distribution of modules per plant), and random networks, (*grey bars*, following the exponential distribution of modules per plant) after 500 replicates of the dynamic model. The distribution is more skewed for the real network than for the random one suggesting that small extinctions are more frequent in real data, but rare events with a high number of extinctions can eventually occur. Most extinctions for the randomized network are mainly in the intermediate range.

networks, but the biggest extinction events occur only in the real data.

What are the structural mechanisms altering the dynamics of the real network when comparing with the randomized ones? It is important to note that the only change that the static null model makes is the number of links for each plant species, but fix both the number of links per herbivore and pollinator-disperser of seeds, and the number of plants with the different types of interactions (23% of plants in the data, 39 out 170 plants). This means that the highly skewed decays of the frequency distribution for real data (i.e., the few species of plants that are embedded in 70% of modules) decays exponentially after the randomization, which implies that all plant species are embedded in a well defined average number of subwebs. Similarly the rest of plant species with only one type of interaction (131 out 170 plants) have after randomization a well defined average number of links. Future studies can provide if the structure of modules altered after the randomization has some implications in the extinction pattern reported.

The community level consequences can be related with the current finding for network topology under random and selective attack (Albert et al. 2000). If the few number of plant species embedded in the most number of modules have bad years (i.e., meaning that the random fluctuation considered in each replicate im-

plies low intrinsic growth rate, high intraspecific competence and a set of herbivores with strong interactions or a set of mutualistic species with weak interactions), this could propagate toward the rest of species in the community and abundances of a high number of species will be extremely small. At the same time, highly frequent small extinctions under random fluctuations of parameters in real data were found. Again, a detailed scrutiny of extinct species in each replicate could uncover the importance of the power law decays in the distribution of modules per plant in real data.

Previous studies have shown that herbivores can modulate the consequences of the interaction between plants and their animal pollinators (Karban and Strauss 1993; Strauss et al. 1996; Gómez 1996; Herrera 2000), and that the persistence of both types of interactors with plants could explain the macroevolutionary patterns of defense and reward systems in some plant lineages (Armbruster et al. 1997). Our results suggest that plants exposed to pollinators are visited significantly by herbivores, and this occurs not only for a subset of species, but at the community level. Future studies integrating more biological detail of each species, as defense and reward systems (Ehrlich and Raven 1964; Herrera 1985; Jordano 1987; Armbruster et al. 1997), within the dynamic modeling framework of random fluctuations with different types of distributions could provide

new insight to understand the structure, diversity, and persistence of large communities with multiple interaction types.

5 Acknowledgements

We thank José Fedriani for suggestions and comments on potential data from the Doñana Ecological Network, Jofre Carnicer, Arndt Hampe, and Alfredo Valido for useful comments on a previous draft, Miguel A. Fortuna for ideas and technical improvements, Pedro Sosa, and Enrique Collado for technical improvements, Santiago Martín and Carmen Mari Pérez, for data organization and typing, and to Juan Amat, Jordi Figuerola, Andy Green, Ramón Soriguer, and Alejandro Rodríguez for providing us with unpublished data. Funding was provided by the Spanish Ministry of Science and Technology (Grants REN2003-04774 to JB and REN2003-00273 to PJ, and Ph.D. Fellowship FP2000-6137 to CJM).

6 References

Allier, C., González Bernáldez, F., and Ramirez, L. (1974). Mapa ecológico de la reserva Biológica de Doñana. División de Ciencias, C.S.I.C., Sevilla.

Albert, R., Jeong, H., & Barabási, A. (2000). Error and attack tolerance of complex networks. *Nature*, **406**:378-382.

Amat, J. A., and Herrera, C. M. (1977). Alimentación de la Garza Imperial *Ardea purpurea* en las Marismas del Guadalquivir durante un periodo de nidificación. *Ardeola*, **24**:95-104.

Amat, J. A., García-Criado, B., and García-Ciudad, A. (1991). Food, feeding behaviour and nutritional ecology of wintering greylag geese, *Anser anser*. *Ardea*, **79**:271-282.

Amat, J. A. (1981). Alimentación primaveral de la garcilla bueyera. *Doñana Acta Vertebrata*, **8**:207-213.

Amat, J. A. (1986). Information on the diet of the Stone Curlew *Burhinus oediconemus* in Doñana, southern Spain. *Bird Study*, **33**:71-73.

Amat, J. A. (1995). Effects of wintering greylag geese *Anser anser* on their *Scirpus* food plants. *Ecography*, **18**:155-163.

Armbruster, W. S., Howard, J. J., Clausen, T. P., Edward, M. D., Loquvam, J. C., Matsuki, M., Cerendolo, B., Andel, F. (1997). Do biochemical exaptations link evolution of plant defense and pollination systems? historical hypotheses and experimental tests with *Dalechampia vines*. *The American Naturalist*, **149**:461-484.

Armbruster, W. S. (1997). Exaptations link evolution of plant-herbivore and plant-pollinator interactions: a phylogenetic inquiry. *Ecology*, **778**:1661-1672.

Berlow, E. L., Neutel, A.-M., Cohen, J. E., DeRuiter, P. C., et al. (2004). Interaction strengths in food webs: issues and opportunities. *J. of Anim. Ecol.*, **73**:585-598.

Cobo, M., and Andreu, A. C. (1988). Seed consumption and dispersal by the spur-thighed tortoise *Testudo graeca*.

Oikos, **51**:267-273.

Cohen, J. E., et al. (1993). Improving food webs. *Ecology*, **74**:252-258.

Chen, X., and Cohen, J. E. (2001). Global stability, local stability, and permanence in model food webs. *J. theor. Biol.*, **212**:223-235.

Ehrlich, P. R., and Raven, P. H. (1964). Butterflies and plants: A study in coevolution. *Evolution*, **18**:586-608.

Fedriani, J., M. (1996). Dieta anual del Zorro, *Vulpes vulpes*, en dos habitats del Parque nacional de Doñana. *Doñana Acta Vertebrata* **23**:143-152.

Figuerola, J., Green, A. J., and Santamaría, L. (2003). Passive internal transport of aquatic organisms by waterfowl in Doñana, south-west Spain. *Global Ecology and Biogeography* (in press).

Gómez, J. M. (1996). Predisersal reproductive ecology of an arid land crucifer, *Moricandia moricandioides*: effect of mammal herbivory on seed production. *Journal of Arid Environments*, **33**:425-437.

Gutiérrez-Yurrita, P. J., Sancho, G., Bravo, M. A., Baltanás, A., and Montes, C. (1998). Diet of the red swamp crayfish *Procambarus clarkii* in natural ecosystems of the Doñana national park temporary fresh-water marsh (Spain). *Journal of Crustacean Biology*, **18**:120-127.

Herrera, C. M. (1982). Defense of ripe fruit from pests: its significance in relation to plant-disperser interactions. *The American Naturalist*, **120**:218-241.

Herrera, C. M. (1985). Aposematic insects as six-legged fruits: incidental short-circuiting of their defense by frugivorous birds. *The American Naturalist*, **126**:286-293.

Herrera, C. M. (2000). Measuring the effects of pollination and herbivores: evidence for non-additivity in a perennial herb. *Ecology*, **81**:2170-2176.

Herrera, J. (1988). Pollination relationships in southern spanish mediterranean shrublands. *Journal of Ecology* **76**:274-287.

Hori, M. (1987). Mutualism and commensalism in a fish community in Lake Tanganyika. In: Kawano, S., Connell, J. H., and Hidaka, T., eds. *Evolution and Coadaptation in Biotic Communities*, University of Kyoto Press, Tokyo.

Janzen, D. H. (1969). Seed eaters versus seed size, number, toxicity and dispersal. *Evolution*, **23**:1-27.

Jordano, P. (1984). Relaciones entre plantas y aves frugívoras en el matorral mediterráneo del área de Doñana. Unpublished PhD. University of Sevilla.

Jordano, P. (1987). Avian fruit removal: effects of fruit variation, crop size, and insect damage. *Ecology*, **68**:1711-1723.

Jordano, P. (1989). Pre-dispersal biology of *Pistacia lentiscus* (Anacardiaceae): cumulative effects on seed removal by birds. *Oikos*, **55**:375-386.

Karban, R., and Strauss, S. Y. (1993). Effects of herbivores on growth and reproduction of their perennial host, *Erigeron glaucus*. *Ecology*, **74**:39-46.

Kokkoris, G. D., Troumbis, A., and Lawton, J. H. (1999). Patterns of species interaction strength in assembled theoretical competition communities. *Ecol. Lett.*, **2**:70-74.

Lawlor, L. R., and Maynard Smith, J. (1976). The co-evolution and stability of competing species. *The American Naturalist*, **110**:79-99.

Levins, R. (1975). Evolution in communities near equilibrium. In: Cody, M. L., and Diamond, J. M., eds. *Ecology and Evolution of Communities*. Harvard Univ. Press. Cambridge, Massachusetts, USA.

Martín, R. (1981). Ecología trófica del Tejón, *Meles meles*, en la Reserva Biológica de Doñana. Unpublished PhD. University of Sevilla.

Martín, R., Rodríguez, A., and Delibes, A. (1995). Local feeding specialization by badgers *Meles meles* in a mediterranean environment. *Oecologia*, **101**:45-50.

Palacios, F. (1975). Estudio Ecológico del Lirón Careto grande, *Eliomys quercinus ssp. lusitanicus*, (Reuvens, 1890), en la Reserva Biológica de Doñana. *Bol. Est. Cent. Ecol.*, **24**:65-76.

Palomares, F. Delibes, M. (1991). Alimentación del meloncillo *Herpestes ichneumon* y de la gineta *Genetta genetta* en la reserva biológica de Doñana, S. O. de la Península Ibérica. *Doñana Acta Vertebrata*, **18**:5-20.

Rau, J. R. (1987). Ecología del Zorro en la Reserva Biológica de Doñana. Unpublished PhD. University of Sevilla.

Ringel, M. S., Hu, H. H., and Anderson, G. (1996). The stability and persistence of mutualisms embedded in community interactions. *Theor. Pop. Biol.*, **50**:281-297.

Rivas-Marínez, S. M., Costa, M., Castroviejo, S., and Valdés, E. (1980). Vegetación de Doñana (Huelva, España). *Lazaroa*, **2**:5-189.

Rodríguez, R. Hiraldo, F. (1975). Régimen alimenticio del calamón (*Porphyrio porphyrio*) en las Marismas del Guadalquivir. *Doñana Acta Vertebrata*, **2**:201-213.

Soriguer, R.C. (1988). Alimentación del conejo (*Oryctolagus cuniculus* L. 1758) en Doñana. SO, España. *Doñana Acta Vertebrata*, **15**:141-150.

Soriguer, R. C., Rodríguez, A., Domínguez, L. (2001). Análisis de la incidencia de los grandes herbívoros en la marisma y vera del Parque Nacional de Doñana. Ministerio de Medio Ambiente, Organismo Autónomo Parques Nacionales.

Strauss, S. Y., Conner, J. K., and Rush, S. L. (1996). Foliar herbivory affects floral characters and plant attractiveness to pollinators: implications for male and female plant fitness. *The American Naturalist*, **147**:1098-1107.

Strauss, S. Y. (1997). Floral characters link herbivores, pollinators, and plant fitness. *Ecology*, **78**:1640-1645.

Strauss, S. Y., Irwin, R. E. (2004). Ecological and evolutionary consequences of multispecies plant-animal interactions. *Annu. Rev. Ecol. Evol. Syst.*, **35**:435-466.

Thompson, J. N. (2002). Plant-animal interactions: future directions. In: Herrera, C. M., and Pellmyr, O., eds., *Plant-animal interactions. An evolutionary approach*. Blackwell, Oxford.

Valverde, J. A. (1958). An Ecological Sketch of the Coto Doñana. *Brit. Birds*, **LI**:1-23.

Valverde, J. A. (1967). Estructura de una comunidad de vertebrados terrestres. *Monografías de la Estación Biológica de Doñana*. N° 1.

Venero, J. L. (1984). Dieta de los grandes fitófagos silvestres de Doñana. *Doñana Acta Vertebrata*, **11**. N° especial.

Yuma, M. (1993). Competitive and cooperative interactions in Tanganykan fish communities. In: Kawanabe, H., Cohen, J. E., and Iwasaki, K., eds. *Mutualism and Community Organization*, Oxford Univ. Press.

7 Appendix

7.0.1 Doñana situation.

Most studies introduced here were carried out in the area of the Doñana Biological Reserve ($37^{\circ}1'N, 6^{\circ}33'W$), southwestern Spain. This reserve includes approximately 68 km^2 (6800 ha) inside the limits of the Doñana National Park, situated on the right bank of the mouth of the river Guadalquivir. The altitude above sea level varies between 0m and 32m . The reserve is located in a sandy coastal area where Mediterranean scrub constitutes the main and dominant vegetation. A more detailed description of the area can be found in Valverde (1958), Allier et al. (1974), and Rivas-Marínez et al. (1980).

7.0.2 Construction of the Doñana Ecological Network: source of empirical data

The present study includes only a subset of the Doñana Ecological Network by including feeding activities from 23 studies (with a total number of 394 species) carried out in the area of the Doñana Biological Reserve. Data comes from analysis of stomach contents and feces captured in the field mainly during the decade 1975-1985 (15 out 23 studies within this period). Although different studies have shown the importance of anthrophagous herbivores and frugivorous insect communities (both pulps and seed predators) for the reproductive cycle of higher plants (Jordano 1987, 1989), we have discarded these species in the present analysis because current information is mainly restricted to a small number of higher plants. We have discarded domestic horse, sheep and cow despite of their importance for the plant community structure and dynamics in the Doñana Biological Reserve (Soriguer et al. 2001). The most important limitation of the current work is that data were obtained using heterogeneous methodologies, and field studies were carried out in different years and seasons. However, it is interesting to note that the duration of 12 studies is equal or greater than two years, which implies an important sampling effort for almost 80% of species in this network. The sign of the interactions has been measured in 45% of the studies (10 out 23). Table 1 and Table 2 provide information for each species recorded following guidelines by Cohen et al. (1993).

7.0.3 Table 1: List of Species and Statistics.

Column one shows species codes. Plant species codes go from number 2 to 201, with a total number of 170 plants. Codes for invertebrate species go from 202 to 381 (180 species). Codes for seed dispersers go from 382 to 402, and from 418 to 423 (27 species). Herbivores go from 403 to 417 (15 species). Column two shows the scientific name of each species. Columns three and four show the number of links of each plant (k_{out}), and for each herbivore or pollinator-disperser (k_{in}). Columns five to seven show the number of modules in which each plant ($N^{\circ} mp$), pollinator-disperser ($N^{\circ} mm$), or herbivore ($N^{\circ} ma$) is present. Two species showed both types of interactions, *Testudo graeca*, code 402 when dispersing 34 plant species, and with the 410 when eating on 6 plant species, and *Porphyrio porphyrio* code 412 (disperse and eat on 6 and 4 plant species respectively). Column eight shows the reference from where specific species was introduced in the present analysis.

Code	Species	k_out	k_in	$N^{\circ} mp$	$N^{\circ} mm$	$N^{\circ} ma$
2	<i>Pistacia lentiscus</i>	18	—	32	—	—
3	<i>Foeniculum vulgare</i>	1	—	0	—	—
4	<i>Hydrocotyle vulgaris</i>	2	—	0	—	—
7	<i>Echium sp.</i>	1	—	0	—	—
8	<i>Callitriche platycarpa</i>	1	—	0	—	—
9	<i>Lonicera periclymenum</i>	10	—	0	—	—
11	<i>Loeflingia baetica</i>	1	—	0	—	—
13	<i>Sagina apetala</i>	1	—	0	—	—
14	<i>Silene nocturna</i>	1	—	0	—	—
15	<i>Spergula arvensis</i>	1	—	0	—	—
16	<i>Ceratophyllum demersum</i>	1	—	0	—	—
17	<i>Cistus libanotis</i>	29	—	0	—	—
18	<i>Cistus salvifolius</i>	29	—	54	—	—
19	<i>Halimium apeninnum subsp. stoechadifolium</i>	3	—	0	—	—
20	<i>Halimium calycinum</i>	13	—	12	—	—
21	<i>Halimium halimifolium</i>	23	—	76	—	—
22	<i>Xolantha guttata</i>	2	—	0	—	—
23	<i>Andryala arenaria</i>	1	—	0	—	—
24	<i>Anthemis cotula</i>	1	—	0	—	—
25	<i>Anthemis mixta</i>	1	—	0	—	—
26	<i>Artemisia campestris</i>	1	—	0	—	—
27	<i>Carduus meoanthus</i>	1	—	0	—	—
28	<i>Carduus pycnocephalus</i>	1	—	0	—	—
29	<i>Carduus sp.</i>	1	—	0	—	—
30	<i>Chamaemelum fuscatum</i>	1	—	0	—	—
31	<i>Chamaemelum mixtum</i>	3	—	0	—	—
32	<i>Evax pygmaea</i>	1	—	0	—	—
33	<i>Hypochaeris italicum subsp. serotinum</i>	19	—	0	—	—
34	<i>Hypochaeris glabra</i>	1	—	0	—	—
35	<i>Leontodon maroccanus</i>	1	—	0	—	—

36	<i>Leontodon taraxacoides</i>	5	—	4	—	—
37	<i>Senecio jacobaea</i>	1	—	0	—	—
38	<i>Senecio sp.</i>	2	—	0	—	—
39	<i>Tolpis barbata</i>	1	—	0	—	—
40	<i>Cressa cretica</i>	1	—	0	—	—
47	<i>Malcolmia lacera</i>	2	—	1	—	—
49	<i>Malcolmia sp.</i>	1	—	0	—	—
50	<i>Teesdalia coronopifolia</i>	1	—	0	—	—
51	<i>Juniperus oxycedrus subsp. macrocarpa</i>	1	—	0	—	—
52	<i>Juniperus phoenicea</i>	2	—	0	—	—
53	<i>Carex distans</i>	1	—	0	—	—
54	<i>Carex divisa</i>	3	—	0	—	—
55	<i>Carex sp.</i>	1	—	0	—	—
56	<i>Cyperus longus</i>	2	—	0	—	—
57	<i>Eleocharis multicaulis</i>	1	—	0	—	—
58	<i>Eleocharis palustris</i>	1	—	0	—	—
59	<i>Scirpoides holoschoenus</i>	5	—	2	—	—
61	<i>Scirpus lacustris subsp. lacustris</i>	1	—	0	—	—
62	<i>Scirpus litoralis</i>	2	—	0	—	—
63	<i>Scirpus maritimus</i>	12	—	11	—	—
64	<i>Scirpus setaceus</i>	2	—	0	—	—
65	<i>Scirpus sp.</i>	1	—	0	—	—
66	<i>Arthrocnemum sp.</i>	7	—	0	—	—
67	<i>Sarcocornia perennis</i>	2	—	0	—	—
68	<i>Tamus communis</i>	4	—	0	—	—
69	<i>Pseudoscabiosa diandra</i>	1	—	0	—	—
70	<i>Corema album</i>	3	—	2	—	—
71	<i>Arbutus unedo</i>	2	—	0	—	—
72	<i>Calluna vulgaris</i>	23	—	22	—	—
73	<i>Erica ciliaris</i>	14	—	13	—	—
74	<i>Erica scoparia</i>	1	—	0	—	—
75	<i>Erica sp.</i>	1	—	0	—	—
76	<i>Astragalus pelecinus</i>	1	—	0	—	—
78	<i>Cytisus grandiflorus</i>	2	—	1	—	—
79	<i>Genista triacanthos</i>	1	—	0	—	—
80	<i>Lathyrus annuus</i>	1	—	0	—	—
81	<i>Lotus hispidus</i>	1	—	0	—	—
82	<i>Lotus sp.</i>	2	—	0	—	—
83	<i>Lotus subbiflorus</i>	1	—	0	—	—
85	<i>Ononis sp.</i>	2	—	1	—	—
86	<i>Ornithopus sativus</i>	1	—	0	—	—
87	<i>Ornithopus sp.</i>	1	—	0	—	—
88	<i>Stauracanthus genistoides</i>	6	—	8	—	—
90	<i>Trifolium repens</i>	1	—	0	—	—
91	<i>Trifolium sp.</i>	2	—	0	—	—
92	<i>Ulex australis</i>	1	—	0	—	—
93	<i>Ulex minor</i>	7	—	6	—	—

94	<i>Ulex parviflorus</i>	4	—	0	—	—
96	<i>Quercus suber</i>	3	—	0	—	—
97	<i>Frankenia laevis</i>	1	—	0	—	—
99	<i>Lepiota sp.</i>	2	—	0	—	—
100	<i>Erodium cicutarium</i>	1	—	0	—	—
102	<i>Geranium molle</i>	1	—	0	—	—
103	<i>Hypericum elodes</i>	1	—	0	—	—
104	<i>Myriophyllum verticillatum</i>	1	—	0	—	—
105	<i>Pteridium aquilinum</i>	4	—	0	—	—
106	<i>Crocus serotinus subsp. salzmannii</i>	1	—	0	—	—
107	<i>Juncus effusus</i>	3	—	0	—	—
108	<i>Juncus heterophyllus</i>	2	—	0	—	—
109	<i>Juncus maritimus</i>	4	—	0	—	—
110	<i>Juncus sp.</i>	1	—	0	—	—
111	<i>Juncus striatus</i>	1	—	0	—	—
112	<i>Lavandula stoechas</i>	18	—	17	—	—
113	<i>Rosmarinus officinalis</i>	25	—	84	—	—
114	<i>Thymus mastichina</i>	23	—	22	—	—
115	<i>Lemna minor</i>	1	—	0	—	—
116	<i>Asparagus aphyllus</i>	21	—	0	—	—
117	<i>Asphodelus aestivus</i>	3	—	0	—	—
119	<i>Scilla peruviana</i>	1	—	0	—	—
120	<i>Smilax aspera</i>	21	—	0	—	—
121	<i>Urginea maritima</i>	1	—	0	—	—
123	<i>Malva parviflora</i>	2	—	0	—	—
124	<i>Myrtus communis</i>	16	—	28	—	—
127	<i>Olea europaea subsp. sylvestris</i>	12	—	20	—	—
128	<i>Phillyrea angustifolia</i>	14	—	13	—	—
129	<i>Serapias lingua</i>	1	—	0	—	—
130	<i>Chamaerops humilis</i>	8	—	15	—	—
131	<i>Pinus pinea</i>	1	—	0	—	—
132	<i>Plantago coronopus</i>	2	—	0	—	—
133	<i>Plantago sp.</i>	1	—	0	—	—
134	<i>Armeria gaditana</i>	1	—	0	—	—
135	<i>Armeria pungens</i>	1	—	0	—	—
136	<i>Armeria velutina</i>	19	—	0	—	—
137	<i>Agrostis sp.</i>	1	—	0	—	—
138	<i>Agrostis stolonifera</i>	3	—	0	—	—
139	<i>Ammophila arenaria</i>	1	—	0	—	—
140	<i>Anthoxanthum ovatum</i>	3	—	2	—	—
142	<i>Avena longiglumis</i>	1	—	0	—	—
143	<i>Briza maxima</i>	3	—	2	—	—
144	<i>Briza minor</i>	1	—	0	—	—
145	<i>Bromus diandrus</i>	1	—	0	—	—
146	<i>Bromus matritensis</i>	1	—	0	—	—
147	<i>Bromus sp.</i>	2	—	0	—	—
148	<i>Corynephorus sp.</i>	1	—	0	—	—

149	<i>Cynodon dactylon</i>	6	—	5	—	—
150	<i>Chaetopogon fasciculatus</i>	1	—	0	—	—
151	<i>Glyceria declinata</i>	1	—	0	—	—
152	<i>Glyceria sp.</i>	1	—	0	—	—
153	<i>Holcus sp.</i>	1	—	0	—	—
154	<i>Hordeum marinum</i>	3	—	0	—	—
155	<i>Lagurus ovatus</i>	1	—	0	—	—
156	<i>Lolium sp.</i>	2	—	0	—	—
157	<i>Oryza sativa</i>	2	—	0	—	—
158	<i>Panicum repens</i>	4	—	3	—	—
159	<i>Paspalum sp.</i>	2	—	1	—	—
160	<i>Paspalum vaginatum</i>	1	—	0	—	—
161	<i>Phalaris sp.</i>	1	—	0	—	—
162	<i>Phragmites australis</i>	2	—	0	—	—
163	<i>Phragmites sp.</i>	1	—	0	—	—
164	<i>Poa annua</i>	1	—	0	—	—
165	<i>Poa trivialis</i>	1	—	0	—	—
166	<i>Poaceae</i>	1	—	0	—	—
167	<i>Polypogon maritimus</i>	2	—	1	—	—
168	<i>Sporobolus sp.</i>	1	—	0	—	—
169	<i>Vulpia alopecurus</i>	2	—	0	—	—
170	<i>Vulpia sp.</i>	2	—	1	—	—
174	<i>Rumex bucephalophorus</i>	5	—	4	—	—
177	<i>Rumex sp.</i>	2	—	0	—	—
178	<i>Potamogeton polygonifolius</i>	1	—	0	—	—
179	<i>Anagallis arvensis</i>	5	—	4	—	—
180	<i>Cytinus hypocistis</i>	2	—	0	—	—
181	<i>Ranunculus bulbosus</i>	1	—	0	—	—
182	<i>Ranunculus peltatus</i>	1	—	0	—	—
183	<i>Ranunculus peltatus subsp. baudotii</i>	1	—	0	—	—
184	<i>Ranunculus sardous</i>	1	—	0	—	—
185	<i>Ranunculus sceleratus</i>	1	—	0	—	—
186	<i>Ranunculus sp.</i>	2	—	1	—	—
187	<i>Reseda media</i>	1	—	0	—	—
188	<i>Rhamnus lycioides</i>	13	—	0	—	—
189	<i>Crataegus monogyna</i>	5	—	4	—	—
190	<i>Pyrus bourgaeana</i>	4	—	4	—	—
191	<i>Rubus ulmifolius</i>	41	—	180	—	—
192	<i>Rubia peregrina</i>	3	—	0	—	—
194	<i>Salix alba</i>	1	—	0	—	—
195	<i>Osyris alba</i>	9	—	8	—	—
196	<i>Osyris quadripartita</i>	15	—	0	—	—
197	<i>Linaria sp.</i>	1	—	0	—	—
198	<i>Sparganium erectum</i>	1	—	0	—	—
199	<i>Daphne gnidium</i>	93	—	0	—	—
200	<i>Typha angustifolia</i>	3	—	0	—	—
201	<i>Typha sp.</i>	1	—	1	—	—

202	<i>Heliotaurus ruficollis</i>		2	---	4	---
203	<i>Bruchidae (NI1)</i>		1	---	4	---
204	<i>Anthaxia parallela</i>		1	---	0	---
205	<i>Anthaxia Dimidiata</i>		1	---	4	---
206	<i>Acmaeodera sp.</i>		2	---	4	---
207	<i>Malthodes sp.</i>		1	---	2	---
208	<i>Cantharidae(NI2)</i>		4	---	8	---
209	<i>Nustera distigma</i>		2	---	0	---
210	<i>Delius sp.</i>		2	---	2	---
211	<i>Cerambycidae(NI3)</i>		1	---	2	---
212	<i>Palleira femorata</i>		1	---	0	---
213	<i>Tropinota squalida</i>		2	---	6	---
214	<i>Coptocephala unifasciata</i>		2	---	5	---
215	<i>Coptocephala scopolina</i>		1	---	4	---
216	<i>Tychius sp.</i>		1	---	0	---
217	<i>Curculionidae(NI4)</i>		1	---	3	---
218	<i>Lobonyx aeneus</i>		5	---	7	---
219	<i>Anthrenus sp.</i>		9	---	13	---
220	<i>Attagenus sp.</i>		1	---	1	---
221	<i>Cardiophorus bipunctatus</i>		1	---	0	---
222	<i>Helodidae(NI5)</i>		1	---	2	---
223	<i>Malachius sp.</i>		3	---	3	---
224	<i>Malachiidae(NI6)</i>		1	---	2	---
225	<i>Melilidae(NI7)</i>		2	---	2	---
226	<i>Mylabris sp.</i>		1	---	4	---
227	<i>Chasmatopterus sp.</i>		2	---	4	---
228	<i>Hymenoptia sp.</i>		1	---	0	---
229	<i>Mordellistena sp.</i>		5	---	3	---
230	<i>Nitidulidae(NI8)</i>		4	---	10	---
231	<i>Oedemeridae(NI9)</i>		1	---	4	---
232	<i>Bombylius argentifrons</i>		1	---	1	---
233	<i>Bombylius ater</i>		2	---	1	---
234	<i>Bombylius fulvescens</i>		1	---	1	---
235	<i>Bombylius torquatus</i>		3	---	6	---
236	<i>Dischistus senex</i>		1	---	1	---
237	<i>Conophorus fumivervis</i>		2	---	2	---
238	<i>Lomatia infernalis</i>		2	---	1	---
239	<i>Exoprosopa italica</i>		1	---	0	---
240	<i>Petrorossia sp.</i>		2	---	2	---
241	<i>Phthiria sp.</i>		11	---	17	---
242	<i>Calliphoridae(NI9)</i>		17	---	17	---
243	<i>Eristalis tenax</i>		10	---	13	---
244	<i>Eristalis arbustorum</i>		1	---	0	---
245	<i>Eristalis pratorum</i>		3	---	3	---
246	<i>Eristalodes taeniops</i>		3	---	1	---
247	<i>Episyrphus balteatus</i>		3	---	1	---
248	<i>Episyrphus auricollis</i>		4	---	5	---

249	<i>Chrysotoxum intermedium</i>		1	---	0	---
250	<i>Lathyrophthalmus aeneus</i>		2	---	1	---
251	<i>Lathyrophthalmus quinquelineatus</i>		2	---	1	---
252	<i>Melanostoma mellinum</i>		1	---	0	---
253	<i>Metasyrphus corollae</i>		5	---	5	---
254	<i>Sphaerophoria scripta</i>		5	---	4	---
255	<i>Sphaerophoria rueppelli</i>		1	---	1	---
256	<i>Syrirta pipiens</i>		1	---	0	---
257	<i>Paragus tibialis</i>		1	---	0	---
258	<i>Volucella elegans</i>		1	---	0	---
259	<i>Tachinidae(NI10)</i>		5	---	5	---
260	<i>Andrena bicolor subsp. nigrosterna</i>		1	---	4	---
261	<i>Andrena bimaculata</i>		1	---	0	---
262	<i>Andrena assimilis subsp. gallica</i>		1	---	5	---
263	<i>Andrena hispania</i>		4	---	10	---
264	<i>Andrena nigroaenea</i>		2	---	2	---
265	<i>Andrena squalida</i>		2	---	5	---
266	<i>Andrena sp.</i>		1	---	2	---
267	<i>Panurgus sp.</i>		1	---	2	---
268	<i>Amegilla fasciata</i>		4	---	3	---
269	<i>Amegilla 4-fasciata</i>		2	---	1	---
270	<i>Anthophora acervorum</i>		1	---	1	---
271	<i>Anthophora dispar</i>		2	---	5	---
272	<i>Anthophora sp.</i>		1	---	2	---
273	<i>Epeolus fallax</i>		1	---	1	---
274	<i>Eucera hispaliensis</i>		1	---	1	---
275	<i>Ceratina cucurbitina</i>		7	---	12	---
276	<i>Ceratina cyanea</i>		4	---	1	---
277	<i>Ceratina mocsaryi</i>		3	---	5	---
278	<i>Nomada mutabilis</i>		1	---	4	---
279	<i>Tetralonia berlandi</i>		2	---	5	---
280	<i>Xylocopa cantabrita</i>		7	---	11	---
281	<i>Xylocopa violacea</i>		1	---	0	---
282	<i>Apis mellifera</i>		14	---	23	---
283	<i>Bombus lucorum</i>		2	---	6	---
284	<i>Colletes acutus</i>		3	---	2	---
285	<i>Colletes caspicus subsp. dusmeti</i>		4	---	1	---
286	<i>Colletes fodiens subsp. hispanicus</i>		1	---	0	---
287	<i>Colletes Succincta</i>		3	---	2	---
288	<i>Colletes sp.</i>		2	---	2	---
289	<i>Lasioglossum aegyptiellum</i>		1	---	0	---
290	<i>Lasioglossum albocinctum</i>		4	---	6	---
291	<i>Lasioglossum callizonium</i>		1	---	0	---
292	<i>Lasioglossum immunitum</i>		8	---	9	---
293	<i>Lasioglossum littorale</i>		7	---	5	---
294	<i>Lasioglossum pallens</i>		1	---	1	---
295	<i>Lasioglossum prasinum</i>		10	---	11	---

296	<i>Lasioglossum punctatissimum</i>		7	---	3	---
297	<i>Lasioglossum villosulum</i>		1	---	0	---
298	<i>Lasioglossum sp.</i>		6	---	7	---
299	<i>Halictus 4-cinctus</i>		6	---	8	---
300	<i>Halictus fulvipes</i>		1	---	0	---
301	<i>Halictus gemmeus</i>		1	---	0	---
302	<i>Halictus scabiosa</i>		1	---	0	---
303	<i>Halictus seladonia-smaragdulus</i>		1	---	0	---
304	<i>Sphecodes hirtellus</i>		1	---	0	---
305	<i>Sphecodes pellucidus</i>		1	---	2	---
306	<i>Anthidiellum strigatum</i>		2	---	1	---
307	<i>Stelis signata</i>		2	---	0	---
308	<i>Megachile maritima</i>		3	---	6	---
309	<i>Megachile leachella</i>		1	---	2	---
310	<i>Megachile pilidens</i>		3	---	3	---
311	<i>Heriades crenulatus</i>		1	---	0	---
312	<i>Osmia sp.</i>		1	---	0	---
313	<i>Dasypoda cingulata</i>		4	---	6	---
314	<i>Dasypoda iberica</i>		1	---	0	---
315	<i>Eumenes dubius</i>		1	---	0	---
316	<i>Odynerus sp.</i>		1	---	0	---
317	<i>Eumenidae (NI11)</i>		3	---	1	---
318	<i>Camponotus lateralis</i>		2	---	5	---
319	<i>Camponotus sicheli</i>		2	---	0	---
320	<i>Cataglyphis viatica</i>		1	---	0	---
321	<i>Crematogaster auberti</i>		1	---	0	---
322	<i>Lasius niger</i>		7	---	8	---
323	<i>Tapinoma erraticum</i>		1	---	3	---
324	<i>Tapinoma sp.</i>		1	---	0	---
325	<i>Pompilidae (NI12)</i>		3	---	1	---
326	<i>Elis villosa</i>		3	---	1	---
327	<i>Ammophila heydeni</i>		1	---	0	---
328	<i>Bembex flavescens</i>		1	---	0	---
329	<i>Bembex olivacea</i>		1	---	0	---
330	<i>Cerceris arenaria</i>		2	---	1	---
331	<i>Cerceris rybiensis</i>		2	---	1	---
332	<i>Diodontus insidiosus</i>		1	---	2	---
333	<i>Gorytes sp.</i>		1	---	0	---
334	<i>Lindenius luteiventris</i>		2	---	0	---
335	<i>Mellinus arvensis</i>		1	---	1	---
336	<i>Philanthus triangulum</i>		1	---	0	---
337	<i>Philanthus venustus</i>		1	---	1	---
338	<i>Podalonia tydei senilis</i>		1	---	4	---
339	<i>Pryonix kirbii</i>		1	---	0	---
340	<i>Meria tripunctata</i>		3	---	1	---
341	<i>Meria sp.</i>		3	---	1	---
342	<i>Tiphia morio</i>		2	---	0	---

343	<i>Aricia agestis subsp. cramer</i>		2	---	1	---
344	<i>Laeosopis roboris</i>		2	---	5	---
345	<i>Lampides boeticus</i>		1	---	0	---
346	<i>Lycaena phlaeas</i>		1	---	4	---
347	<i>Plebejus argus</i>		3	---	6	---
348	<i>Polyommatus icarus</i>		2	---	1	---
349	<i>Leptotes pirithous</i>		5	---	2	---
350	<i>Gegenes nostrodamus</i>		2	---	1	---
351	<i>Colias crocea</i>		1	---	0	---
352	<i>Gonepteryx cleopatra</i>		1	---	0	---
353	<i>Pieris brassicae</i>		1	---	0	---
354	<i>Artogeia rapae</i>		2	---	5	---
355	<i>Pontia daplidice</i>		1	---	0	---
356	<i>Pyronia cecilia</i>		1	---	0	---
357	<i>Macroglossum stellatarum</i>		2	---	0	---
358	<i>Eilema complana</i>		1	---	0	---
359	<i>Rhodometra sacraria</i>		1	---	0	---
360	NI13		1	---	0	---
361	<i>Hoplodrina ambigua</i>		1	---	0	---
362	<i>Agrotis puta</i>		1	---	0	---
363	<i>Mythimna vitellina</i>		1	---	0	---
364	<i>Metachrostis dardouinii</i>		1	---	0	---
365	<i>Metachrostis velox</i>		1	---	0	---
366	<i>Heliothis armigera</i>		1	---	0	---
367	<i>Heliothis nubigera</i>		1	---	0	---
368	<i>Heliothis peltigera</i>		1	---	0	---
369	<i>Cerocala scapulosa</i>		1	---	0	---
370	<i>Discestra sodae</i>		1	---	0	---
371	<i>Pechipogo plumigeralis</i>		1	---	0	---
372	<i>Autographa gamma</i>		1	---	0	---
373	<i>Spodoptera exigua</i>		1	---	0	---
374	<i>Acrobasis porphyrella</i>		1	---	0	---
375	<i>Pempeliella plumbella</i>		1	---	0	---
376	<i>Psorosa brephiella</i>		1	---	0	---
377	<i>Psorosa genistella</i>		1	---	0	---
378	<i>Evergestis politalis</i>		1	---	0	---
379	<i>Mecyna sp.</i>		1	---	0	---
380	<i>Palpita unionalis</i>		1	---	0	---
381	<i>Udaea martialis</i>		1	---	0	---
382	<i>Sylvia atricapilla</i>		14	---	16	---
383	<i>Sylvia borin</i>		12	---	11	---
384	<i>Erithacus rubecula</i>		9	---	12	---
385	<i>Sylvia melanocephala</i>		12	---	13	---
386	<i>Turdus merula</i>		12	---	13	---
387	<i>Turdus philomelos</i>		5	---	8	---
388	<i>Sylvia communis</i>		4	---	6	---
389	<i>Sylvia hortensis</i>		4	---	8	---

390	<i>Sylvia cantillans</i>		7	---	10	---
391	<i>Ficedula hypoleuca</i>		4	---	3	---
392	<i>Phoenicurus phoenicurus</i>		4	---	7	---
393	<i>Sylvia undata</i>		2	---	4	---
394	<i>Luscinia megarhynchos</i>		3	---	7	---
395	<i>Muscicapa striata</i>		3	---	7	---
396	<i>Sturnus sp.</i>		4	---	7	---
397	<i>Cyanopica cyanus</i>		4	---	9	---
398	<i>Carduelis chloris</i>		5	---	10	---
399	<i>Vulpes vulpes</i>		6	---	13	---
400	<i>Eliomys quercinus subsp. lusitanicus</i>		2	---	5	---
401	<i>Meles meles</i>		3	---	7	---
402	<i>Testudo graeca*</i>		34	---	39	---
403	<i>Dama dama</i>		55	---	---	152
404	<i>Cervus elaphus</i>		50	---	---	246
405	<i>Sus scrofa</i>		20	---	---	89
406	<i>Oryctolagus cuniculus</i>		9	---	---	2
407	<i>Lepus capensis</i>		27	---	---	37
408	<i>Procambarus clarkii</i>		4	---	---	37
409	<i>Genetta genetta</i>		2	---	---	50
410	<i>Testudo graeca</i>		34	---	---	47
411	<i>Bubulcus ibis</i>		0	---	---	0
412	<i>Porphyrio porphyrio**</i>		10	---	8	2
413	<i>Ardea purpurea</i>		2	---	---	1
414	<i>Gallinula chloropus</i>		10	---	---	4
415	<i>Anser anser</i>		2	---	---	1
416	<i>Burhinus oedicephalus</i>		1	---	---	1
417	<i>Cyphosoma lawsoniae</i>		1	---	---	1
418	<i>Anas acuta</i>		1	---	0	---
419	<i>Anas clypeata</i>		2	---	11	---
420	<i>Anas crecca</i>		1	---	0	---
421	<i>Anas platyrhynchos</i>		3	---	0	---
422	<i>Anas strepera</i>		1	---	0	---
423	<i>Fulica atra</i>		1	---	0	---

7.0.4 Table 2: Data sources and Data features.

From column one to column six, the following information is included: (1) species codes equal to Table 1, (2) data source, (3) the number, type and duration of sampling, (4) the period of the study, (5) feeding location, and (6) the area of the study. Interrogants mean that not explicit information is given in the original reference.

368	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
369	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
370	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
371	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
372	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
373	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
374	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
375	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
376	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
377	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
378	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
379	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
380	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
381	Herrera (1985, 1988)	plot weekly visited between 1982 and 1984	year round	RBD	4 has
382	Jordano (1984)	634 samples (1981-1983)	year round	Hato Ratón	20km2
383	Jordano (1984)	153 samples (1981-1983)	year round	Hato Ratón	20km2
384	Jordano (1984)	289 samples (1981-1983)	year round	Hato Ratón	20km2
385	Jordano (1984)	195 samples (1981-1983)	year round	Hato Ratón	20km2
386	Jordano (1984)	65 samples (1981-1983)	year round	year round	20km2
387	Jordano (1984)	11 samples (1981-1983)	year round	Hato Ratón	20km2
388	Jordano (1984)	11 samples (1981-1983)	year round	Hato Ratón	20km2
389	Jordano (1984)	5 samples (1981-1983)	year round	Hato Ratón	20km2
390	Jordano (1984)	21 samples (1981-1983)	year round	Hato Ratón	20km2
391	Jordano (1984)	48 samples (1981-1983)	year round	Hato Ratón	20km2
392	Jordano (1984)	14 samples (1981-1983)	year round	Hato Ratón	20km2
393	Jordano (1984)	12 samples (1981-1983)	year round	Hato Ratón	20km2
394	Jordano (1984)	46 samples (1981-1983)	year round	Hato Ratón	20km2
395	Jordano (1984)	15 samples (1981-1983)	year round	Hato Ratón	20km2
396	Jordano (1984)	3 samples (1981-1983)	year round	Hato Ratón	20km2
397	Jordano (1984)	2 samples (1981-1983)	year round	Hato Ratón	20km2
398	Jordano (1984)	80 samples (1981-1983)	year round	Hato Ratón	20km2
399	Fedriani (1996)/Rau et al. (1987)	293 faecal pellets (1993-1994)/436 faecal/month (1982)	year round	Coto del rey	10km2
400	Palacios (1975)	27 stomach contents, 11 nested (1973)	year round	RBD	??
401	Martín (1981)/ Martín et al. (1995)	250 faecal pellets (1977-1978)	year round	RBD	??

402	Cobo and Andreu (1988)	170 faecal pellets (1983-1986)	Spr. & Autm.	RBD	56 has
403	Venero (1984)	484 dir. obs., 74 sto. cont. (76-81), 120 fae. (79-81)	year round	RBD	All ar.
404	Venero (1984)	534 dir. obs., 54 sto. cont. (76-81), 120 faecal (79-81)	year round	RBD	All ar.
405	Venero (1984)	138 dir. obs., 65 sto. cont. (76-81), 120 faecal (79-81)	year round	RBD	All ar.
406	Soriguer (1988)	130 fresh pellets (1977)	Summer	RBD(Mart.)	—
407	Soriguer (1982-1985), Unp. data.	2123 faecal pellets (1982-85)	year round	RBD	??
408	Gutiérrez-Yurrita et al. (1998)	502 stomachs (1992)	Spring	RBD	??
409	Palomares and Delibes (1991)	246 faecal pellets (1985-1986)	year round	RBD	??
410	Cobo and Andreu (1988)	170 faecal pellets (1983-1986)	Spr. & Autm.	RBD	56 Has
411	Amat and Soriguer (1981)	?? faecal pellets (1977)	Spring	RBD (L. Mari)	??
412	Rodríguez and Hiraldo (1975)	141 stomach contents (1968-1974)	All year	Clo. RBD	??
413	Amat and Herrera (1977)	??(1977-1978)	Summer	PND (L. Mari)	??
414	Amat and Soriguer (1984)	??	??	??	??
415	Amat et al. (1991)/ Amat (1995)	+250 fresh droppings (1981-82 to 1983-1984)	Winter	RBD	??
416	Amat (1986)	55 fresh droppings (1984)	Summer	PND (C. Gua.)	??
417	Amat (1986)	??	??	??	??
418	Figuerola et al. (2003)	44 fresh droppings (1998-1999)	Winter	Veta la Palma	4567 H.
419	Figuerola et al. (2003)	38 fresh droppings (1998-1999)	Winter	Veta la Palma	4567 H.
420	Figuerola et al. (2003)	24 fresh droppings (1998-1999)	Winter	Veta la Palma	4567 H.
421	Figuerola et al. (2003)	87 fresh droppings (1998-1999)	Winter	Veta la Palma	4567 H.
422	Figuerola et al. (2003)	17 fresh droppings (1998-1999)	Winter	Veta la Palma	4567 H.
423	Figuerola et al. (2003)	146 fresh droppings (1998-1999)	Winter	Veta la Palma	4567 H.

5.2 What is New?

The introduction of real data with two interaction types in a large ecological network is completely new. The static and dynamic model explored with data is a first approach to detect interactions between structure and dynamics. It is interesting to note that the theoretical introduction of different types of interactions between agents in large matrices is not new (see Nowak and Sigmund (2004) for a review; Doebeli et al. 2004). What is really new is the synthesis of a large number of species with different interaction types, and testing this data against a null static and dynamic model.

5.3 Current and Future Work

The integration of historical and current ecological data with multiple interaction types in a set of communities and the exploration of the structure and its dynamical implications is still far clear. But large data sets and methods to analyze data are becoming more resolved and accurate respectively. This work to the community level should not be disconnected from previous studies introducing adaptive behaviour or different interaction types in a small subset of species (Herrera 1982; Jordano 1987; Armbruster 1997), multilevel selection theory (Stanley 1975; Wilson 1976; Wilson and Swenson 2003), and current theoretical studies introducing a set of interactions in multispecies communities (Otto and Nuismer 2004).

How could the introduction of two interaction types change our view of structure, assembly and dynamics of species-rich communities? Let me try to explain it briefly with an analogy. Let's imagine a small island. Suppose that we have 100 species in the regional pool that can reach the island. How many species could we find on the island? Is the number of species in the island independent of species interactions? Suppose that each species has a code number and a ticket with the codes of the species which this species interact with. For example, species number 1 interact with the species number 4 and number 7. We suppose that first interaction is a strong dependence. That is, if number 4 is in the island, number 1 can be present, if not, number 1 can not be present. Second interaction is a strong conflict, that is, if number 7 is in the island, number 1 can not be present. Before starting to introduce species, we calculate the degree of the 100 species for both types of interactions. Once we have the topology of the system, we start to assemble

it. How does topology alter the size and function of the ecosystem?

Let me make one more assumption. We introduce in each replicate 10 species considered basic for the ecosystem dynamics. Then, we start the assembly process by choosing randomly one species from the pool, check dependences and conflicts with the rest of species, and whether they are or not in the island. If the selected species enter into conflict with an already present one, it is discarded and never will be part of the island. If there are not conflicts with the introduced species, we check whether some of the species on which it depends both directly or indirectly has been discarded or has a conflict with an already introduced species. If so, it is discarded too. Otherwise it is introduced with all the species on which it depends both directly and indirectly. The process continues until no more species are available to be included (i.e., species excluded by the assembly temporal sequence due to their conflicts with species already introduced). Imagine that we assembled 1000 replicates following the same process. How would be the community size of each replicate?, and how would be the distribution of the community size? Our first conclusion is that community size will change dramatically depending on the initial topology of the system (see Fig. 1 and figure caption). That is, if we have most species with few of both types of interactions and few species with many of them (i.e., the topology follows a power-law decays), the system will be bigger than if most species have a well defined average number of both types of interactions (i.e., the topology follows an exponential decays). Why is so important the number of species in an ecosystem? Because size alters structure, dynamics, and the function of real communities (Naeem et al. 1994; Naeem and Li 1997; Wilmers et al. 2002).

It is interesting to note that the previous assumptions are crude for species assemblages. Determining interactions between species before the assemblage is a first step. We have explored the process previously described for a real complex network (see Fig. 1 and caption for details). Although the real data explored to detect the final size of a complex network does not come from ecological studies, it could be an interesting analogy to (1) explore theoretically the assembly of species communities by integrating multiple interaction types with different qualitative and quantitative distributions, (2) study thresholds and limits to diversity in communities changing the interaction types ratio, and (3) allow adaptive behaviour of each species during the assemblage and

take into account both weak and strong interactions.

Literature Cited

Doebeli, M., Hauert, C., and Killingback, T. (2004). The Evolutionary origin of cooperators and defectors. *Science*, **306**:859-862.

Fortuna, M. A., and Melián, C., J. (2004). Scale-free regulatory networks are bigger than random ones. Submitted.

Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H., Woodfin, R. M. (1994). Declining biodiversity can affect the functioning of ecosystems. *Nature*, **368**:734-737.

Naeem, S., Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature*, **390**:507-509.

Nowak, M. A., and Sigmund, K. (2004). Evolutionary dynamics of biological games. *Science*, **303**:793-799.

Otto, S. P., and Nuismer, S. L. (2004). Species interactions and the evolution of Sex. *Science*, **304**:1018-1020.

Stanley, S. M. (1975). A Theory of Evolution Above the Species Level. *Proc. Nat. Acad. Sci. USA*. **72**:646-650.

Wilmers, C. C., Sinha, S., and Brede, M. (2002). Examining the effects of species richness on community stability: an assembly model approach. *Oikos*, **99**:363-367.

Wilson, D. S. (1976). Evolution on the level of communities. *Science*, **192**:1358-1360.

Wilson, D. S., and Swenson, W. (2003). Community genetics and community selection. *Ecology*, **84**:586-588.

Fig. 1

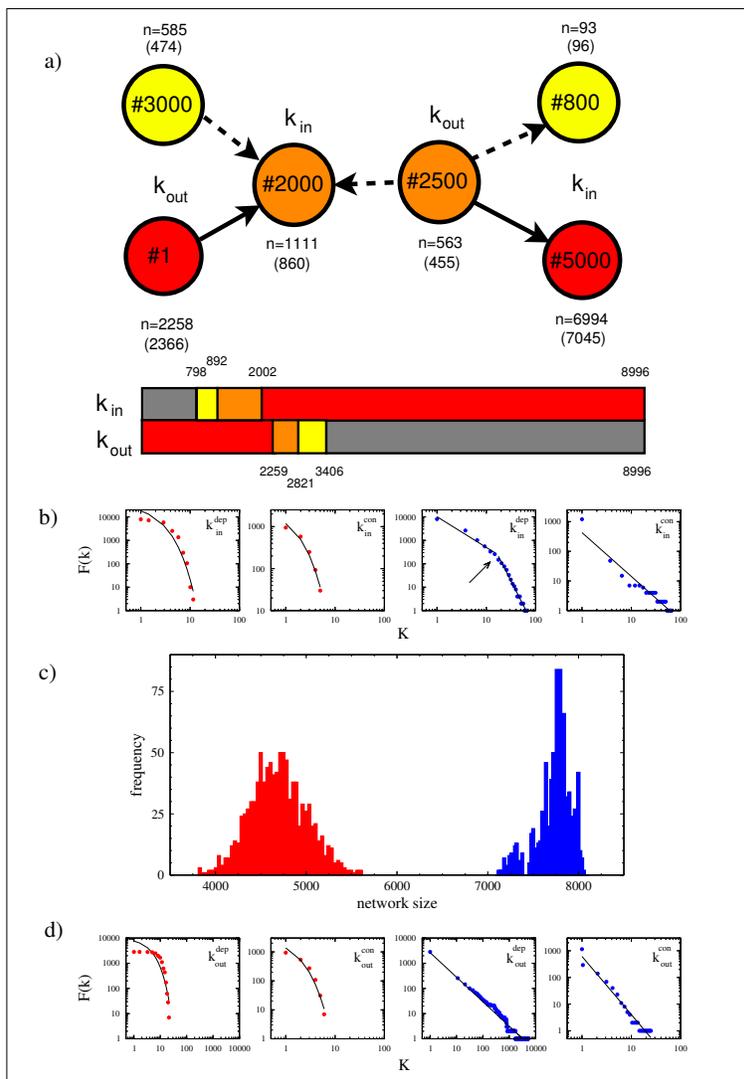


Fig. 1 synthesizes what we have done using real data from the *Debian GNU/Linux* operating system. It includes 8996 nodes (*packages*), and 31904 regulatory interactions (30003 dependences, and 1901 conflicts, which implies a 6% of conflicts or 1 conflict each 15 dependences approximately). Fig. 1a represents an hypothetical graph illustrating the type of packages as a function of their k_{in} (number of incoming edges per node) and k_{out} (number of outgoing edges per node), and types of interactions (solid arrows represent dependences k^{dep} (number of dependences per node), and dotted arrows conflicts k^{con} (number of conflicts per node)). Packages with k_{in}^{dep} (e.g., package number 5000), k_{in}^{con} (e.g., package number 800) or both (e.g., package number 2000), mean that they depend on other packages, and/or have a conflict with other packages, respectively. Packages with k_{out}^{dep} (e.g., package number 1) or k_{out}^{con} (e.g., package number 3000) or both (e.g., package number 2500), mean that other packages depend on them and/or enter into conflict with them, respectively. n is the total number of packages with each type of link in the network (in brackets the average value after 1,000 replicates of the null model (see ** for the description of the null model)). Colors in the horizontal bars correspond to the number of each type of packages in the null model. Yellow are packages with k_{in}^{con} or k_{out}^{con} . Red are packages with k_{in}^{dep} and or k_{out}^{dep} . Orange are packages with k_{in}^{dep} and k_{in}^{con} or k_{out}^{dep} and k_{out}^{con} . Gray regions are packages without k_{in} or k_{out} interactions (not shown in the graph).

Fig. 1b represents the cumulative k_{in} degree distributions of null model (*red circles*) and real data (*blue circles*). All degree distributions are marginally significant for both null model (k_{in}^{dep} , $n=7894$; k_{in}^{con} , $n=944$), and real data (k_{in}^{dep} , $n=8105$; k_{in}^{con} , $n=1204$), decaying exponentially ($P = 0.07$, and $P = 0.07$ respectively) for the null model, and as a power law for real data ($P = 0.1$ for the first regression, and $P = 0.1$ for the second with a breakpoint in $k = 15$ (solid arrow), and $P = 0.07$ respectively). Degree distribution of the null model represents the average value for ten replicates.

Fig. 1c represents the size frequency distribution differs from a normal distribution for real data (blue, Jarque-Bera test, $P < 0.05$, with an average network size of 7,647 packages) and does not differ from a normal distribution for the null model (red, Jarque-Bera test $P = 0.2$, with an average network size of

4,750 packages). No replicate from the null model distribution is equal or higher than any replicate from the real data distribution ($P < 0.0001$).

Fig. 1d represents the cumulative k_{out} degree distributions of null model (*red circles*) and real data (*blue circles*). Degree distributions for the null model are significant (k_{out}^{dep} , $n=2821$), and marginally significant (k_{out}^{con} , $n=941$), decaying exponentially in both cases ($P < 0.05$ and $P = 0.09$ respectively). Degree distribution for real data are significant (k_{out}^{dep} , $n=2821$), and marginally significant (k_{out}^{dep} , $n=1148$), decaying in both cases as a power law ($P < 0.05$ and $P = 0.08$ respectively). Degree distribution of the null model represents the average value for ten replicates.

**To test the effect of the topology of a large regulatory network on its activated network size we develop a null model that (1) preserves the total number of dependences and conflicts as in the real network, and (2) randomizes packages maintaining statistically their input and output interactions for dependences and conflicts (Fig 1a), forcing them to an exponential degree distribution (Fig. 1b,d). As commented before we assembled 1,000 replicates from both real data and the null model, and counted the total number of packages installed in each replicate. This represents the active network size of each replicate. Therefore, each replicate from real data and data from the null model has a different number of packages installed. After 1000 replicates we obtain the frequency distribution of the active network size from both real data and data from the null model (Fig. 1c).

Chapter 6

Conclusions

1. A few highly connected species tend to interact significantly among each other generating a cohesive pattern in complex food webs. This has implications for the robustness of food webs to different perturbations.
2. Simple trophic subwebs (i.e., omnivory, apparent competition, intraguild predation) studied both empirically and theoretically are well represented in complex food webs.
3. Strongly interacting tri-trophic food chains are underrepresented in a large Caribbean marine food web. Even when they do occur, they tend to be accompanied by strong omnivory. These quantitative modules reduce the likelihood of community-wide trophic cascades.
4. Food web structure affects the extinction threshold of species after habitat loss.
5. The combination between dispersal, competition, and trophic structure alters local abundances of basal, intermediate and top species.
6. Plants exposed to mutualist species are visited significantly more often by herbivores in the Doñana ecological network. This structure affects the dynamics of the community by changing the frequency distribution of extinct species.

6.1 Conclusiones

1. Unas pocas especies altamente conectadas tienden a interactuar significativamente entre ellas y entre el resto de las especies, generando un patrón cohesivo en redes tróficas. Esta estructura tiene implicaciones para la robustez de las redes tróficas a las perturbaciones.
2. Las subredes sencillas estudiadas tanto de forma empírica como teórica están bien representadas en las redes tróficas.
3. Las cadenas tróficas con interacciones fuertes no están significativamente presentes en la red trófica del Caribe. Estas cadenas tienden a estar acompañadas con una interacción omnívora fuerte. Los módulos cuantitativos con omnivoría reducen la probabilidad de ocurrencia de las cascadas tróficas al nivel de comunidad.
4. La estructura de las redes tróficas altera los umbrales de extinción de las especies tras la destrucción del hábitat.
5. La combinación de dispersión, competencia y estructura trófica altera significativamente las abundancias locales de las especies tanto basales, intermedias como la de los niveles tróficos más altos.
6. Las plantas expuestas a interacciones con especies mutualistas son visitadas significativamente por las especies herbívoras en la red ecológica de Doñana. Esta estructura afecta la dinámica de la comunidad al cambiar la distribución de las especies extinguidas.