UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

CENTRO DE INVESTIGACIONES
EN ECOSISTEMAS

BIODIVERSIDAD VEGETAL Y GENERACIÓN DE SERVICIOS ECOSISTÉMICOS: ACERCAMIENTOS A DIFERENTES ESCALAS ESPACIALES

TESIS

QUE PARA OBTENER EL GRADO ACADÉMICO DE

DOCTORA EN CIENCIAS

PRESENTA

SANDRA QUIJAS FONSECA

TUTORA PRINCIPAL DE TESIS: DRA. PATRICIA BALVANERA LEVY

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MÉXICO, D.F. **MAYO, 2012**

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Ciencias Biológicas

COORDINACIÓN

Dr. Isidro Ávila Martínez
Director General de Administración Escolar, UNAM
Presente

Por medio de la presente me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 7 de mayo del 2012, se acordó poner a su consideración el siguiente jurado para el examen de DOCTORA EN CIENCIAS de la alumna **QUIJAS FONSECA SANDRA** con número de cuenta **91158822,** con la tesis titulada: **"Diversidad vegetal y generación de servicios ecosistémicos: acercamientos a diferentes escalas espaciales"**, bajo la dirección de la **Dra. Patricia Balvanera Levy.**

Presidente:	Dr. Gerardo Héctor R. Bocco Verdinelli
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El Comité Académico, aprobó que la integración del jurado se realizará a solicitud del alumno, **con cinco sinodales**, en apego a la nueva normatividad, acogiéndose al artículo **QUINTO TRANSITORIO**, con base en lo establecido en el Artículo 31 del Reglamento General de Estudios de Posgrado.

Sin otro particular, quedo de usted.

Atentamente
"POR MI RAZA HABLARA EL ESPIRITU"
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Al posgrado en Ciencias Biológicas de la Universidad Nacional Autónoma de México (UNAM), al personal académico y administrativo del Centro de Investigaciones en Ecosistemas (UNAM), al Consejo Nacional de Ciencia y Tecnología (CONACyT) por la beca otorgada (Beca No. 172589), al Programa de Apoyo a los Estudios de Posgrado (PAEP) de la UNAM, por el apoyo económico otorgado para la asistencia a cursos, congresos y estancias de investigación. A SEP-CONACyT (proyecto 50955) por el financiamiento del proyecto que alberga a esta tesis. A la Fundación-Telmex (Beca No. 062003376) por la beca otorgado.

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A mi familia, Luis Enrique y Santiago

En esta tesis se analizó el papel de la diversidad vegetal sobre la generación de servicios ecosistémicos, utilizando distintos enfoques de análisis a diferentes escalas espaciales. La biodiversidad juega un papel fundamental en el funcionamiento del ecosistema y por lo tanto como regulador de la capacidad que tienen los ecosistemas para generar servicios o beneficios para la sociedad. En este trabajo los enfoques que se utilizaron para caracterizar la relación fueron: i) una revisión cualitativa de la literatura sobre el tema a distintas escalas y para distintos estudios de caso, ii) un meta-análisis de estudios experimentales de la biodiversidad a escala local, iii) una evaluación del conocimiento de expertos a escala de paisaje, y iv) el desarrollo de modelos espacialmente explícitos a escala regional. Para avanzar en la comprensión de cómo componentes específicos de la biodiversidad están afectando la generación de servicios, el trabajo se enfocó en las plantas vasculares terrestres como unidad proveedora de servicios. La revisión cualitativa de la literatura mostró cambios importantes en la forma en que la diversidad se relaciona con los servicios entre escalas y entre servicios así como grandes huecos en el conocimiento. El meta-análisis arrojó un claro efecto positivo de la diversidad sobre la generación de servicios a escala local. La consulta a expertos mostró que la mayoría de los expertos consultados reconocen un efecto positivo de la diversidad en la generación de servicios a escala de paisaje, pero también se encontraron discrepancias de opinión entre expertos. A escala de una cuenca hidrológica se encontró que los patrones espaciales de diversidad vegetal mostraron diferencias importantes entre las distintas formas de vida e índices de la diversidad, aunque fue posible detectar varias áreas de altos valores de diversidad para todos los índices. La comparación sistemática a través de las escalas espaciales mostró que el efecto positivo de la diversidad vegetal sobre la generación de unos pocos servicios se ha derivado de manipulaciones experimentales, pero se requiere la comprobación de nuevas hipótesis y las mediciones directas de una variedad más amplia de servicios a escalas que son relevantes para el manejo. Finalmente, se propone la necesidad de considerar los patrones espaciales de la diversidad y los servicios para analizar sus relaciones funcionales y espaciales, y entender sus vínculos que son poco conocidos a escalas de paisaje y regional. Los distintos enfoques de análisis señalan la importancia de mantener la diversidad vegetal para garantizar y aumentar la generación de servicios ecosistémicos que benefician el bienestar humano.

In this dissertation, I examined the role of plant diversity on ecosystem services generation, using various approaches of analysis at different spatial scales. Biodiversity plays a critical role in ecosystem functioning and therefore as a regulator of the ability of ecosystem to generate services or benefits to society. In this project, the approaches used to characterize the relationship included: i) a review of the publications on the topic at different scales and for different case studies, ii) a meta-analysis of experimental studies of biodiversity at local scale, iii) an expert assessment at landscape scale and iv) the development of spatially explicit models at a regional scale. To advance the understanding of how specific components of biodiversity are affecting the generation of services, we focused on terrestrial plants as services provider units. The qualitative review of publications showed significant changes in how diversity is related to services between scales and between services as well as large gaps in knowledge. The meta-analysis showed a clear positive effect of diversity on the generation of services at local scale. The survey of expert knowledge showed that most of expert recognize a positive effect of diversity in the generation of services at the landscape scale, but also found differences of opinion among them. A watershed scale we found that the spatial patterns of plant diversity showed significant differences among various life forms and indices of diversity, although it was possible to detect several areas of high diversity values for all indices. The systematic comparison across spatial scales showed that the positive effect of plant diversity on the generation of a few services have been derived from experimental studies, but it requires the testing of new hypotheses and direct measurements for a wider variety of services at scales relevant to management. Finally, I propose the need to consider the spatial patterns of diversity and services to analyze their functional and spatial relationships, and understand the links that are poorly understood at landscape and regional scales. The different approaches of analysis indicate the importance of plant diversity to ensure and increase the generation of ecosystem services that benefit human welfare.

Introducción

En los últimos 50 años, los seres humanos han transformado los ecosistemas rápida y extensivamente, generado una pérdida considerable, en gran medida irreversible de biodiversidad (Chapin et al. 2000; Rockstrom et al. 2009). Estas transformaciones no sólo tienen consecuencias negativas sobre el funcionamiento de los ecosistemas, sino también sobre su capacidad para seguir generando servicios ecosistémicos (MA 2005). La amplia investigación sobre la biodiversidad y funcionamiento del ecosistema, claramente ha mostrado el importante papel que desempeña la biodiversidad como regulador de la capacidad que tienen los ecosistemas para generar servicios o beneficios para la sociedad (Hooper *et al.* 2005, MA 2005; Balvanera *et al.* 2006; Naeem *et al.* 2009, Cardinale *et al.* 2011).

La generación de servicios ecosistémicos es resultado de la interacción entre los diferentes componentes del ecosistema y los procesos que en estos ocurren y las sociedades (Fig. 1). Los componentes del ecosistema incluyen elementos bióticos (diversidad vegetal y de otros organismos), elementos abióticos (condiciones y recursos) y las interacciones entre ellos (los procesos ecosistémicos). La cantidad de especies (riqueza) y las características de estas (composición, atributos funcionales) tienen efectos sobre la magnitud, tasa, variabilidad y dirección de los procesos, los cuales determinan a su vez la provisión de servicios ecosistémicos (Hooper *et al.* 2005; Balvanera *et al.* 2006; Díaz *et al.* 2006). Estas interacciones se dan a distintas escalas espaciales y temporales, y determinan la capacidad de los ecosistemas para generar los distintos tipos de servicios (MA 2005).

Cuando las propiedades y funciones ecosistémicas son directamente consumidas, disfrutadas o contribuyen a condiciones ambientales favorables para el desarrollo de la vida humana, se puede hablar de servicios ecosistémicos (Boyd & Banzhaf 2007; Luck *et al.* 2009). Los servicios ecosistémicos (MA 2003, Maass et al 2005) son de tres tipos: *i)* los de *provisión*, o bienes tangibles de apropiación directa que se pueden medir y cuantificar, *ii)* los de *regulación*, producto de las complejas interacciones entre los componentes físicos de los ecosistemas, y *iii)* los *culturales*, cuya importancia surge de la percepción individual o colectiva de su existencia, y fuertemente dependientes del contexto cultural. Una categoría adicional, la de los servicios de soporte, fue descrita por la Evaluación de los Ecosistemas del Milenio (MA 2003), pero que consideramos en realidad procesos ecosistémicos básicos puesto que indirectamente benefician a la sociedad y permiten los otros tres tipos de servicios de provean (Maass *et al.* 2005; Lamarque *et al.* 2011).

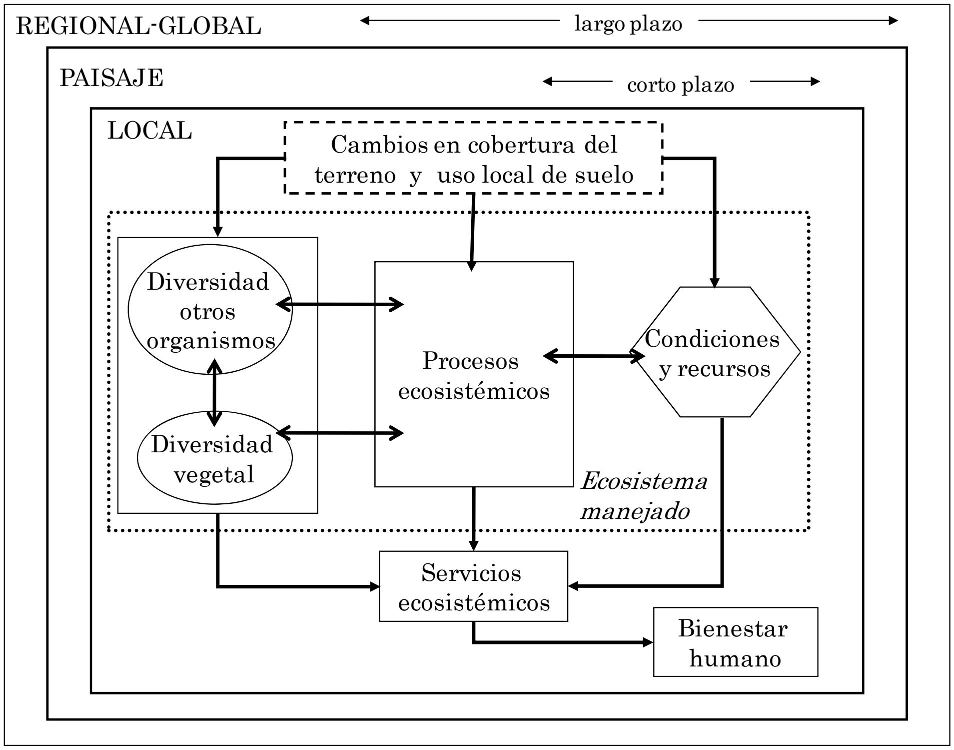


Figura. 1. Generación de servicios ecosistémicos a partir de los distintos componentes del ecosistema. Modificado de Díaz *et al.* 2006; MA 2005.

El papel que desempeña la biodiversidad sobre la generación de servicios ecosistémicos ha sido evaluado en diferentes escalas espaciales. A escala local existe una amplia literatura que evalúa de forma experimental los impactos de los cambios en riqueza de especies sobre el funcionamiento de los ecosistemas. Las síntesis de esta gran cantidad de información tienden a mostrar un efecto positivo de la riqueza de especies sobre la magnitud de las funciones del ecosistema (Balvanera *et al.* 2006; Worm *et al.* 2006; Schmid *et al.* 2009; Cardinale *et al.* 2011).

A escalas de paisaje se cuenta con estudios basados en experimentos naturales y en observaciones de patrones que ocurren en los paisajes. A esta escala la cantidad de estudios es relativamente reducida. Además se observa una gran diversidad de tipos de respuestas. Las relaciones entre la diversidad y la generación de servicios a esta escala pueden ser el resultado de efectos de la biodiversidad sobre el servicio, o el resultado de efectos de los cambios en condiciones abióticas o decisiones de manejo sobre la biodiversidad y los procesos y/o los servicios (Tscharntke *et al.* 2005; Barbier *et al.* 2008, Lavorel *et al.* 2011).

A escalas regionales las relaciones entre la diversidad y los servicios ecosistémicos se pueden explorar a través de los resultados obtenidos de modelos espacialmente explícitos. Los resultados obtenidos a la fecha muestran escasa o nula concordancia espacial entre la biodiversidad y los servicios (Chan *et al.* 2006; Nelson *et al.* 2009), así como asociaciones funcionales débiles (Anderson *et al.* 2009).

Actualmente, se reconoce que el avance en la investigación sobre los servicios requiere de una caracterización de la contribución de los distintos componentes de la biodiversidad a la generación de servicios (Kremen 2005; Luck *et al.* 2009). Se ha reconocido que una amplia variedad de organismos actúan como proveedores de servicios ecosistémicos (Luck *et al.* 2009).De esta gran gama de proveedores de servicios ecosistémicos pocos han sido estudiados de forma sistemática.

Las plantas terrestres son un grupo proveedor de servicios ecosistémicos particularmente relevante. Las plantas son el primer eslabón en los sistemas terrestres en la cadena trófica; existe además amplia información acerca del papel que pueden estar jugar en la generación de servicios (Hooper *et al.* 2005; Díaz *et al.* 2005).

Para avanzar en el entendimiento de la relación de la diversidad vegetal y la generación de servicios, se pueden considerar distintos enfoques (Fig. 2). Un primer enfoque es una síntesis cualitativa de la literatura disponible a la fecha sobre la biodiversidad y los servicios considerando distintas escalas espaciales y para distintos servicios ampliamente estudiados (Fig. 2, Capítulo I). Un segundo enfoque es una síntesis cuantitativa o meta-análisis de la amplia investigación generada durante los últimos 50 años a escalas locales, sobre los efectos de la manipulación experimental de la riqueza de especies sobre las funciones del ecosistema que están directamente relacionadas con la generación de servicios (Fig. 2, Capítulo II). Un tercer enfoque es el compensar la falta de información a escalas de paisaje sobre la relación entre la diversidad vegetal y la generación de servicios ecosistémicos con una consulta a expertos que permita generar nuevas hipótesis sobre la relación de la diversidad vegetal (Fig. 2, Capítulo III). Un cuarto enfoque es el desarrollo de modelos espacialmente explícitos de la diversidad vegetal, que permita comparar los patrones espaciales para distintas formas de vida y sus índices de diversidad; enfoque que permitirá explorar si estos son una herramienta poderosa para la identificación de áreas con altos valores de diversidad (Fig. 2, Capítulo IV). Un enfoque que queda pendiente es el análisis conjunto de los patrones espaciales de la diversidad y los de los servicios para examinar sus relaciones funcionales y espaciales, aspectos poco conocidos a escalas de paisaje y regional (Fig. 2, Capítulo V).

Preguntas de investigación

Ante este panorama, el presente proyecto de tesis pretende responder las siguientes preguntas:

1- ¿Qué se sabe a la fecha sobre la relación de la biodiversidad y la generación de servicios ecosistémicos?

2- ¿Cuál es el efecto de la riqueza de especies vegetales sobre la generación de los servicios considerando la investigación acumulada durante los últimos 50 años acerca de los efectos de la manipulación experimental de la riqueza sobre el funcionamiento del ecosistema?

3- ¿Cuál es la percepción de los expertos sobre el papel de la diversidad vegetal en la generación de servicios ecosistémicos a escala de paisaje?

4- ¿La selección de la forma de vida vegetal y el índice de diversidad afectan la exactitud y predicción de las áreas prioritarias de conservación dentro de una cuenca hidrológica?

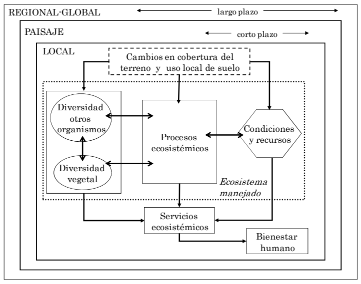
¿Cuál es la relación entre la diversidad vegetal y los servicios ecosistémicos?

Estructura de la tesis

LO QUE SE SABE

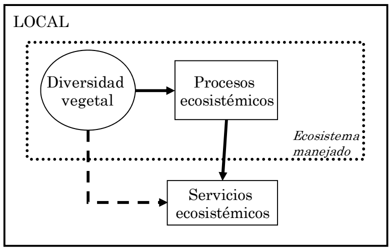
Capítulo I

Revisión de la literatura sobre la biodiversidad y los servicios ecosistémicos a distintas escalas y para distintos estudios de caso



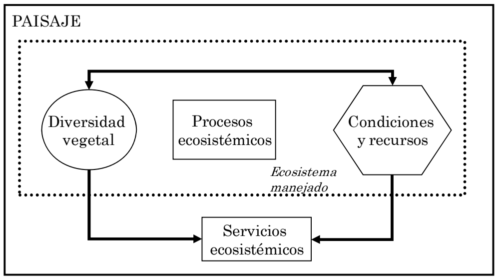
Capítulo II

Relación entre la diversidad vegetal y los servicios ecosistémicos: meta-análisis de información disponible



Capítulo III

Percepción de los expertos sobre el efecto de la diversidad vegetal en la generación de servicios ecosistémicos



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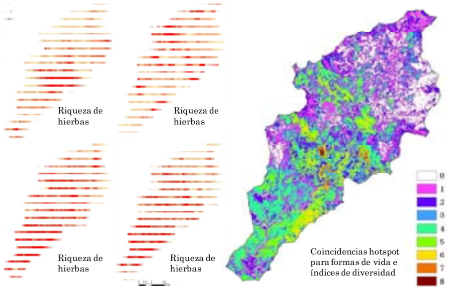
Capítulo IV

Modelación y mapeo de la diversidad vegetal en una cuenca hidrológica: formas de vida e indicadores de diversidad



Capítulo V

Contribución al conocimiento y preguntas relevantes que fomentan la investigación futura sobre la relación de la diversidad vegetal y la generación de servicios ecosistémicos

LO QUE HACE FALTA

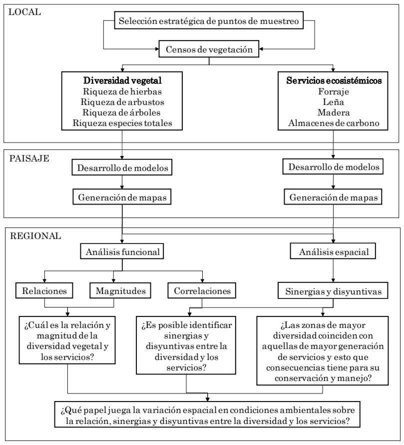


Figura 2. Estructura de la tesis y que aspecto de la relación entre la diversidad vegetal y los servicios ecosistémicos que se abordan en cada capítulo.

Objetivos

General

Analizar el papel de la diversidad vegetal sobre la generación de servicios ecosistémicos, utilizando distintos enfoques de análisis a diferentes escalas espaciales.

Particulares

1- Revisar la literatura disponible a la fecha sobre la biodiversidad y los servicios ecosistémicos.

2- Sintetizar la amplia investigación experimental sobre biodiversidad y funcionamiento del ecosistema, traduciendo el efecto de la diversidad vegetal dentro del contexto de los servicios ecosistémicos.

3- Determinar qué atributos de la diversidad vegetal son los más relevantes para la generación de diferentes servicios ecosistémicos, así como su importancia relativa con respecto a las condiciones y recursos a través de la consulta a expertos.

4- Analizar la distribución espacial de distintas formas de vida e índices de diversidad a partir de su cuantificación local y modelación en una cuenca hidrológica.

Estructura de la tesis

En esta tesis se analizó el papel de la diversidad vegetal sobre la generación de servicios ecosistémicos, utilizando distintos enfoques de análisis a diferentes escalas espaciales.

En el capítulo I se hace una revisión cualitativa de la literatura disponible a la fecha sobre la biodiversidad y la generación de servicios, se hace una introducción a conceptos claves; se muestran los complejos vínculos entre la biodiversidad y los servicios ecosistémicos considerando estudios de caso; se analizan los principales encuentros y vacíos de información de la relación a diferentes escalas espaciales.

En el capítulo II se realizo un meta-análisis de la amplia investigación experimental sobre biodiversidad y funcionamiento del ecosistema, traduciendo la importancia de la diversidad vegetal dentro del contexto de los servicios ecosistémicos.

En el capítulo III se determino qué atributos de la diversidad vegetal son los más relevantes para la generación de diferentes servicios ecosistémicos, así como su importancia relativa con respecto a las condiciones y recursos a través de la consulta a expertos que estudian la biodiversidad, el funcionamiento del ecosistema y los servicios ecosistémicos.

En el capítulo IV de la tesis se identificaron de los patrones espaciales de distintas formas de vida vegetal e índices de diversidad a partir de su cuantificación local y modelación en una cuenca hidrológica. Además, se identificaron las áreas de mayor concentración de diversidad y sus implicaciones en la conservación.

En la discusión final del Capítulo V se destacan las aportaciones específicas de cada uno de los capítulos para el entendimiento de la relación que existe entre diversidad vegetal y los servicios ecosistémicos a diferentes escalas espaciales; se propone la necesidad de analizar los patrones espaciales de la diversidad y los servicios para analizar sus relaciones funcionales y espaciales, y entender sus vínculos que son poco conocidos a escalas de paisaje y regional; se plantean una serie de preguntas avanzar en la investigación sobre diversidad y servicios. Finalmente, basándome en los resultados de esta tesis, se subrayan las conclusiones más relevantes.

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Capítulo I

Biodiversity and ecosystem services*

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*Manuscrito en prensa en Encyclopedia of Biodiversity

Abstract

Biodiversity is tightly linked to ecosystem services and thus to human well-being in complex ways. The roles played by biodiversity in key ecosystem services such as agricultural food production, regulation of soil productive potential, crop pollination and human disease regulation have been intensively studied and show very different patterns and mechanisms. Experimental manipulations of biodiversity at local spatial scales, observational studies at landscape scales, and the development of spatially explicit models at regional to global scales have also contributed to test hypotheses, develop models and inform management on the role played by biodiversity in ecosystem service delivery.

Keywords

Ecosystem Process; Ecosystem Service; Ecosystem Service Provider; Experimental Manipulations; Food; Functional Diversity; Human Health; Human Well-Being; Meta-analysis; Observational Studies; Pollination; Spatial Scale; Species Composition; Species Richness

Glossary

Biodiversity- Variety of living genotypes, populations, species, communities, and landscapes; for the case of species it includes the number of different species, their relative abundance, differences their composition or functional attributes, their spatial patterns, and the complexity of their trophic interactions.

Ecosystem process- Transfers of energy and materials given by interactions among abiotic (non-living) and biotic (living) components of ecosystems.

Ecosystem resilience- Ability of an ecosystem to maintain its functioning in the face of changing environmental conditions and disturbances.

Ecosystem service- Ecosystem component or process that directly contributes to human well-being as it is consumed, experienced, or it regulates the environmental conditions in which humans live.

Ecosystem service provider- Components of populations, communities, trophic groups, landscapes and habitats that are necessary for the delivery of ecosystem services.

Human well-being- People's condition and capacities allowing secure access to food, water, energy, and shelter of adequate quality to meet the needs, and ensure good health as well as social connections.

Meta-analysis- statistical synthesis of the results of separate studies (quantitative research synthesis).

Spatial and temporal scale- Spatial or temporal extent within which biodiversity interacts with ecosystem processes, ecosystem processes operate, and ecosystem services are delivered.

I. Why worry about the links between biodiversity and ecosystem services?

We are growingly concerned about the impacts of the human enterprise on biodiversity and ecosystem functioning, and their ability to continue to deliver the ecosystem services that are essential for human life. To meet humanity's rapidly increasing demand for fuel, water and food, human impacts on ecosystem have also been increasing, accumulating and interacting, leading to irreversible changes in the way ecosystems function. Anthropogenic climate change caused by an increase in the atmospheric concentration of greenhouse gases, large additions of nitrogen and phosphorus activated by humans to soil, water and atmosphere resulting from modern agriculture, and rates of biodiversity loss have all crossed boundaries for sustainable functioning of the Earth system (Rockstrom *et al* 2009).

Species are lost today at rates 10 to 100 times higher than those found in the fossil record. Predictions for extinction rates in the 21st century are up to 100 times higher than those found today (Millennium Ecosystem Assessment, 2005; Rockstrom *et al.*, 2009).

Given that ecosystem processes depend on living organisms, and that ecosystem functioning is given by the combination of such ecosystem processes, a key question to be answered is how will biodiversity loss impact the ability of ecosystems to continue meeting human needs.

The concept of ecosystem services was developed to show explicitly the tight connections between human well-being and the adequate provision of ecosystem services. The drive to satisfy human needs is threatening the maintenance of ecosystem functioning, while at the same time human impacts on ecosystems threaten their continued ability to satisfy human's needs.

II. Introduction to the concepts

New concepts have been coined in the past few years to advance key frontiers of knowledge, and old ones have been used in different contexts to address the multifaceted nature of the relationships between biodiversity and ecosystem services.

A. Biodiversity

Biodiversity is a termed used to encompass all the variability found in living organisms in terrestrial and aquatic systems. This variability can be observed at different levels of organization. The variability among genomes of individuals, among populations of individuals within the same species, among species within a community, or among communities within a landscape can all be analyzed and may be linked to ecosystem services (Diaz *et al* 2006). Various mechanisms can generate biodiversity effects on ecosystem functioning. Species can be complementary in the way they contribute to the function and thus higher species richness leads to higher magnitude of the function. Sampling (or selection) effect is given by the increasing probability of including a highly efficient species for a particular function with increasing species richness increasing the probability of choosing this species as a result of random sampling. These two mechanisms are those that are the most frequently called for; in fact, the most common is the combination of both. Facilitation occurs when a given species has a positive effect on the functional contribution of another one. To date, despite the accepted importance of these mechanisms, actual tests of their operation are much less frequent (Cardinale *et al* 2011).

The simplest and more direct way to analyze the variability is simply through the count of the number of different types of units, otherwise called richness. The most common use of this term is to refer to species richness, the number of species found in a community. The relative abundance of species is also part of this variability, given that an ecosystem largely dominated by a single species will function in a different way than one with the same richness but with even abundance of species. Differences in species composition, not only in terms of their taxonomic identity, but also in terms of the differences in the way they respond to environmental conditions and contribute to ecosystem functions, will lead to changes in ecosystem services. The variability in morphological or functional attributes of species is called functional diversity. The distribution patterns of species in space are also relevant to ecosystem functioning, and species can either be evenly distributed across space or rather clumped into patches of different sizes. The structure of a food web, in terms of the number of trophic levels and the number of linkages between species, is also relevant to ecosystem functioning and has been referred to as vertical diversity.

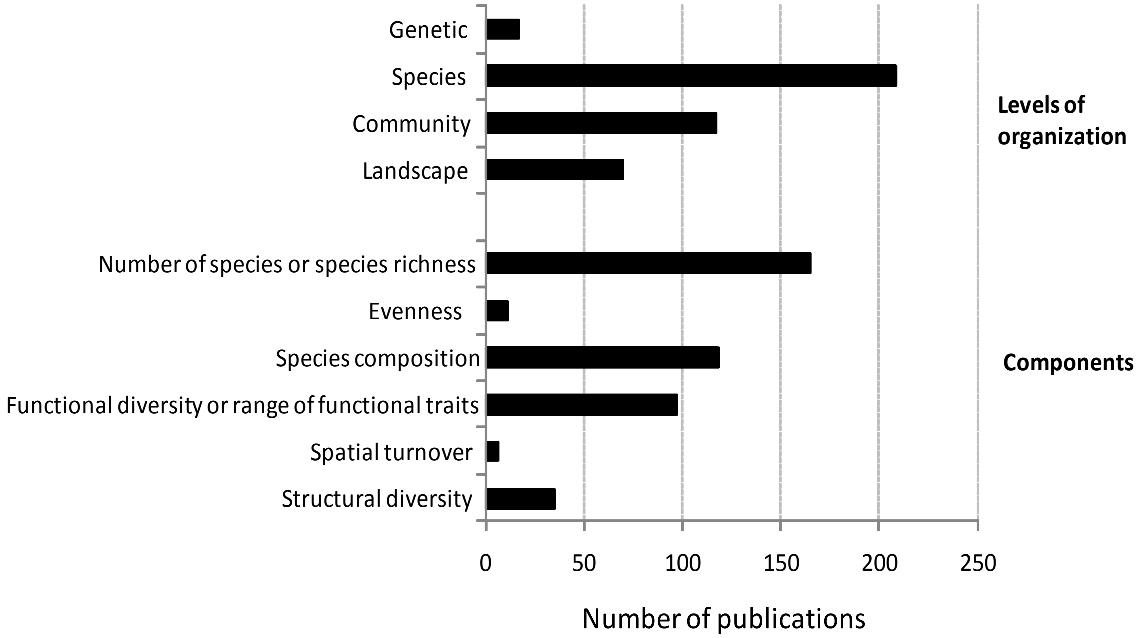


Figure 1 Components and levels of organization of biodiversity that have been related to ecosystem services. Results are derived from a search in ISI Web of Science and Biological Abstracts in May 2011 for all past references using the term in the graph and "(plant or invertebrates or non vascular plants or microbes or aquatic plants or vertebrates) and ecosystem services".

A rich literature has developed, exploring the links between biodiversity and ecosystem services in many ways. Such a wealth of data and theory has led to syntheses on the role of species richness in ecosystem functioning and provision of ecosystem services that will be discussed below. A large fraction of the explorations of the links between biodiversity and ecosystem services focus on species richness (Figure 1).

Table I Selected examples of ecosystem services and their ecosystem service providers. Characteristics of the providers refer to the level of organization or the components of diversity involved in service delivery.

Ecosystem service provider	Characteristics of the providers	Processes	Service	Type of ecosystem service	Spatial scale	References
Soil invertebrates; soil micro-organisms, plant and animal	Populations, species, functional groups	Elemental transformation Soil structure modification	Soil generation	Supporting	Local	van der Heijden et al (1998) Barrios (2007)
Vegetation	Populations, species, communities, ecosystems	Primary production	Agricultural food production	Provisioning	Local-landscape	Jackson et al (2009)
Leaf litter and soil invertebrates; soil micro-organisms; nitrogen-fixing plants; plant and animal production of waste products	Populations, species, functional groups	Decomposition, Nutrient cycling	Regulation of soil productive potential	Regulating	Local	van der Heijden et al (1998) Barrios (2007)
Insects, birds, mammals	Populations, species, functional groups	Trophic interactions Movement of pollen and seeds by animals	Pollination	Regulating	Local and landscape	Kremen et al (2007) Klein et al (2009)
Micro-organisms, invertebrate parasitoids, vertebrate predators	Populations, species, functional groups	Trophic interaction	Regulation of human disease vectors	Regulating	Local to global	Jones et al (2008) Keesing et al (2010)
Many types of organisms	Populations, species, communities, ecosystems	Ecological-social dynamics	Aesthetic and spiritual inspiration, sense of identity	Cultural	Local to global	Chan et al (2011)

Yet, the roles of species composition or identity, functional diversity, species' relative abundance, species' spatial distribution patterns and trophic diversity are increasingly being recognized and investigated (Table 1); the same is true for the roles of genetic diversity in ecosystem functioning and ecosystem services.

B. Ecosystem processes and ecosystem functioning

Ecosystem processes are the interactions among abiotic or non-living and biotic or living component of terrestrial and aquatic ecosystems. Such interactions encompass transfers of energy and materials (Chapin *et al* 2000).

One of the central processes in terrestrial and aquatic ecosystem is the transformation of solar energy into biomass through photosynthesis. Primary productivity, the change in primary producer biomass per unit area and time, is the result of photosynthesis, respiration and decomposition leading to net plant growth. Numerous studies have explored the links between biodiversity and some component measures of this process, largely as total biomass of primary producers or the rates at which this biomass accumulates. To date there is a very large amount of evidence available that indicate that increased producer species richness increases the efficiency by which plants and algae convert these into standing biomass; this is true for temperate grasslands, agricultural systems, marine coastal systems and lakes (Cardinale et al. 2011).

The biomass stored in primary producers is either consumed or decomposed. The effects of biodiversity have been frequently studied for secondary production (consumption) or decomposition. Such studies have measured biomass consumed or decomposed, amounts of carbon liberated to the atmosphere, as well as respiration rates to assess the activity of decomposers.

The cycling of several key elements - phosphorus, nitrogen, sulfur and carbon- can also be linked to biodiversity. The loss of species of primary producers, particularly plants in temperate grasslands, has been shown to reduce the efficiency by which they assimilate inorganic resources such soil nitrate (Cardinale et al. 2011). Yet, the information available to date does not allow generalizing these findings to other elements or to other ecosystems. This is particularly worrying given that the concentrations and cycles of these elements have been substantially altered by human activities over the past two centuries, strongly modifying the functioning of ecosystems and their ability to deliver ecosystem services (Millennium Ecosystem Assessment, 2005; Rockstrom *et al.*, 2009).

We know little about the role of biodiversity in the different components of the water cycle. Plant diversity, in the form of functional and structural diversity may play a key role on evapotranspiration, surface and underground runoff (Chapin et al., 2002, Diaz et al. 2006). The diversity of soil organisms (such as earthworms, micro-arthropods and microbes) is related to soil physical properties such as the presence of macropores to aid infiltration (Barrios 2007). Yet, not enough experimental nor observational data is consistently available to confirm the role of biodiversity on these processes.

Ecosystem functioning encompasses many of the above-mentioned processes and the interactions among them. Functioning includes the ability of the ecosystem to cope with natural and anthropogenic disturbance by converging around a particular state rather than changing dramatically into a very different condition for the components and processes that make them up. The latter is called ecosystem resilience.

The potential links between biodiversity and multiple ecosystem processes or ecosystem functioning are often referred to in scientific literature. Yet, only a fraction of such references correspond to actual data on such links.

C. Ecosystem services

Ecosystem services are the links between ecosystems and human societies. In the broadest sense they are the benefits societies obtain from ecosystems (Millennium Ecosystem Assessment 2005). More specifically, services are produced by living or non-living components of ecosystems, through the conditions and processes in ecosystems (see Tallis *et al.*). They contribute to human well being in different ways: they can be directly consumed, as in the case of water or food. They can be experienced, as in the case of the scenic beauty or the sense of awe that a waterfall, a mountain covered by vegetation or a monarch butterfly can inspire in us. They also contribute to the fundamental environmental conditions for human life, such as the regulation of relatively stable climatic conditions and the protection against extreme events.

Ecosystem services have also been defined as those components and processes of ecosystems that contribute directly to human well-being (Luck *et al* 2009). By emphasizing on the direct nature of such connection an effort is being made to distinguish ecosystem processes from ecosystem services.

There is a fine line between ecosystem processes and ecosystem services. Some authors have considered ecosystem processes as those ecosystem services that support the delivery of all other types of services. The advantage of this position is that it is possible to encompass both direct benefits to human societies as well as ecosystem functions and the origin and maintenance of biodiversity within the term ecosystem services. This approach can be very useful when communicating with decision makers.

Yet, in order to quantify the amount of services a clear distinction between supply, service and value can be useful. Supply is the contribution of ecosystem processes and components to a service that can potentially benefit societies. Service is the actual benefit societies obtain from the service, which can include water consumption or the number of people that benefit from regulation of flooding. Value reflects how societies consider the relative importance of a service; it can be monetary, as an expression of markets or preferences or embedded into cultural perspectives (Chan *et al.*, 2011). In this chapter we will dissect ecosystem processes from ecosystem services in this way.

The key message is that services or benefits to human societies depend on ecosystems and their functioning. In turn, such functioning is dependent to some degree on biodiversity.

The Millennium Ecosystem Assessment (2005) classifies services into four types: supporting, provisioning, regulating and cultural services. We did not include supporting services, as we considered them to be ecosystem processes that indirectly benefit societies by supporting one of the other three types of services.

i. Provisioning services

Provisioning services are the tangible resources – or goods – that people obtain from ecosystems. These are finite, can be renewable, and can be directly consumed, appropriated, and traded.

Food provision is among the most important services. Food can be obtained from agricultural activities, aquaculture, hunting, gathering and fisheries. Other key provisioning services include fodder, wood, fibers, biofuels, and a diversity of abiotic and biotic resources derived from terrestrial and aquatic systems.

ii. Regulating services

Regulating services result from the contribution of multiple ecosystem processes to ecosystem functioning, specifically to the regulation of the conditions where humans live and make a living. Such regulation determines both the average and the variance in such conditions.

Regulating services include the regulation of local or global climate, of disease vectors and incidence, of pests, crop pollination, soil fertility, and soil erosion. They also regulate the amount, temporality and quality of water provision, as well as the impacts of severe weather conditions on ecosystem and people.

iii. Cultural services

Cultural services are ecosystem's contribution to the non-material benefits that arise from the interaction between people and ecosystems. These benefits include a range of capabilities and experiences (Chan *et al* 2011).

Cultural ecosystem services include the sense of place or identity linked to a particular ecosystem and its management. They also include activities such as recreation and work. The existence and bequest value of a site or a species for future generations, or the sense of awe and spiritual or aesthetic inspiration are also considered cultural services.

D. Ecosystem service provider

An ecosystem service provider is a biotic component of an ecosystem that is necessary for the delivery of an ecosystem service. Ecosystem providers can include populations, communities, trophic groups, landscapes and habitats (Kremen 2005; Luck *et al* 2009).

The concept of ecosystem service provider was developed to identify the component(s) of the ecosystem that should be managed in order to ensure the sustained delivery of each service. Vascular and non-vascular plants, terrestrial and aquatic invertebrates, microbes and vertebrates have been explicitly recognized as ecosystem service providers (see Table 1). Genetic diversity, species diversity, species richness, functional diversity and vertical diversity have also been identified as such.

E. Human well-being

Human well-being is a complex concept that is not universal but rather context dependent. The different components of such well-being as well as their relative importance depend on the cultural, geographic and historic development of societies.

The Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005) identified to food, water and other materials, security, good health and good social relations as the key components of well-being. A recent report by another interdisciplinary international team (Stiglitz *et al* 2010) emphasizes the need to simultaneously consider the following dimensions: material living standards (income, consumption and wealth), health, education, personal activities including work, political voice and governance, social connections and relationships, environment (present and future conditions), and insecurity (of an economic as well as physical nature). To assess them both people's objective conditions and capabilities should be taken into account.

Human well-being is directly linked to the biodiversity that surrounds the many rural communities of the world, from which they obtain food, medicine, materials and inspiration. The role that biodiversity plays in ecosystem processes, the services they provide and thus human well-being will be discussed below.

F. The shape of the relationship between species diversity and ecosystem functions and services

The shape of the relationship between the species diversity and the magnitude of ecosystem function or service is quite relevant for management. If the shape is asymptotic this means that loosing the few first species may have little effect on the function, but the magnitude of the impacts of loosing further species can increase in non-linear ways leading to a dramatic decline in the function or service once enough species have been lost (Figure 2). Experimental studies much more frequently find such a pattern, rather than a linear relationship, or one where losing the first few species has the most dramatic effects (Cardinale *et al.*, 2011). Similarly, observational studies have also found such an asymptotic pattern (Balvanera *et al.*, 2005).This means that loosing species in already depauperate systems can have dramatic consequences of ecosystem functioning and ecosystem services.

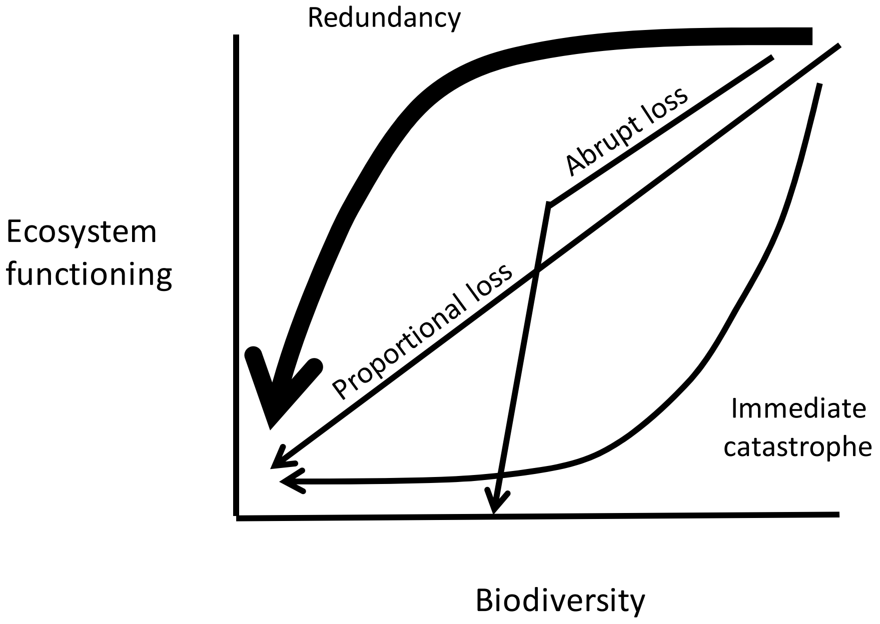


Figure 2 Possible ecological consequences of diversity loss: (1) the redundancy response predicts that initial losses of diversity will be accompanied by minimal change in the ecosystem process because some fraction of species are redundant for that process; however, at some point, loss of species leads to rapid declines in ecological function; (2) ecosystem function declines proportionally to species loss; (3) an abrupt loss in ecosystem functioning is given by the loss of a keystone species or last member of a key functional group, or the addition of a new species trait; (4) even minimal species loss leads to an immediate catastrophe and large declines in the functioning of ecosystems. A thicker line for the redundancy model indicates that it is the most frequently found pattern (modified from Hooper and Vitousek 1997; Chapin et al. 2000).

G. Spatial and temporal scales

Spatial or temporal scale refers to the extent of the area or the duration of time. A related but different issue is the resolution, or grain, that refers to the smallest detectable event or property at a particular scale. Given that distribution patterns of biodiversity vary at different spatial and temporal scales, given that ecosystem processes operate at different scales, and given that services are delivery at different scales it is essential to clearly define the scale of analysis.

Spatial and temporal scales are continuous and dissected in a variety of ways, but for analytical purposes we have arbitrarily defined three contrasting scales here. The local spatial scale was defined here for areas up to 1 ha. This scale encompasses the area used for many of the local biodiversity assessments in terrestrial habitats (e.g. 0.1 ha assessment, or 1 ha assessment). Also, the experimental manipulations of biodiversity have used experimental units within this area range; for the case of those involving primary producers (the most frequent ones) the median size of the experimental unit is 0.003 ha, and the largest ones have an area of 0.5 ha.

The landscape scale was defined as that ranging from 1 to 1,000 hectares. This range encompasses the area included into an individual piece of land to the whole area one can see from an elevated point under low to very wide visibility. This area encompasses well-known gradients in environmental conditions, a combination of individual lots of lands with natural, semi-natural and anthropogenic conditions (e.g. agriculture, agroforestry), and can include one or various rural settlements. The regional scale to global scale was defined as that includes 1,000 hectares and more. This range of areas can include a few rural settlements, one or many municipalities or urban settlements, and all the way to whole states and countries. At this spatial scale use of remotely sensed data and/or spatially explicit models are needed to assess biodiversity distribution patterns as well as the magnitude of ecosystem processes and services.

III. The complex linkages between biodiversity and ecosystem services: selected examples

What would happen if we lost most of the biodiversity? Would the delivery of ecosystem services be dramatically impaired? Do all the ecosystem services show the same sensitivity to the loss of biodiversity? How universal is the asymptotic relationship between biodiversity and service provision?
All these are very complex and profound questions that have not been addressed thoroughly and systematically for all ecosystem services and at all spatial scales. We focus below on four very important and intensively studied ecosystem services. We show that they all depend on biodiversity, though in

very different ways. We also show how they have been analyzed in very different ways.

A. Agricultural food production

Understanding the complex links between food production derived from agriculture and biodiversity is as relevant as ever, as feeding an expected nine billion people pose a paramount challenge. Most of food production today is derived from highly intensive agricultural systems with low diversity. In fact, the sites with the highest agricultural yields (e.g. sites in China with 1.3 metric tons per hectare by year [MT]; FAO 2011) are those where most plants correspond to only one species and to one or a few genetic combinations (e.g. wheat and rice with 0.32 MT in China or sugar cane with 0.78 MT in Brazil; FAO 2011). Also, the expansion and intensification of agricultural systems are the major driver of biodiversity loss of terrestrial habitats. On the other hand, the ability of diverse cropping systems, diverse agricultural landscapes, and biodiversity friendly agricultural systems (e.g. organic) to meet the global food needs is being debated.

Food production derived from agriculture depends on a wide diversity of crop species found across the planet. As many as 100 different crops used for human food are registered in global agricultural databases, and many more are locally grown and consumed. Yet, 63% of food production (as measured on a dry biomass basis) relies on only five species: sugar cane, maize, wheat, rice and potatoes (FAO 2011).

The diversity of plant crops, as well as that of soil microorganisms and vertebrates, weeds, herbivores and carnivores that interact with them are all relevant to the provision of this service. Also, diversity at different trophic levels, ranging from genetic diversity within populations to the diversity of communities within landscapes is relevant.

Agrobiodiversity, that is the variety and variability of living organisms that contribute to food and agriculture as well as the knowledge associated with them, can enhance agricultural food production. A recent meta-analysis of 552 experiments (Letourneau *et al* 2011) showed a general trend for positive effects of biodiversity. Diverse cropping schemes (polycultures) have shown to have a significantly lower abundance of pests (herbivores), higher abundance of natural enemies of such pests (predators and parasites), decreased damage by pests, though at a cost of a small but significant reduction in crop yield (Figure 3).

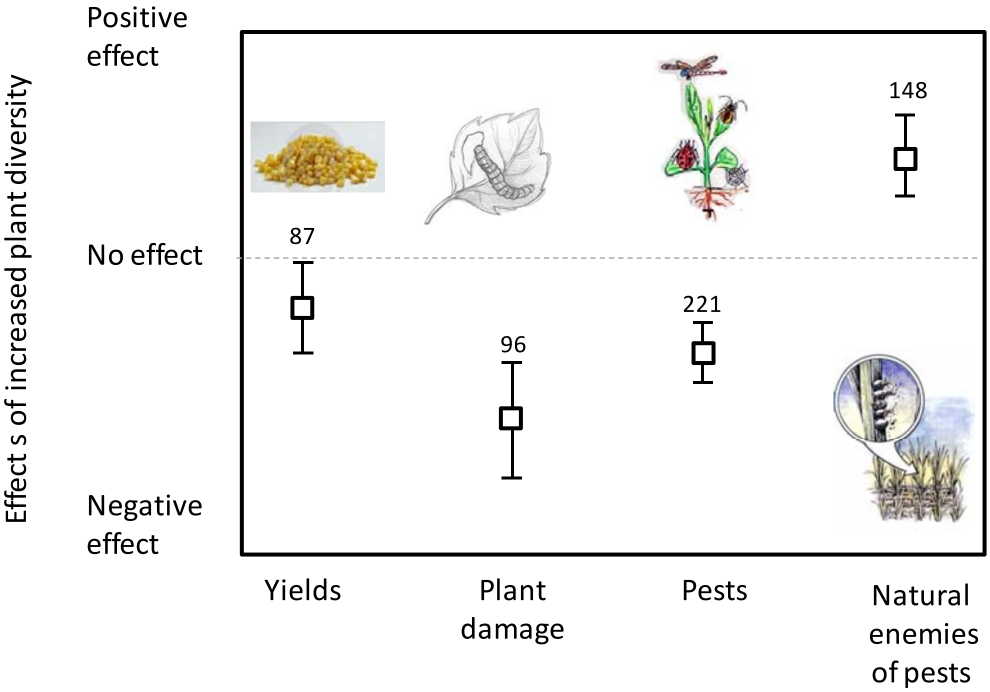


Figure 3 Effects of increased diversity associated to more diverse cropping schemes (polycultures) relative to less diverse ones or crop monocultures on various ecosystem services. The mean of the proportional effects of diversity and the 95% confidence intervals values derived from the meta-analysis are shown for each response variable. Significant effects correspond to average and confidence interval values that do not overlap with the non-effect line. Numbers above each result indicate the number of independent measurements found in the literature used for the analyses (modified from Letourneau et al 2011).

Genetic diversity within populations, population diversity within crop species and community diversity within agricultural landscapes contribute to food production derived from agriculture. Farmers, particularly in developing countries, use a wide variety of traditional crop local varieties, or landraces, that still dominate production in many rural landscapes. Genetic and population diversity confers resilience in the face of abiotic (e.g. drought) and biotic (e.g. pests) stress, leading to more stable yields and higher adaptation to stressful conditions; various study cases support this well, though a systematic broader assessment is still needed to test for the generality of such statements. Also, diversity of communities within agricultural landscapes, including low to high diversity agro-ecosystems and a mosaic of well-connected successional (recovering after agricultural use) and conserved patches of habitat provide increased resilience (Jackson *et al* 2009).

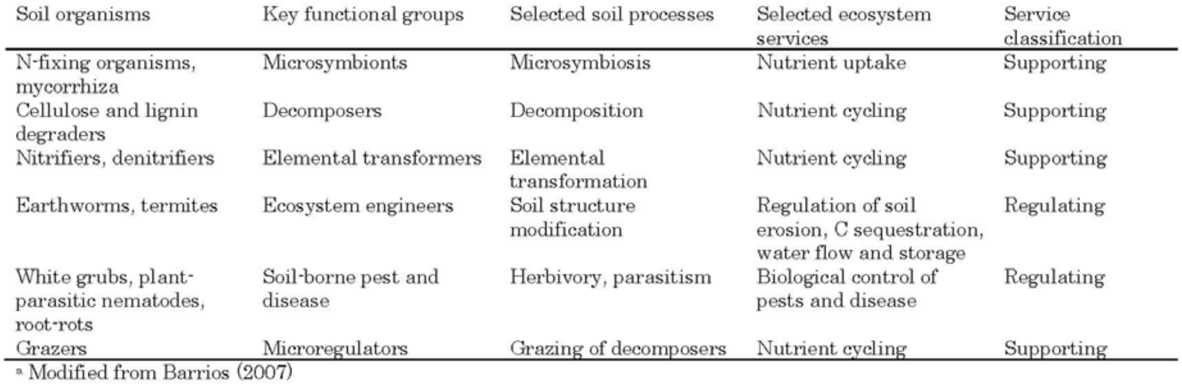
B. Regulation of soil productive potential

A tight but much more complex and less understood link exits between biodiversity and soil productive potential. The maintenance of the functioning of a large array of different types of organisms within soils is critical for maintaining agricultural, pastoral and forestry yield over the long term. Managing for increasing short term yield, such as the addition of inorganic fertilizers, may jeopardize the long term maintenance of biodiversity and this service. Yet, management is complex as it can hardly me targeted to specific groups or functions we understand little.

Soils provide physical support, as well as water and nutrients needed for plants to grow, all of which can be encompassed into the regulation of soil productive potential. Services such as food production from agricultural systems, firewood, timber and biofuel production, and indirectly the regulation of soil erosion depend on the adequate regulation of soil conditions.

Many different types of organisms (Table 2) participate in the regulation of soil productive potential (Barrios 2007). Plants establish symbiotic associations with microorganisms that enhance the availability of otherwise limiting nutrients; soil bacteria (e.g. Rhizobium) in symbiosis with leguminous plants fix atmospheric nitrogen into the soil, while soil-borne fungi in symbiosis with roots of many vascular plants, particularly the so-called arbuscular mycorrhizal fungi enhance phosphorus acquisition through the branching filamentous structure of fungi (hyphae). Decomposition of organic materials into simpler molecules is given by small invertebrates that break down dead tissues; by bacteria, fungi protozoa and invertebrates that chemically degrade dead organic matter further with enzymes; and by microorganisms that generate soluble and volatile organic and inorganic compounds. Earthworms, ants and termites modify soil structure by removing soil and creating structures given by their activity; root-rots, plant-parasitic nematodes and scarab beetle larvae are responsible for soil-borne diseases, while soil grazer, predators or parasites drive the local food-web (Table 2).

Table 2 Soil organisms and key functional groups of soil biota, soil processes they influence and ecosystem services they provide [a]



Soil organisms	Key functional groups	Selected soil processes	Selected ecosystem services	Service classification
N-fixing organisms, mycorrhiza	Microsymbionts	Microsymbiosis	Nutrient uptake	Supporting
Cellulose and lignin degraders	Decomposers	Decomposition	Nutrient cycling	Supporting
Nitrifiers, denitrifiers	Elemental transformers	Elemental transformation	Nutrient cycling	Supporting
Earthworms, termites	Ecosystem engineers	Soil structure modification	Regulation of soil erosion, C sequestration, water flow and storage	Regulating
White grubs, plant-parasitic nematodes, root-rots	Soil-borne pest and disease	Herbivory, parasitism	Biological control of pests and disease	Regulating
Grazers	Microregulators	Grazing of decomposers	Nutrient cycling	Supporting

[a] Modified from Barrios (2007)

Richness of various types of organisms is linked to some of the processes related to the regulation of soil productive potential. Recent meta-analyses (Balvanera *et al* 2006; Hoeksema *et al* 2010; Quijas *et al* 2010) have shown that higher plant species richness contributes to significantly higher plant root biomass and decomposer activity, higher mycorrhizal richness leads to higher plant nutrient concentration, and higher decomposer richness to higher decomposer activity. Instead, higher plant species richness contributes to lower decomposer biomass and soil nutrient supply.

Species composition and particularly functional composition and diversity are expected to have a paramount importance for the regulation of soil productive potential given the wide range of organism involved in the different processes. Growth form composition (e.g. legume, hemiparasitic plants) and growth form diversity (e.g., life form, root depth, photosynthetic capacity, nitrogen fixing capacity) contribute to higher nutrient uptake through increased functional diversity (de Bello *et al* 2010).

The links between biodiversity and the regulation of soil productive potential occur at local scales (Barrios 2007). Soils are highly heterogeneous in terms of their physical, chemical and micro-climatic characteristics, as well as in terms of the spatial (horizontal and vertical) distribution of the soil biota, at scales ranging from microns to meters. Soil biota is concentrated in hot-spots of activity that are mostly associated with the availability of carbon substrates and water availability.

A better understanding of the spatial distribution patterns of soil biota at a wide range of spatial scales and the consequent impacts on soil processes is needed to allow for managing soils and maintaining the range of ecosystem services they provide.

C. Pollination

Mobile organisms pollinate many important crops and other plant species of commercial and social importance. In absence of the native organisms that have contributed to this service, domestic European bees (*Apis mellifera*) have been introduced; in few cases, pollination has been performed by hand by humans.

Pollination, a regulation service, provides benefits to human populations by increasing the production of those commercial and subsistence crops, fiber, fodder, wood and non-timber forest products that require a mobile organism to transport male pollen grains into feminine floral structures for seed production.

Pollination is also a supporting service, or ecosystem process, that enables the reproduction of many wild plants.

Pollination is important for 35% of global crop production. Between 60 and 90% of wild plants (depending on the type of biome) require pollination; a larger proportion of the species benefit from flower visitation by mobile organisms.

Mobile organisms that visit flowers provide pollination services at the local scale at which such interaction occurs. Yet, these organisms move freely within and among habitats, and thus their individual, population and community dynamics depend on the spatial distribution of resources at landscape or larger spatial scales (Kremen *et al* 2007).

Pollination is provided by wild animals. Bees are the most important pollinators. Yet, butterflies, moths, flies, beetles, wasps, birds, bats, and other invertebrates and mammals are important for this service. Commercially managed bees are very important for the provision of the service in agricultural contexts; *Apis mellifera* is the most important pollination service provider globally to farmers.

Rich pollinator assemblages enhance pollination in different ways. Richer species are often the most abundant and show the highest contribution to pollination. Different species pollinate different species within a diverse agro-ecosystem. Also, different species visit preferentially different parts of the plant and thus contribute to a more thorough pollination. Different species respond differently to changes in climatic conditions and in resource availability. They are also differently sensitive to the impacts of agricultural intensifications. Thus richer pollinator communities show higher resilience (Klein *et al* 2009).

Landscape structure and diversity determine the spatial and temporal availability of food, and sites most suitable for nesting, hibernating and mating. Thus landscape quality is determinant for the maintenance of pollinators and the services they provide.

Wild and managed pollinators have suffered dramatic declines in recent years. Severe declines in *Apis mellifera* populations, those of the major groups of pollinators and of the plants that they pollinate have been document, despite the pervading lack of long-term, globally distributed data (though the data records for *A. mellifera* begin in 1908). Land use change and changes in landscape structure are the major drivers of this change. Also, agricultural intensification, particularly the use of pesticides, that directly affect pollinator populations, and that of herbicides, fertilizers, irrigation, tillage or fire, that affects the availability and spatial distribution of resources as well as environmental conditions, change the total abundance, composition and richness of pollinator assemblages (Winfree *et al* 2009). Yet, the reduced amount of independent experiments or observations has hindered testing for the generality of the impacts of the above factors. To date, only habitat change has shown consistent negative significant effects on bee richness and abundance (Figure 4).

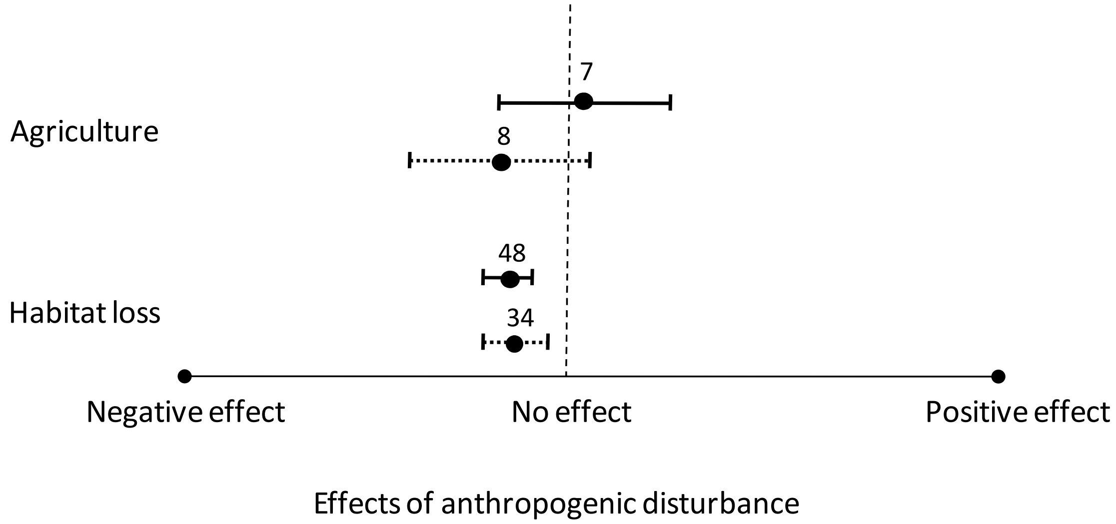


Figure 4 Effects of different anthropogenic disturbance factors on (a) bee abundance (solid line) and (b) bee richness (dashed line). Mean effect and 95% confidence intervals are shown for each type of disturbance. Significant effects correspond to average and confidence interval values that do not overlap with the non-effect line. Numbers above each result indicate the number of independent measurements found in the literature used for the analyses (modified from Winfree et al 2009).

The above results show that pollinator decline is undeniable and that decline in the abundance and richness of pollinators has negative consequences for pollination. Yet, the consequent threats to global agricultural food production are still under debate.

D. Regulation of human infectious disease

It is not possible to assert that the most diversity the better the regulation of human infectious diseases. In fact, evidence to date shows that the maintenance of some of the biodiversity can cause disease, while the maintenance of other elements of biodiversity is key to regulating both the incidence and prevalence of disease.

Regulation of the appearance and transmission of infectious diseases to human populations is a regulating service. The service is provided by several processes such as the regulation of population sizes of vectors, hosts and pathogens, the regulation of interactions between them and human populations, and the regulation of their natural enemies.

Infectious diseases result from the interaction of pathogens or parasites, vectors, hosts and the environment. Frequently many species are involved, including many hosts, many vectors, and a wide range of species with which they interact. Pathogens include helminthes, fungi, protozoa, viruses or prions and bacteria or rickettsiae; nearly bacteria and rickettsiae caused 55% of infectious diseases. Zoonotic pathogens are those that complete their whole life cycle within animal species but can also infect humans, through links with other vertebrates. More than 70% of human diseases are caused by such pathogens associated to wild fauna, and their incidence is increasing through time (Jones *et al* 2008).

The nature of the links between biodiversity and the regulation of infectious diseases is quite complex. On one hand, higher biodiversity can be associated with a larger diversity of new pathogens; on the other, higher biodiversity has been associated with reduced transmission probability of already established pathogens and with the reduced establishment of new ones. Yet the most evidence points to the latter. Mathematical models, individual studies and recent syntheses have shown that a higher diversity of hosts is associated with less frequent and slower disease transmission, and thus reduced disease incidence (Keesing *et al* 2010).

Table 3 Diseases whose transmission is affected by habitat or biodiversity loss and the associated mechanism. S indicates a suggested mechanism, while D denotes that tmechanisms have been demonstrated in diverse studies [a]

Disease	Mechanism	Main organisms that affects the disease
Coral diseases	Changes in host/vector abundance ^{D}	Coral reefs
Malaria	Changes in host/vector abundance ^{D}	Humans (mammals, vertebrates)
Helminthic parasite of fish	Changes in host/vector abundance ^{S}	Aquatic vertebrates (fishes and sharks)
Puccinia rust infection of ryegrass	Changes in host/vector abundance ^{S}	Plants
Amphibian limb malformation	Changes in host/vector/parasite behavior ^{D}	Amphibian (salamanders, frogs and toads)
Bacteriophage of Pseudomonas syringae	Changes in host/vector/parasite behavior^{D}	Plants
Fungal disease of Daphnia	Changes in host/vector/parasite behavior ^{D}	Plank tonic crustaceans
Schistosomiasis	Changes in host/vector/parasite behavior ^{D}	Humans (invertebrates, vertebrates)
Trematode diseases of snails and birds	Changes in host/vector/parasite behavior ^{D}	Invertebrates, vertebrates
Hantavirus disease	Changes in host/vector abundance and Host/vector/parasite behavior ^{D}	Humans (mammals, vertebrates)
Lyme disease	Changes in host/vector abundance and host/vector/parasite behavior ^{D}	Humans (mammals, vertebrates)
West Nile fever	Changes in host/vector abundance ^{S}, Host/vector/parasite behavior ^{S}	Humans (birds, vertebrates)

[a] Modified from Keesing et al. (2010)

At local to regional scales (Keesing *et al* 2010), biodiversity loss affects the emergence and transmission of infectious disease through changes the abundance of hosts or vectors, changes in the behavior of hosts, vectors or parasites and changes the condition of hosts or parasites (Table 3). Anthropogenic impacts on ecosystems have led to impacts on the regulation of infectious diseases through losses of natural enemies of vectors, increases in population densities of host species, changes in genetic diversity of vectors or pathogens (such as antibiotic resistant bacteria or pesticide resistant mosquitoes), as well as increased frequency of soil, water or airborne transmission of pathogens.

At global scales, many social and ecological factors are related to the increasing incidence of infectious diseases (that peaked in the 80's). The highest incidence occurs at high latitudes (30-60 degrees north and 30-40 degrees south), in areas with the highest population density. Yet, host species richness is a significant predictor of the appearance of infectious diseases associated to zoonotic transmissions from wild species (Jones *et al* 2008).

Overall, reduced species richness has been related to increased disease incidence. Yet, further understanding of the role played by biodiversity in the regulation of infectious diseases is needed to better assess the risks of biodiversity loss on human health.

IV. Analyzing the links between biodiversity and ecosystem services at different spatial scales

The links between biodiversity and ecosystem services have been studied at a wide range of spatial scales. The approaches used, hypotheses tested and the types of results change clearly across these scales.

A. Local scale

A large amount of work has been done to explore the links between biodiversity and ecosystem functioning at local scales, some of which has been used to assess the effects of biodiversity on ecosystem services. Experimental studies, observational studies and modeling efforts have led to recent syntheses of this vast literature.

Quantitative syntheses have addressed the role played by various types of diversity. The first qualitative synthesis (Hooper *et al* 2005) emphasized the strong influence that species' functional characteristics have on ecosystem processes, independently of their relative abundance. Another one (Diaz *et al* 2006) suggested multiple potential links between genetic diversity, species richness, functional composition and landscape structure on a range of ecosystem services. Yet the generality of the patterns was debated.

Quantitative meta-analyses have assessed the generality of the effects of species richness on ecosystem functioning derived from experimental studies.

Higher plant species richness leads consistently and significantly to increased standing biomass of primary producers and increased efficiency in the assimilation of inorganic resources by these primary producers in terrestrial and aquatic systems. Data for other functions and groups is still insufficient to draw general conclusions (Cardinale *et al* 2011).

Experimental studies have also been used to assess the role of biodiversity in the provision of ecosystem services and synthesized using meta-analysis (Figure 5). Higher plant species richness leads to higher provision of plant products, greater pest regulation (lower primary consumer biomass), greater erosion control and higher regulation of invasive species and pathogens. Also, increased micorrhizae richness led to higher provision of plant products and higher erosion control. Yet, higher species richness led to lower low or non-significantly different soil fertility regulation (Balvanera *et al* 2006; Quijas *et al* 2010).

The effects of species richness on ecosystem stability, measured as the inverse of the variance of an ecosystem process through time, have been assessed in a few long-term experiments. Higher species richness led to higher stability in some cases and to non-significant changes in stability in others (Balvanera *et al* 2006). Higher plant species richness consistently contributed to higher security (less variance) in the provision of plant products (Quijas *et al* 2010).

The above results are derived from extrapolations from links between ecosystem processes actually measured in experiments and ecosystem services that are potentially associated with them. Focusing on individual ecosystem service providers, and making explicit these links have helped clarify these connections (Quijas *et al* 2010). Yet, direct measures of services from biodiversity experiments are needed.

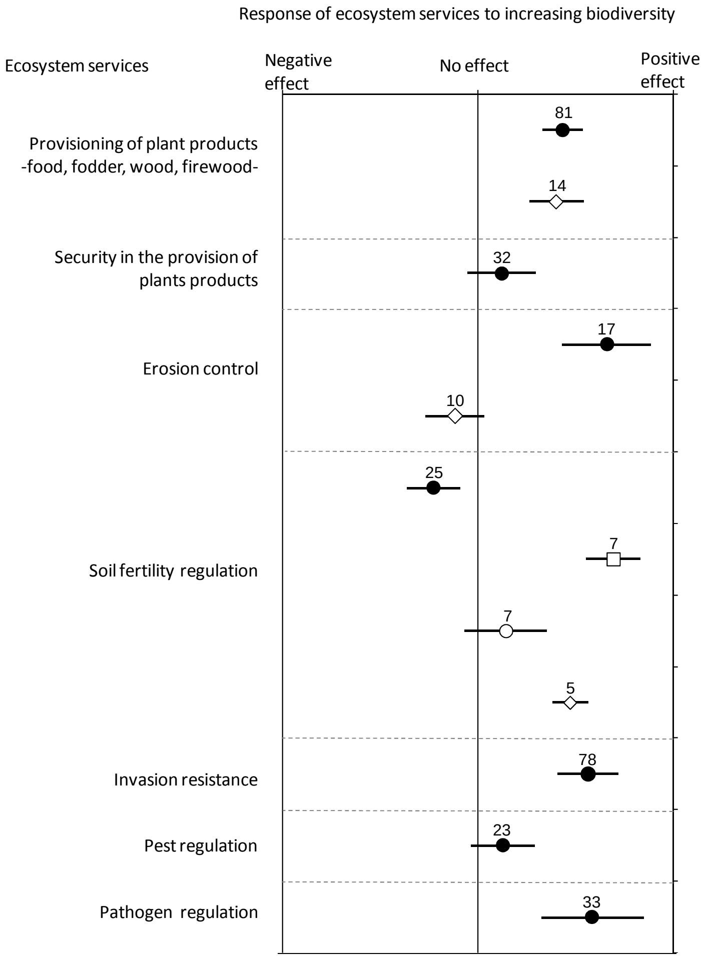


Figure 5 Effects of experimental manipulations of biodiversity on ecosystem services. Symbols show differential effects of trophic level manipulated: circle, primary producers; diamond, mycorrhiza; square, decomposer. Numbers above each result indicate the number of independent measurements found in the literature used for the analyses (modified from Balvanera et al 2006, clear open symbol; Quijas et al. 2010; solid symbol).

Observational studies have in many cases measured ecosystem services directly. Recent syntheses for the case of agricultural food production, pollination and regulation of infectious diseases have been summarized above. A meta-analysis of the effect of richness in tree plantations has shown that mixing tree species generally increases plantation growth rate.

Experimental and observational studies seldom address cultural ecosystem services. Yet, one experiment in temperate grasslands showed that people perceive changes in species richness, composition and evenness. People were most attracted to the most diverse arrays (Lindemann-Matthies *et al* 2010).

Functional attributes of species and communities have strong influence on ecosystem service provision through their effect on ecosystem processes. A recent synthesis has shown that quantitative associations between species' traits and ecosystem services are available to date for a range of organisms, with a large proportion of data for plants and soil invertebrates. Key traits such as body size, canopy size and specific leaf area or root architecture are related to a suite of ecosystem services (de Bello *et al* 2010).

Individual species have differential contributions to a particular function. The functional structure approach can be used to assess the relative contribution of each individual species to an additive ecosystem function, in the same way that rank-abundance curves assess the relative contribution of each species to the total abundance. Pollination in watermelon organic farms of California found within conserved matrices is provided by 11 bee species; eight of these species contribute with quite similar amounts of pollen grains. Instead, in organic farms found within agricultural matrices only four species pollinate watermelon; only one species contributes to more than 90% of the pollen grains deposited. Also, the relationship between species' relative abundance and relative functionality can be used to identify abundant species that are functionally important, or rare species that contribute little to the function, or species whose relative contribution to the function is significantly different than that expected by their relative abundance. Carbon stocks in the tropical rain forest of Chiapas, Mexico, are provided by 169 tree species; one abundant species with dense wood and large trunks, *Dialium guianense*, contributes to more than 10% of the abundance and of the carbon stocks; a fast growing species with thin stems, the pioneer species *Cecropia obtusifolia*, contributes less to carbon than expected from its relative abundance; various species of the genus *Ficus* contribute to less than 1% of carbon stocks, and to less than 0.1% of the abundance, and yet have been considered keystone species due to their critical interactions with many bird and mammal species (Balvanera *et al* 2005).

Analyses of biodiversity effects on functions or services have mostly focused on a single function. Yet, a key question is how will species loss affect overall ecosystem functioning. Conceptual models and experimental studies and shown that increasing species richness increases the maintenance of multiple ecosystem processes; this is particularly true when there are many species that contribute significantly to various functions (Gamfeldt *et al* 2008).

Evidence from local-scale experimental and observational studies points to positive effects of biodiversity on service provision, and to the paramount role played by species composition or functional attributes. Key functional attributes such as leaf phenology, leaf distribution over stems and canopy size and architecture have been shown to be important in determining plant species' contribution to climate regulation (de Bello *et al.*, 2010).

Overall, while the local-scale experimental approach may provide key insight on the way biodiversity relates to functioning their potential applications to services is somehow limited. To date, only a small range of services have been assessed (e. g. soil fertility, fodder provision, biocontrol). Also, the realism of local scale biodiversity experimental manipulations and their potential applications to management relevant conditions, including larger spatial scales and human interventions, has been debated.

B. Landscape scale

Analyzing the links between biodiversity and ecosystem services at landscape scales offers very different perspectives than those at the local scale. While food production, or soil fertility regulation are provided at local spatial scales, many ecosystem services such as pollination, pest regulation, regulation of landslides or coastal protection depend on ecosystem processes and ecosystem service providers that occur at landscape scales. Mobile organisms that move freely through the landscape provide some of the services; the attributes of the landscape in terms of the types of land-use change found and their spatial arrangement are relevant at this scale; complex trophic cascades that encompass organisms with home ranges at a variety of spatial scales are associated with service provision. Also, societies and ecosystems interact at landscape scales through land-use decisions that often lead to land-cover changes or to agricultural intensification.

Natural experiments, those in which different diversity levels are found due to natural or anthropic causes, replace experimental manipulations of species richness at this scale. As a consequence, correlations between diversity and services can be observed, but can be the result of direct effects of changes in abiotic conditions on diversity, direct effects on the processes or services, or mediate the links between them. Testing for the underlying mechanisms is more complex. Yet, manipulations of some groups of species are possible at this scale.

Experimental manipulations of individual groups of species have shown positive correlations between diversity and ecosystem services. A meta-analysis of experimental bird enclosures in diverse agroecosystems in Central America showed that bird functional species richness, richness of functional groups and functional diversity were positively correlated with pest regulation services, measured as removal of arthropods (Philpott *et al* 2009). The contribution of all species and functional groups were not equal, and one species and two of the functional groups contributed disproportionately to the service. Yet, direct links to a service would require focusing on crop consumer arthropods.

Species loss at one particular trophic level can have cascading effects on many other levels, and thus have profound consequences on ecosystem services. Mathematics models have shown that many species of decomposers can be lost before observing a dramatic reduction in service provision; yet, the fraction of species lost that leads to reduction in ecosystem services increases as upper trophic levels are considered (plants, herbivores and predators). Moreover, rapid declines in service provision are predicted as predators are lost

(Figure 6). Given that the upper trophic levels are more vulnerable to land use change, as they have less functional redundancy, fewer individuals per species and are characterized by larger home ranges, rapid declines in ecosystem services are to be expected (Raffaelli 2004; Dobson *et al* 2006).

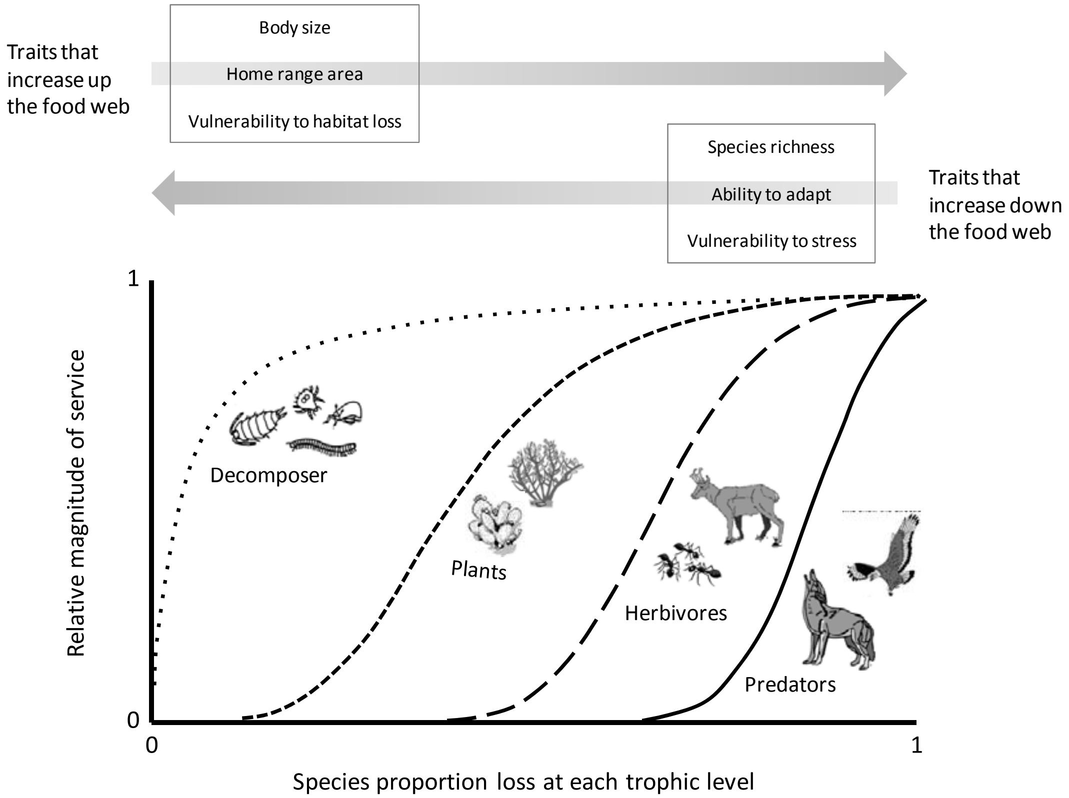


Figure 6 Declines in species diversity and corresponding impacts on ecosystem services for different trophic levels. A mathematical model suggests that declines in ecosystem services will initially be slow but will then accelerate as species from higher trophic levels are lost at faster rates and the consequences of their loss is most dramatic (modified from Dobson et al. 2006).

Yet, the responses of ecosystem processes and services associated with species loss vary between different trophic levels. A meta-analysis of removal experiments in agroecosystems (Mooney *et al* 2010) showed that excluding vertebrate insectivores such as birds, bats and lizards increased the abundance of predaceous and herbivorous arthropods, that is both those species that are considered pests in agroecosystems (herbivores) and their natural enemies (predators); in fact, the strength of the effect of vertebrate insectivores on both groups was the same. Exclusions also showed reduced plant damage and increased plant biomass. Thus the role played by birds, bats and lizards in pest regulation in agroecosystems can be seen both as positive (by decreasing herbivores, decreasing plant damage and increasing plant biomass) and negative (by decreasing natural enemies of herbivores).

One of the main drivers behind species loss in terrestrial environments is habitat loss, or habitat degradation. Thus biodiversity effects on ecosystem services at landscape scales can be assessed indirectly through changes in land cover and in the spatial distribution of habitat patches. The mechanisms underpinning the maintenance of biodiversity in complex landscapes such as agricultural landscapes are growingly being understood. Individual species' dynamics is given by that of individual populations that are found locally as well by the meta-population, given by the group of populations found across the landscape. In similar ways, interactions among species within and among trophic levels occur at different spatial scale. Thus, structurally complex agricultural landscapes allow for the maintenance of biodiversity and are expected to contribute to the maintenance of ecosystem services such as pest regulation while ensuring food production (Tscharntke *et al* 2005).

One well-studied aspect of the role played by landscape structure on ecosystem provision is isolation from natural habitat. A meta-analysis of landscape effects on crop pollination services (Ricketts *et al* 2008) showed a consistent decline in pollinator richness with increasing isolation; richness drops to half of its maximum value at distances of 1,500 m. A faster decay rate was found in visitation rate, which drops to half of its maximum value at a distance of 700 m, with steeper decay rates in tropical regions respective to temperate ones.

Ecosystem services can also be provided by the physical structure that results from the establishment and growth of species. That is the case of coastal protection that is provided by mangroves, salt marshes, coral reefs and sea grass beds. Wave height decreases as it moves inland from a shoreline with mangroves or salt marshes. Decreases in wave height have been associated with increasing habitat distance inland from the shoreline for mangroves and salt marshes. Wave attenuation decreases with increasing water depth above sea grass beds and near-shore coral reefs, and with increasing grass cover in coastal dunes (Barbier *et al* 2008).

Given that changes in species richness, species' functional attributes and land cover characteristics are all relevant to determining change in ecosystem service provision, the integration of many of those aspects is needed to characterize the role played by biodiversity in service provision at landscape scales. Ecosystem processes and services are strongly determined by species' functional characteristics, or functional traits, and largely by those of dominant species. On the other hand, abiotic conditions can have direct effects on the services; also, non-dominant species can have disproportionately large effects on the function. Thus the role played by biodiversity on ecosystem services can be explored using a step-wise analysis by dissecting the individual contribution of the above factors on ecosystem services, and then combining those into the best possible predictive model, as has been suggested recently (Diaz *et al* 2007).

Spatially explicit models of the links between biodiversity and ecosystem services can be built based on the understanding on the tight links between land cover and ecosystem service provision, as well those between species' functional attributes (Lavorel *et al* 2011). Thus land use can have both direct effects on ecosystem services, and those that affect species' functional attributes and in turn affect ecosystem service provision. Given that individual species' traits are relevant to various ecosystem services, and that land use change has impacts on multiple ecosystem services, models have been developed to assess the direct and indirect impacts of land use change on multiple ecosystem services. The recently developed tool to map and model ES called InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs) uses LUC maps as basis for further assessing quantitatively ES delivery in terrestrial and marine ecosystem.

At landscape scale the needs and perceptions of different social actors converge, each leading to different land use change decisions and fostering the provision of particular ecosystem services. Links between biodiversity and ecosystem services would then need to incorporate such complexity. Relevant ecosystem services can be related to species' functional traits and functional diversity based on scientific evidence and local quantifications. Yet this can also be done from the perspective of the local social actors based on their perceptions of such links and their preferences for different ecosystem services. A conceptual framework that integrates all the above has been developed (Diaz *et al* 2011), that result from a combination of approaches into an interdisciplinary (ecological and social sciences) and inter-sectorial (scientists and relevant local actors) perspective of the links between biodiversity and ecosystem services (Figure 7).

C. Regional to global scale

At regional to global scales exploration of the links between biodiversity and ecosystem services is much more related to their potential spatial congruence than their functional relationships. The analyses rely on spatially explicit models that predict both biodiversity and service provision that are based on topographic, climatic and land use information. The key question is whether most diverse areas are also those that are most critical for the provision of individual services or that of combinations of services. To date, less than a dozen of such studies are available at scales ranging from regional to the globe.

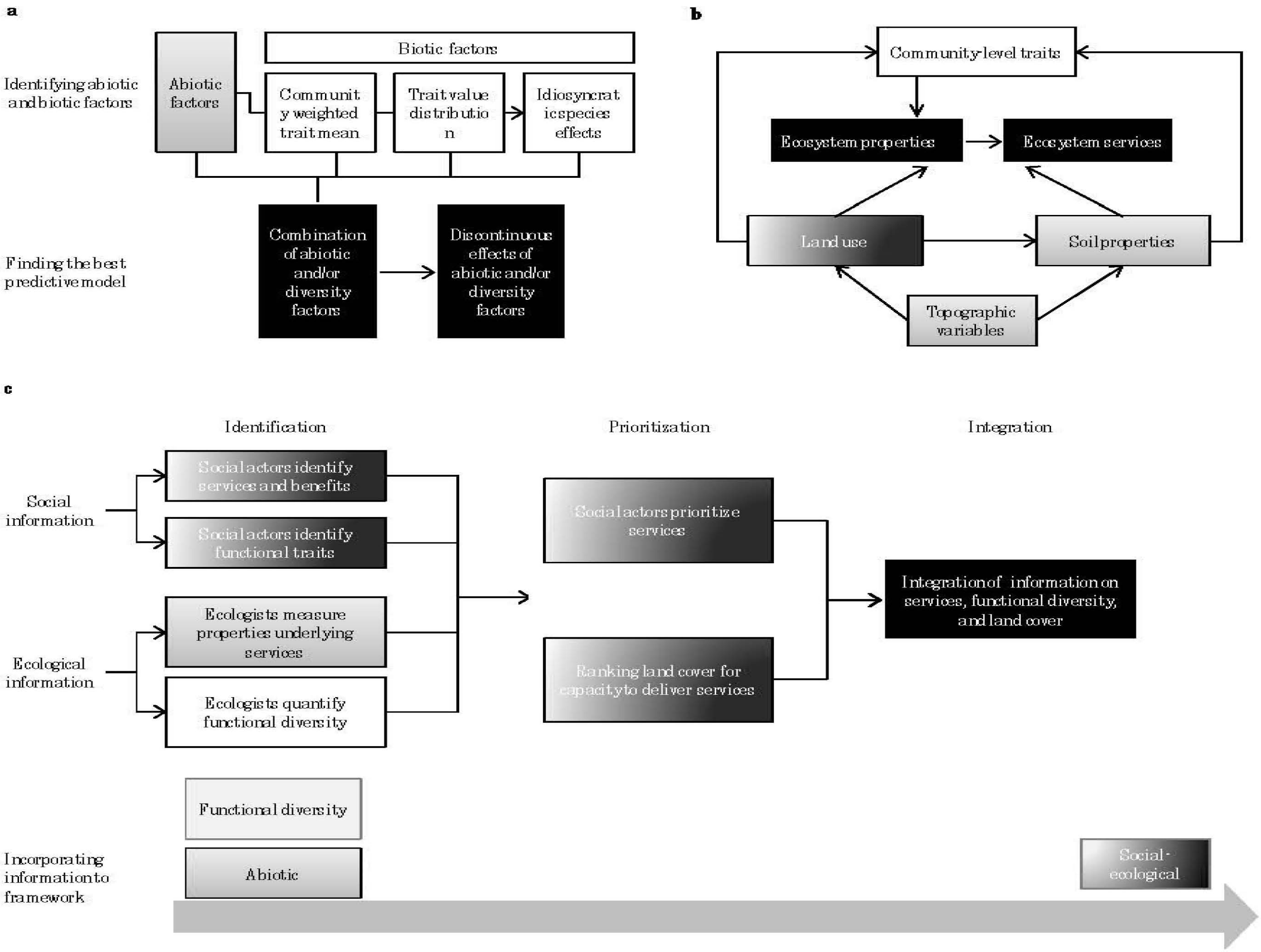


Figure 7 Diagrammatic conceptual frameworks for analyzing the links between functional diversity, ecosystem functioning and ecosystem services. (a) Framework with steps proposed to reduce uncertainty in the prediction of properties and ecosystem services based on plant functional diversity (modified from Diaz et al. 2007); (b) framework for the analysis of ecosystem properties underlying ecosystem services (modified from Lavorel et al. 2011); (c) framework that integrates ecological and social information on the links between biodiversity, ecosystem services and land use (modified from Diaz et al. 2011).

Spatially explicit models to predict the distribution of biodiversity have been developed for the past two decades. Instead, the development of analogous models for the case of ecosystem service delivery is very recent, and started to be developed only a decade ago. To date close to 50 different publications have addressed this issue from different perspectives. Yet, the broadest initiative to date on the subject, both in terms of the types of services analyzed, the range of data sources needed, and the number of places in the globe where it has been applied is the Natural Capital Project initiative (www.naturalcapitalproject.org). The initiative developed spatially explicit models for many ecosystem services as well as analytical tools to assess the management implications of the resulting maps (Kareiva *et al* 2011).

No consistent evidence of spatial concordance between biodiversity and ecosystem services has been found. This is true both for regions within a state (Chan *et al* 2006) and for the whole globe (Naidoo *et al* 2008). Also, the spatial patterns of provision of individual services are not correlated and thus critical areas for the maintenance of one service is not similar to that of another service (Chan *et al* 2006). When combining multiple ecosystem services into a total ecosystem service value the concordance between biodiversity and the services was not found either (Turner *et al* 2007).

The lack of congruence in the spatial patterns of biodiversity distribution and ecosystem service delivery is expected from a conceptual perspective. The lack of congruence in the spatial patterns of different groups of species was found a decade ago, and is consistent with the fact that each group is differentially affected by changes in environmental conditions and that the scale at which such interaction is given changes in the size of the organism. In similar ways, we have seen here that different ecosystem service providers are relevant for the delivery of different services; ecosystem service providers and services respond differently to changes in environmental conditions and to anthropogenic disturbance.

Despite of the lack of congruence in the distribution patterns of biodiversity and ecosystem services, management can be aimed towards maximizing the possibility of protecting both. Reserve selection algorithms have been used to identify the combination of areas that would maximize the conservation of biodiversity conservation that of ecosystem services (Chan *et al* 2006). Spatially explicit models of biodiversity and ecosystem services have been used to predict the outcomes of different land use change scenarios and explore for management alternatives that would maximize conservation of both biodiversity and ecosystem services. Stakeholder preferences for scenarios that provide multiple services while ensuring the conservation of biodiversity in a case study in the state of Oregon suggest opportunities for win-win policies that will ensure both (Nelson *et al* 2009).

To date, the identification of key areas of biodiversity or service provision heavily relies on the limitations inherent to the spatial modeling tools. In general, the analysis of different scales (total area studied) encompasses changes in the resolution (pixel size) of the study. Changes in resolution have been shown to lead contrastingly different patterns of concordance between biodiversity and service provision (Anderson *et al* 2009).

Understanding the links between biodiversity and ecosystem services at regional to global scales is still developing. Systematic comparisons with the equivalent methods are needed among regions and among scales. Also tools for this assessment might need to be refined.

V. Conclusions

Research available to date has shown that biodiversity plays a prominent role in the delivery of many key ecosystem services. A wide range of types of organisms, their genetic, population, and community diversity, as well as the landscape diversity and the trophic networks among them are key ecosystem service providers. Biodiversity is linked to agricultural food provision, soil fertility regulation, pollination, and human disease regulation in a variety of ways; ongoing studies have contributed significantly to understanding the ways in which biodiversity is important for ecosystem services. Most of the research available is concentrated in that derived from experimental manipulations of biodiversity and its effects on ecosystem services or on a few key ecosystem services. Direct measurements of a wide variety of ecosystem services are needed as well as a more data at landscape scales, at which the most relevant connections between biodiversity and services are expected. Systematic comparisons of the role played by biodiversity at a set of spatial scales for many ecosystem services are needed. Also, the final effects on biodiversity and human well-being through ecosystem services are still to be fully understood.

VI. Acknowledgements

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Capítulo II

Plant diversity enhances provision of ecosystem services: a new synthesis*

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Plant diversity enhances provision of ecosystem services: A new synthesis

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Abstract

Biodiversity is known to play a fundamental role in ecosystem functioning and thus may positively influence the provision of ecosystem services with benefits to society. There is a need for further understanding of how specific components of biodiversity are affecting service provision. In this context, terrestrial plants are a particularly important component of biodiversity and one for which a wealth of information on biodiversity–ecosystem functioning relationships is available. In this paper, we consider terrestrial plants as providers of ecosystem services and analyze whether manipulating plant diversity has an effect on the magnitude of ecosystem service provision using a meta-analysis of 197 effect sizes and a vote-counting analysis of 361 significance tests. The results of these analyses are compared with those of a previous meta-analysis that included a wide diversity of service providers. We produce a synthesis table to explicitly link plants as service providers to indicators of ecosystem properties and these to ecosystem services. By focusing on only plants, we found a clear positive effect of biodiversity on six out of eight services analyzed (provisioning of plant products, erosion control, invasion resistance, pest regulation, pathogen regulation and soil fertility regulation). When controlling for pseudoreplication (repeated records from single studies), we found that four of the six positive effects remained significant; only pest regulation and soil fertility showed non-significant effects. Further expanding our basis for inference with the vote-counting analysis corroborated these results, demonstrating that quantitative meta-analysis and vote-counting methods are both useful methods to synthesize biodiversity–ecosystem service studies. Notwithstanding the restricted number of identified services, our results point to the importance of maintaining plant diversity to ensure and increased provision of ecosystem services which benefit human well-being.

Zusammenfassung

Zahlreiche Studien zeigen, dass Biodiversität einen positiven Einfluss auf Ökosystemfunktionen im Allgemeinen hat. Verschiedene dieser Ökosystemfunktionen können von Nutzen für die Gesellschaft sein. Es stellt sich daher die Frage, wie diese sogenannten Ökosystemdienstleistungen im Besonderen durch Biodiversität und ihre Komponenten beeinflusst werden. In diesem Zusammenhang spielen Landökosysteme und hier in erster Linie eine diverse Vegetation eine entscheidende Rolle. Zudem ist die Faktenlage hinsichtlich des Einflusses pflanzlicher Biodiversität auf die Funktionsfähigkeit von Landökosystemen besonders gut. Wir verwenden diese Fakten in zwei Meta-Analysen, um den Einfluss pflanzlicher Biodiversität auf Ökosystemdienstleitungen zu beschreiben. In der ersten Analyse verwenden wir Effektgrössen aus 197 untersuchten Beziehungen, in der zweiten Analyse Signifikanzen aus 361 Beziehungen. Die Synthese der analysierten Beziehungen wird in einer Tabelle

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dargestellt, welche die pflanzliche Biodiversität als Leistungserbringer mit Gruppen von Ökosystemfunktionen (Indikatoren) und diese mit Ökosystemdienstleistungen in Beziehung setzt. Durch die Fokussierung auf einen Leistungserbringer wurden in der ersten Analyse signifikante positive Effekte der Biodiversität auf sechs von acht untersuchten Ökosystemdienstleistungen sichtbar: Pflanzenproduktivität, Erosionsvermeidung, Kontrolle invasiver Arten, Regulation von Schädlingspopulationen, Regulation von Pflanzenkrankheiten und Erhalt der Bodenfruchtbarkeit. Die zweite Analyse bestätigte diese Resultate. Gleichzeitig konnte durch den Vergleich der beiden Analysen gezeigt werden, dass nicht nur Studien mit Effektgrössen sondern auch solche mit Signifikanzen Sinn machen, insbesondere wenn mit Signifikanzen eine grössere Population von Studien erschlossen werden kann. Unsere Ergebnisse zeigen, dass durch den Schutz und die Förderung pflanzlicher Biodiversität Ökosystemdienstleistungen gesteigert werden können und somit direkter Nutzen für die Gesellschaft erzeugt werden kann.

Keywords: Ecosystem property; Ecosystem service; Ecosystem service provider; Meta-analysis; Vote-counting; Terrestrial ecosystems; Terrestrial plant diversity

Introduction

There is growing concern that loss of biodiversity may affect ecosystem functioning and, therefore, may threaten the continued provision of various ecosystem services on which humans depend (Chapin et al. 2000). Recent syntheses have indeed shown many positive effects of biodiversity on ecosystem properties (e.g. plant aboveground and root biomass, biomass of marine plants and algae) related to the provision of ecosystem services (e.g. carbon storage, erosion control, regulation of water quality; Balvanera et al. 2006; Worm et al. 2006). With due care, such results, while based mostly on small-scale biodiversity manipulation experiments, can be extrapolated to estimate the contribution of different components of biodiversity to the provision of services at larger spatial and temporal scales (Schläpfer, Schmid, & Seidl 1999; Roscher et al. 2005; Duffy 2009).

Available syntheses derived from experimental work (Balvanera et al. 2006; Cardinale et al. 2006; Schmid et al. 2009a) have covered various functions, services and habitats, contributing to the generality of results. Yet, there is still need for further understanding of how the specific biodiversity components are involved in ecosystem service provision. Such understanding would allow better management to protect both biodiversity and services in real ecosystems (Kremen 2005; Díaz, Fargione, Chapin, & Tilman 2006; Díaz et al. 2007b; Luck et al. 2009). Unravelling explicit connections between biodiversity components, ecosystem properties and ecosystem services is essential to address this need. For instance, high primary productivity can easily be associated with the provisioning of food in terrestrial ecosystems, but is also a sign of eutrophication in aquatic ecosystems (Srivastava & Vellend 2005). The identification of specific populations, communities, functional groups, or habitat types involved in service provision (Luck et al. 2009) will enhance our understanding of the links between biodiversity and ecosystem service provision.

Taking advantage of the wealth of information available from experimental studies manipulating terrestrial plant diversity, we focus here on terrestrial plants as ecosystem service providers, and analyze if increasing species diversity of a plant community contributes to increasing ability of these systems to provide benefits to human population. Plants as the first trophic level in the ecosystem play a fundamental role in ecosystem functioning (Hooper et al. 2005) and are relevant for the provision of many ecosystem services (Díaz et al. 2006). The experimental work in this research area has involved manipulations of this first trophic level and represents between 29% and 73.4% of the records in databases about biodiversity–ecosystem functioning relationships (Srivastava & Vellend 2005; Benayas, Newton, Diaz, & Bullock 2009; Cardinale et al. 2009; Schmid, Pfisterer, & Balvanera 2009b).

Positive effects of diversity on ecosystem service provision (Balvanera et al. 2006) were based on a wide variety of ecosystem service providers such as primary producers, primary consumers, secondary consumers and detritivores. Further examination of such results focusing on the service provider for that is best-known to date may allow us to confirm or refute its effects on specific ecosystem services. This may be done with quantitative meta-analyses, which assess the magnitude and direction of plant diversity effects on service provision, or with vote-counting methods, which assess the frequency of positive, neutral and negative test results, and thus can use larger samples sizes for analysis (Hedges & Olkin 1980; Gurevitch & Hedges 2001).

In this paper we explore in detail the relationship between terrestrial plant diversity and the provision of ecosystem services. First, we explicitly associate terrestrial plants with specific ecosystem properties and corresponding ecosystem services. Second, we perform a meta-analysis, restricted to studies manipulating terrestrial primary producers, to (a) explore effects of changing diversity on service provision and (b) compare our results to previous analyses considering a wider range of organisms and habitats. This comparison will allow us to assess the pros and cons of focusing only on terrestrial plants as service providers. Third, we perform a vote-counting analysis for results from studies manipulating plant diversity to explore the robustness of conclusions derived from different synthesis methods. Finally, we discuss the most important conclusions that emerge regarding the different ecosystem services identified and the maintenance of these services via the conservation of plant diversity.

Materials and methods

Data base

We used a recently published database compiling experimental work about the effects of biodiversity on ecosystem functioning (Schmid et al. 2009b). The database covers publications from 1954 to June 2004; these publications were identified in the ISI Web of Science and in the Biological Abstracts databases using specific search keywords (biodiversity or species richness and stability or ecosystem function or productivity or yield or food web; Balvanera et al. 2006). The database contains 761 records; including studies reporting *r* values; i.e. the simple (regression) and multiple (analysis of variance) correlation coefficient of the relationship between manipulated diversity and the magnitude of the ecosystem property; as well as studies only reporting direction and significance; i.e. whether relationships between manipulated biodiversity and a given ecosystem property were significantly positive; neutral or significantly negative.

For this new synthesis we only considered studies involving the manipulation of terrestrial plant diversity. By this we mean the manipulation of any attribute of primary producer diversity (richness, evenness, functional richness and diversity). Furthermore, all the response variables were terrestrial ecosystem properties. Given these criteria, we worked with 361 records from 82 experimental studies all of which were used for the vote-counting analysis. A subset of 197 records from 61 studies additionally reported *r* values and were used for the quantitative meta-analysis. Overlaps and differences between the database used here (Schmid et al. 2009b) and the one used by Balvanera et al. (2006) are detailed in Appendix A (Supplementary Data) (Table 1)

Associating ecosystem services with ecosystem properties and indicators

A first step towards the assessment of the effects of manipulated plant diversity on the provision of ecosystem services was to identify the measured ecosystem properties and suggest a corresponding ecosystem service (Hooper et al. 2005; Luck et al. 2009).

By consistently relating specific indicators ("indicator" = group of similar variables measured in the original studies) to ecosystem properties and the corresponding ecosystem services we hope to reduce uncertainties in our theoretical understanding and capacity to manage biodiversity for the provision of ecosystem services. Our mapping of indicators to ecosystem properties and services does not explicitly include the differences in spatial scales at which various properties were measured. In the absence of true large-scale experiments, we argue that all cases analyzed here can be collectively considered as representative of the local scale even if ranging from 0.03 to 500 m^2 (see Roscher et al. 2005 for a demonstration of scale invariance of plant diversity effects within the local scale).

For each record in the database we identified: (i) the trophic level or ecosystem component measured (e.g. primary consumer), (ii) the indicator to which a measured variable belonged, (iii) the ecosystem property (e.g. primary consumer biomass) to which the indicator was related, (iv) the ecosystem service (e.g. pest regulation) that was *a priori* associated to the ecosystem property using the Millennium Ecosystem Assessment service classification (MA 2003) and (v) the definition of this ecosystem service (Table 1).

Ecosystem services are the key conceptual link between ecosystem properties and the benefits they provide to society (Boyd & Banzhaf 2007; MA 2003). Ecosystem properties are physical characteristics of ecosystems – dynamic or static – that encompass their biotic and abiotic components. Ecosystem services are components of ecosystems that are directly consumed, enjoyed or that contribute, through interactions with other components, to conditions for human well-being, e.g. climate regulation or erosion control (Boyd & Banzhaf 2007; Luck et al. 2009). Based on our definitions of ecosystem services we analyzed how ecosystem properties contribute to human well-being. In the case of ecosystem properties that are related to decreased human well-being, we consider a plant diversity effect as positive for the corresponding ecosystem service if it leads to decreased values of the undesirable ecosystem property (Balvanera et al. 2006). For example, the association between invader primary producer biomass (ecosystem property) and invasion resistance (ecosystem service) was considered negative and, as a consequence, a negative effect of plant diversity (service provider) on invader primary producer biomass was considered as a positive effect of plant diversity on invasion resistance.

Data analysis

Meta-analysis of plant diversity effects on ecosystem services

The correlation coefficients, *r* values, were *z*-transformed to obtain effect size measures, *Zr* values. We obtained the *Zr* values using Fisher's *z*-algorthim, $Zr = 0.5 \times \ln((1+r)/(1-r))$. *Zr* values are commonly used in meta-analyses because they should be more normally distributed than *r* values which are restricted to the interval from −1 to +1 (Balvanera et al. 2006). The reciprocal of the variance in the individual *Zr* values was used as a weighting factor to make sure studies with small sample sizes were not over-rated in comparison with studies with large sample sizes (Balvanera et al. 2006; Borestein 2009; Schmid et al. 2009b). We report results of weighted mean *Zr* values and their standard errors for each property (hereafter caller QMA for Quijas meta-analysis). These analyses were carried out with the statistical software GenStat (VSN International 2008).

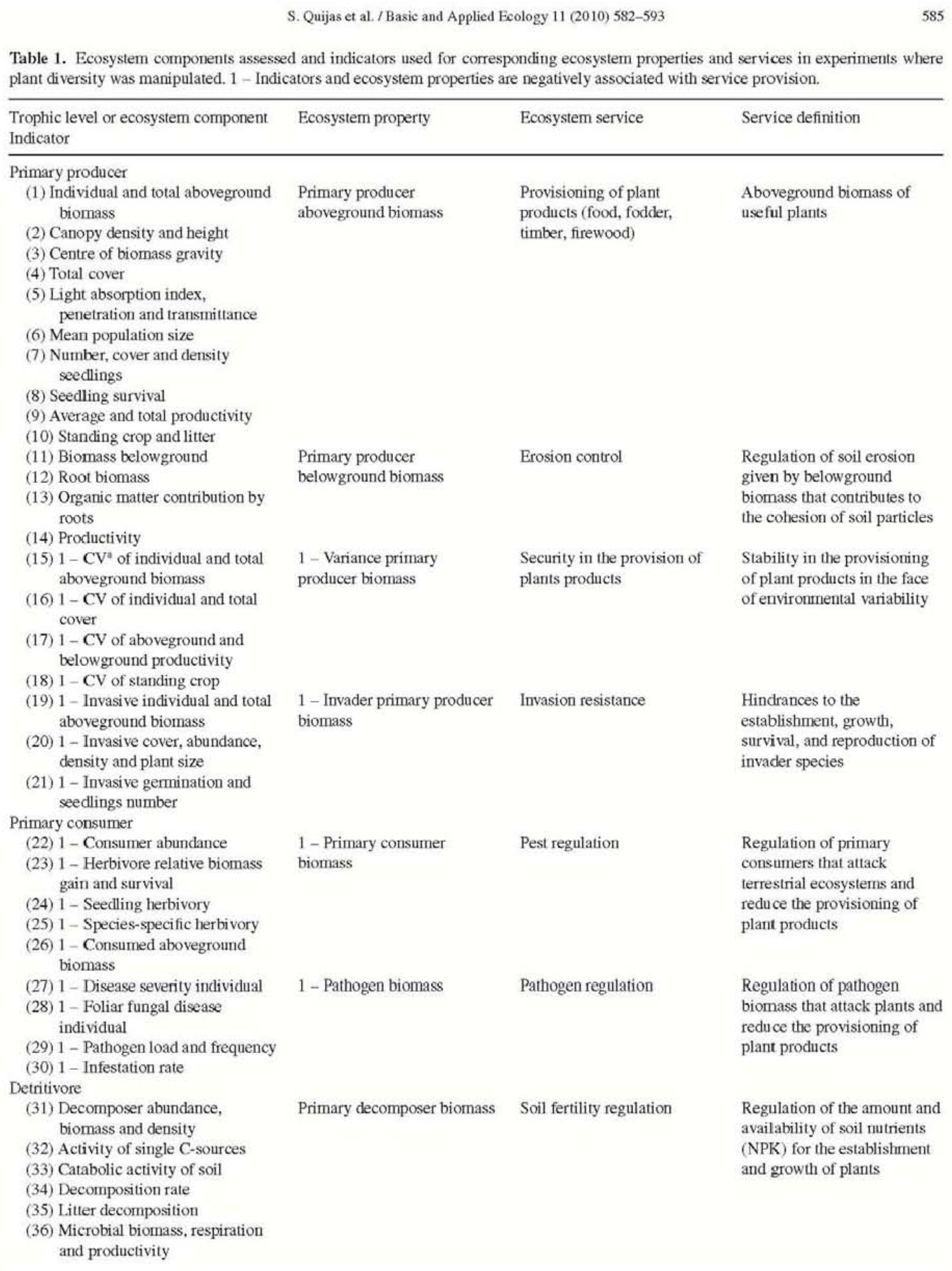

Table 1. Ecosystem components assessed and indicators used for corresponding ecosystem properties and services in experiments where plant diversity was manipulated. 1 – Indicators and ecosystem properties are negatively associated with service provision.

Trophic level or ecosystem component Indicator	Ecosystem property	Ecosystem service	Service definition
Primary producer			
(1) Individual and total aboveground biomass (2) Canopy density and height (3) Centre of biomass gravity (4) Total cover (5) Light absorption index, penetration and transmittance (6) Mean population size (7) Number, cover and density seedlings (8) Seedling survival (9) Average and total productivity (10) Standing crop and litter	Primary producer aboveground biomass	Provisioning of plant products (food, fodder, timber, firewood)	Aboveground biomass of useful plants
(11) Biomass belowground (12) Root biomass (13) Organic matter contribution by roots (14) Productivity	Primary producer belowground biomass	Erosion control	Regulation of soil erosion given by belowground biomass that contributes to the cohesion of soil particles
(15) 1 – CV[a] of individual and total aboveground biomass (16) 1 – CV of individual and total cover (17) 1 – CV of aboveground and belowground productivity (18) 1 – CV of standing crop	1 – Variance primary producer biomass	Security in the provision of plants products	Stability in the provisioning of plant products in the face of environmental variability
(19) 1 – Invasive individual and total aboveground biomass (20) 1 – Invasive cover, abundance, density and plant size (21) 1 – Invasive germination and seedlings number	1 – Invader primary producer biomass	Invasion resistance	Hindrances to the establishment, growth, survival, and reproduction of invader species
Primary consumer			
(22) 1 – Consumer abundance (23) 1 – Herbivore relative biomass gain and survival (24) 1 – Seedling herbivory (25) 1 – Species-specific herbivory (26) 1 – Consumed aboveground biomass	1 – Primary consumer biomass	Pest regulation	Regulation of primary consumers that attack terrestrial ecosystems and reduce the provisioning of plant products
(27) 1 – Disease severity individual (28) 1 – Foliar fungal disease individual (29) 1 – Pathogen load and frequency (30) 1 – Infestation rate	1 – Pathogen biomass	Pathogen regulation	Regulation of pathogen biomass that attack plants and reduce the provisioning of plant products
Detritivore			
(31) Decomposer abundance, biomass and density (32) Activity of single C-sources (33) Catabolic activity of soil (34) Decomposition rate (35) Litter decomposition (36) Microbial biomass, respiration and productivity	Primary decomposer biomass	Soil fertility regulation	Regulation of the amount and availability of soil nutrients (NPK) for the establishment and growth of plants

Table 1. (*Continued*)

Trophic level or ecosystem component Indicator	Ecosystem property	Ecosystem service	Service definition
Abiotic ecosystem components			
(37) N, P availability	Soil nutrient supply	Soil fertility regulation	
(38) N, C organic dissolved			
(39) N mineralization, immobilization, release and retention			
(40) N-pool size in soil			
(41) P,K accumulation soil			
(42) Recirculation of nutrients			
(43) N, P, S concentration soil			

[a] Coefficient of variation.

To avoid pseudoreplication due to multiple records from of a single study (each reference was given an ID) and a single site (each site was given an ID), we used mixed-effects models, where *reference ID* + *site ID* were the random effects that influence the variance of the variable, and the ecosystem property was the fixed effect (hereafter we refer to this analysis as "nops" for "no pseudoreplication"). This allowed us to calculate adjusted means and adjusted standard errors of Zr for each of the properties (hereafter called QMA_{nops}).

Comparison of this meta-analysis with the meta-analysis of Balvanera et al. (2006)

Unadjusted, weighted means reported by Balvanera et al. (2006) (hereafter called BMA) were compared to those of QMA to explore whether there is a benefit in focusing solely on manipulations of plant diversity (QMA) rather than considering all biodiversity manipulations (BMA). We did not compare the adjusted means of our meta-analysis (QMA_{nops}) with BMA, because Balvanera et al. (2006) only presented unadjusted means.

In QMA we reduced the number of ecosystem services considered by combining some ecosystem properties that had been treated separately in BMA. Invader fitness, invader diversity and invasion resistance from BMA were all included into invasion resistance (invader primary producer biomass) in QMA. Drought resistance, resistance to other disturbance and natural variation in BMA were all included into security in the provision of plant products in QMA.

Positive or negative diversity effects on each ecosystem service from QMA and BMA were identified by plotting 95% confidence intervals for mean Zr values and comparing this to zero as the reference value indicating no effect (Borestein 2009). Changes in the significance and direction of diversity effects on each ecosystem service between QMA and BMA were identified when (i) confidence intervals of mean Zr values did not coincide with 0, and (ii) confidence intervals of mean Zr values of each meta-analysis (e.g. BMA vs. QMA) did not overlap. Also, changes in the variance of Zr values among records for each service were evaluated using an F test, based on the ratio of the mean variance of values from BMA and the mean variance from QMA (or the inverse in case the denominator was larger than the nominator).

We also compared the results of our weighted mean Zr values and their standard errors without control for pseudoreplication (QMA) with the results of the analysis controlling for pseudoreplication (QMA_{nops}).

When QMA and BMA yielded different results, we compared the total number of measurements, the trophic level manipulated and the ecosystem type used for each ecosystem property to identify possible sources of discrepancies. When QMA and QMA_{nops} yielded different results, we identified the control for pseudoreplication as the source of such discrepancy.

Vote-counting of plant diversity effects on ecosystem services

Vote-counting analysis (VC) allowed the inclusion of a larger number of records from Schmid et al. (2009b), including those with information only on the significance and direction of the relationship between biodiversity and ecosystem property. For each ecosystem service we registered the frequency of different significant responses to plant diversity according to the following possibilities: (i) the greater the diversity, the lower the provision of the service (−1), (ii) a greater diversity does not modify the provision of the service (0), and (iii) the greater the diversity, the greater the provision of the service (+1). Using standard vote-counting analysis procedures (Bushman & Wang 2009) we first tested for significant differences in frequencies of positive, neutral and negative responses to biodiversity of the different services with a χ^2 test (Sokal & Rohlf 1995). We further used adjusted residuals (residuals divided by their variance) as an a posteriori test for identifying the frequencies responsible for a significant chi-square value to check whether frequencies for +1, 0 or −1 were less or more frequent than expected from a null model where +1, 0 and −1 were equally frequent (Everitt 1992).

To check the appropriateness of using VC, we repeated the analysis with logistic mixed-model analysis as described by Schmid et al. (2009a). The dependent variables were the probability of observing a significant vs. no significant effect and the probability of observing a positive vs. a negative effect among the significant ones. The same basic model as in the analysis of Zr values was used, but instead of an identity link we used the logit link function and instead of normal errors we assumed binomial errors. The fixed-effects factor ecosystem property was then tested conservatively against the random-effects term *site ID* using an analysis of deviance with approximate F-tests (McCullagh & Nelder 1989). After we had confirmed a highly significant difference among ecosystem properties for both dependent variables, we analyzed for each ecosystem property separately if there was a significant difference between the probabilities of observing a significant vs. no significant effect or between the probabilities of observing a positive vs. a negative effect. For this we tested the intercept against the *site ID* in logistic regressions with the data set restricted to each single ecosystem property in turn. Results of this logistic mixed-model analysis were similar to the ones obtained using VC but reached less often significance because of the more restrictive test using *site ID* as error term. Below, we mainly report the results of VC. We do this for better compatibility with other studies using VC as an alternative to meta-analysis of effect sizes.

The results of VC were compared with those obtained from QMA_{nops}. We explored whether there was concordance of the significance and direction of diversity effects on each ecosystem service between VC and QMA_{nops} (e.g. significantly positive effects in both cases vs. one significantly positive and the other no-effect). When there were discrepancies, we explored the proportion in which the additional measurements contributed to more positive, neutral or negative responses to explain them.

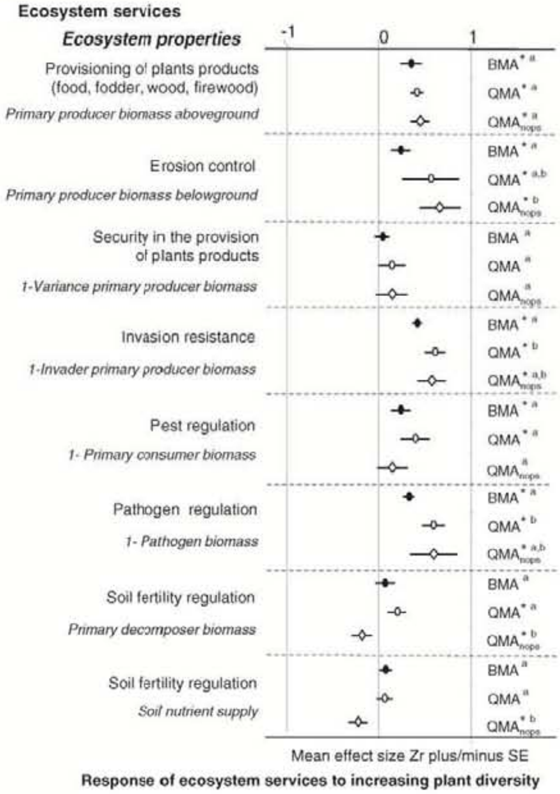

Fig. 1. Magnitude and direction of plant diversity effects on ecosystem services comparing a more comprehensive meta-analysis (Balvanera et al. 2006; BMA, solid circles) and the present meta-analysis, which was restricted to studies manipulating plant diversity in terrestrial ecosystems. Ecosystem properties in italics are listed below the corresponding ecosystem services; 1 – property is used when it is negatively associated with service provision. Mean values and SEs of normalized effect sizes Zr, weighted by the reciprocal of the variance of the individual Zr values, are shown. There are two versions of the meta-analysis restricted to plant diversity manipulating: one analyzing the raw data set (QMA, clear open circle) and one controlling for pseudoreplication (QMA_{nops}, open diamond). *Significant plant diversity effects; superscripts indicate significant differences among mean Zr values.

Results

Associating ecosystem services with ecosystem properties

We grouped all measures reported in the original papers into 43 indicators (second column in Table 1). These were then associated with eight ecosystem properties (third column in Table 1) which were again associated with seven ecosystem services (fourth column in Table 1). Soil fertility was associated with the two ecosystem properties primary decomposer biomass and soil nutrient supply.

Effects of plant diversity on the provision of ecosystem services

This meta-analysis (QMA) vs. Balvanera meta-analysis (BMA)

A clear positive effect of plant diversity on ecosystem service provision was obtained for QMA; and this was consistent with results of BMA that used a wider range of ecosystem service providers (Fig. 1, Table 2). Positive effects of plant diversity on the provision of services were found in both QMA and BMA for provisioning of plant products, erosion control, invasion resistance, pest regulation and pathogen regulation. Non-significant effects were found in both QMA and BMA for security in the provision of plant products and one aspect of soil fertility regulation (soil nutrient supply). The only discrepancy between QMA and BMA was observed with regard to the other aspect of soil fertility regulation (primary decomposer biomass), where a significantly positive effect was found in QMA but not in BMA.

Table 2. Comparison between studies used in this meta-analysis and in a previous meta-analysis (Balvanera et al. 2006). Number of measurements is shown in parentheses following each ecosystem property, provider, or type). 1 - property is used when it is negatively associated with service provision.

This meta-analysis				Balvanera et al. (2006)			
Ecosystem services	Ecosystem property	Service provider	Ecosystem type	Ecosystem services	Ecosystem property	Service provider	Ecosystem type
Provisioning of plants products (food, fodder, wood, firewood)	PP biomass AB	PP (63)	CS (9), F (1), G (49), R (3), SM (1)	Primary productivity	PP abundance	PP (57), PC (5), D (2), Mu (3), My (14)	AF (11), CP (1), F (13), G (46), MA (3), R (3), SC (3), SM (1)
Erosion control	PP BG biomass	PP (6)	G (6)	Erosion control	Plant root biomass	PP (6), D (1), My (10)	F (9), G (7), SC (1)
Security in the provision of plants products	1 – variance PP biomass	PP (18)	F (1), G (17)	Stability	Drought Res + Res other + natural variation	PP (21), PC (5), SCo (1), D (2), Mu (3)	AF (10), BM (2), F (1), G (16), SC (3)
Invasion resistance	1 – IN PP biomass	PP (28)	G (28)	Invasion resistance	1 – IN fitness + 1 – IN diversity + IR	PP (66), PC (7), D (1), Mu (4)	AF (23), AM (5), BM (1), G (49)
Pest regulation	1 – PC biomass	PP (17)	G (16), R (1)	Secondary productivity	PC abundance	PP (12), PC (7), Mu (4)	AF (5), AM (7), BM (1), G (9), R (1)
Pathogen regulation	1 – pathogen biomass	PP (33)	G (33)	Regulation of biological diversity	PC (plant disease severity)	PP (33)	G (33)
Soil fertility regulation	PD biomass	PP (16)	G (14), R (1), SC (1)	Nutrient cycling	D activity	PP (14), D (7), Mu (4)	AF (6), AM (2), BM (1), G (9), L (2), OF (2), R (1), SC (2)
Soil fertility regulation	Soil nutrient supply	PP (16)	G (12), R (2), SC (2)	Nutrient cycling	Nutrient supply from soil	PP (21), PC (3), Mu (6), My (1)	AM (9), G (15), L (2), OF (3), R (2)

Abbreviations: AF: aquatic fresh; AM: aquatic marine; BM: bacterial microcosm; CP: crop/plantation; CS: crop/sucessional; F: forest; G: grassland; L: litter; OF: old field; R: ruderal; SM: salt marsh; SC: soil community; PP: primary producer; PC: primary consumer; PD: primary decomposer; SCo: secondary consumer; D: detritivores; Mu: multitrophic; My: mycorrhiza; AB: aboveground; BG: belowground; Res: resistance; IN: invader; IR: invasion resistance.

No significant differences in variances of records within services were found between QMA and BMA for any of the analyzed services.

Meta-analysis without (QMA) vs. with control for pseudoreplication (QMA_{nops})

While QMA found significant positive effects of plant diversity on ecosystem services for six of the analyzed services, only four of them remained significantly positive when controlling for pseudoreplication in QMA_{nops} (provisioning of plant products, erosion control, invasion resistance and pathogen regulation; Fig. 1). Pest regulation showed a significantly positive effect in QMA but not in QMA_{nops}; one aspect of soil fertility regulation (primary decomposer biomass) showed a significantly positive effect in QMA and a significantly negative one in QMA_{nops}. The other aspect of soil fertility regulation (soil nutrient supply) was non-significant in QMA but significantly negative for QMA_{nops}.

Overall, the effect of pseudoreplication tended to be small given that the degrees of freedom in the comparison among ecosystem services was reduced from 190 (total number of records − number of ecosystem services) to 138.7 in the mixed-effects model. Yet, when different ecosystem services were recorded in a single study this did not contribute to pseudoreplication. The magnitude of variance among records within each service was in general similar for QMA and QMA_{nops}. Only in the case of pathogen regulation variance was significantly lower in QMA than in QMA_{nops} ($F_{32,32} = 2.75$, $p = 0.003$).

Focusing on plant diversity vs. controlling for pseudoreplication: which is explaining our results?

No discrepancies between BMA, QMA and QMA_{nops} were found for four services (provisioning of plant products, erosion control, security in the provision of plant products and invasion resistance; Fig. 1). Discrepancies between BMA and QMA_{nops} were found for three services (pest regulation, two aspects of soil fertility regulation (primary decomposer biomass and soil nutrient supply; Fig. 1)). Focusing on only plants (QMA) rather than all trophic levels (BMA) led to shifts towards higher *Zr* values, while focusing on only plants *and* controlling for pseudoreplication (QMA_{nops}) led to shifts towards lower or even negative *Zr* values.

Meta-analysis (QMA_{nops}) vs. vote-counting (VC)

The results of VC were similar to those of QMA_{nops} (Figs. 1 and 2). The positive effect of plant diversity was consistent in both analyses for four services: provisioning of plant products, erosion control, invasion resistance and pathogen regulation. For two services (security in the provision of plants products, pest regulation) results from QMA_{nops} and VC did not consistently support positive effects of plant diversity. For the two aspects of soil fertility regulation results were not consistent; while a negative effect was found for primary decomposer biomass from QMA_{nops} a significantly smaller frequency of negative effects was found from VC; while a negative effect was found for nutrient supply from QMA_{nops}, no significant differences in frequencies were found from VC.

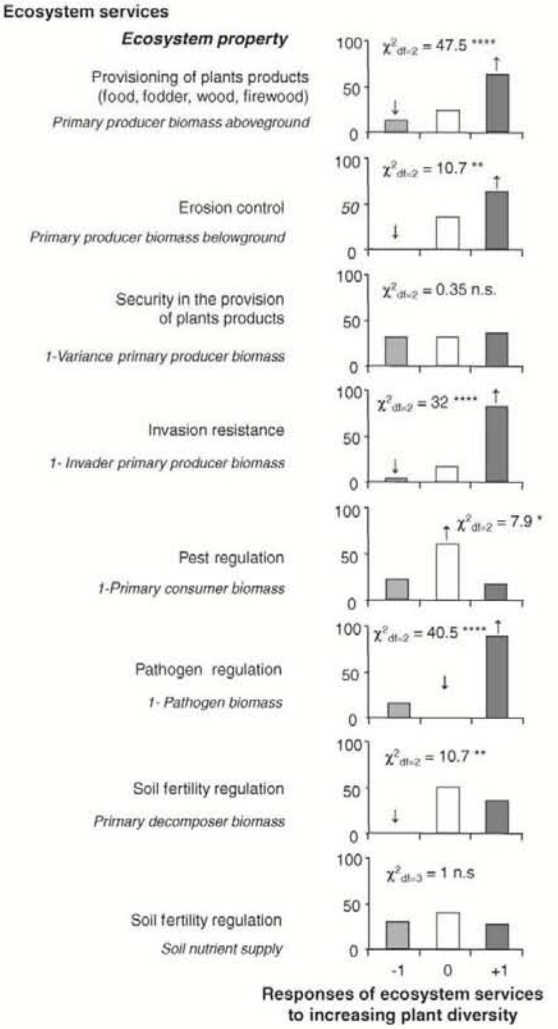

Fig. 2. Frequency of measurements showing negative (−1 = the more diversity the less service), neutral (0 = no effect) or positive (+1) effects of terrestrial plant diversity on the provision of ecosystem services. Ecosystem properties in italics are listed below the corresponding ecosystem services; 1 − property is used when it is negatively associated with service provision. Arrows represent significantly lower (↓) or higher (↑) frequencies than expected from a null model. $*p < 0.05$; $**p < 0.01$; $****p < 0.0001$; n.s.: not significant.

The logistic mixed-model analyses found significantly more positive than negative significant effects for three services: provisioning of plant products (approx. $F_{1,34} = 22.89$, $p < 0.001$), erosion control (approx. $F_{1,10} = 10.00$, $p = 0.010$) and invasion resistance (approx. $F_{1,10} = 8.60$, $p = 0.015$).

However, the results were not significant for pathogen regulation (approx. $F_{1,2} = 1.98$, $p < 0.294$), because a large number of significant positive effects were reported from a single site.

Discussion

Associating ecosystem services with ecosystem properties

In this synthesis we take advantage of the large amount of published results available about experimental effects of manipulating biodiversity on ecosystem functioning (BEF). We apply these results to explore effects of biodiversity on the provision of ecosystem services (BES). By focusing on a single ecosystem service provider, terrestrial plants, we could provide an explicit proposal for the links between ecosystem properties and ecosystem services, and thus translate the results from BEF studies into insights about BES relationships. Uncertainty in the process of deriving indicators of ecosystem properties related to ecosystem services was greatly reduced by this focused approach. We believe that explicit associations between measured indicators, ecosystem properties and corresponding ecosystem services should be developed for other ecosystem service providers as well, in order to foster better understanding of biodiversity effects on the provision of services. To our knowledge, this is the first study that explicitly dissects the different properties measured and the corresponding ecosystem services; it intends to go beyond previous syntheses of biodiversity effects (Balvanera et al. 2006; Worm et al. 2006) and previous generalizations on associations between traits and ecosystem services (Díaz et al. 2007a; Wallace 2007).

The use of the ecosystem service provider framework (Luck, Daily, & Ehrlich 2003; Kremen 2005; Luck et al. 2009) was particularly useful in this task. It allowed us to disentangle the complexity involved in the relationships between biological levels of organization, types of ecosystems, ecosystem properties, ecosystem processes and the provision of ecosystem services (Luck et al. 2009). Further developments along these lines are urgently needed for a variety of ecosystem services at a variety of spatial and temporal scales.

Advantages of focusing on plants

By reducing the number of ecosystem service providers from six to one (only plants) and the number of habitat types from ten to five (with a marked predominance of grasslands) from BMA to QMA (Table 2), we found one more positive effect of plant diversity on the provision of ecosystem services (five positive effects in BMA and six in QMA). This additional positive effect concerned one aspect of soil fertility regulation (primary decomposer biomass), a service for which this is one of the most recent studies to report a positive effect of plant diversity (Wardle, Yeates, Barker, & Bonner 2006; Ball, Bradford, Coleman, & Hunter 2009). The overall consistency of results between BMA and QMA is surprising given that the mean number of analyzed records per ecosystem service in QMA was half that in BMA and that the range of service providers and habitat types changed dramatically. This result reinforces the message given in BMA (Balvanera et al. 2006) about the strongly consistent effects of diversity in the provision of services and is concordant with the only previous meta-analysis addressing this particular question (Worm et al. 2006).

Advantages of controlling for pseudoreplication

The more frequent discrepancies between QMA and QMA_{nops}, in comparison with those between BMA and QMA, suggest a need to control for pseudoreplication in these meta-analyses. This can successfully be done by applying mixed-effects models (Schmid et al. 2009a) or by avoiding multiple records obtained for the same ecosystem service from single publications or sites (Borestein 2009; Shadish & Haddock 2009) in meta-analyses. Recent meta-analysis literature shows an increasing interest in controlling for pseudoreplication as demonstrated by a search in ISI Web of Science and Biological Abstracts for 2009, for which close to 30% of the studies ($N = 25$) used procedures for that purpose.

Complementarily between meta-analysis (QMA_{nops}) and vote-counting (VC)

Consistent results between QMA and VC, and between QMA_{nops} and VC (logistic mixed-model analysis), were found for six and five of the analyzed services, respectively. Using up to two (provisioning of plant products) or even three times (erosion control) as many records for VC as for QMA_{nops}, we were able to provide increased support for the observed patterns. It has been discussed that vote-counting does not adequately control for sample size and thus may lead to biased effects estimates. Furthermore, increasing the number of records and thus the variance among records may decrease the power of VC (Gurevitch, Curtis, & Jones 2001; Bushman & Wang 2009). These problems can be resolved using logistic mixed-model analysis with a weighting variable accounting for different sample sizes and testing fixed-effects factors against appropriate random-effects terms as we did here and in a previous study (Schmid et al. 2009a). The results of this analysis were very similar to those of the VC analysis, although significances were lower and in one case not reached due to the accounting for pseudoreplication. This is a difference similar to the one between QMA and QMA_{nops}. The consistency of our results across the different types of analysis parallels other findings from synthesis work on biodiversity effects on ecosystem properties (Cardinale et al. 2009; Schmid et al. 2009a). The use of complementary methods for performing syntheses, such as meta-analysis and vote-counting, has seldom been applied (but see Huberty & Denno 2004; Attwood, Maron, House, & Zammit 2008) but can increase support for observed patterns.

Lessons learned about effects of plant diversity on the provision of ecosystem services

Our results confirm previously suggested relationships between plant diversity and the provision of ecosystem services for six of the analyzed services. We found that, consistently with the many previous studies (Hector et al. 1999; van Ruijven & Berendse 2003), plant diversity increases the amount of aboveground plant biomass derived from primary productivity and thus the provisioning of useful plant products such as food, fodder, timber and firewood (Díaz et al. 2006; Schmid et al. 2009a). Plant diversity also had a positive effect on erosion control, through increased belowground biomass contributing to greater cohesion of soil particles (Gyssels, Poesen, Bochet, & Li 2005).

Resistance to plant invasions consistently increased with plant diversity; the lower the invasive species biomass will be, the higher the regulation of its presence and impacts, and the lower the detrimental effects incurred by humans and society (Díaz et al. 2006; Schnitzler, Hale, & Alsum 2007). Yet, a previous meta-analysis of non-experimental work found that native species diversity was positively correlated with the establishment of exotic species (Schnitzler et al. 2007). Discrepancies between meta-analyses synthesizing observational vs. experimental studies may be due to the following factors: (i) experimental studies by manipulating diversity can move a system away from its equilibrium and thus reveal processes that led to the equilibrium (Schmid & Hector 2004); (ii) correlations in observational studies may be due to a third variable which affects the two variables under study, if the influence of the third variable could be removed (as in an experimental study), the correlation may disappear or turn its sign (Mwangi et al. 2007); (iii) scale effects, the spatial scale of observational studies usually being much larger than the one of experimental studies, under the condition that different mechanisms are operating at the different scales (Fridley et al. 2007).

Increasing plant diversity also leads to a better regulation of plant pathogens. This is in agreement with the focused meta-analysis mentioned above (Schmid et al. 2009a) and with the qualitative analysis by Díaz et al. (2006). The role played by plant diversity in the regulation of pathogens may become even more important in the future as rates of pathogen attacks on plants are predicted to increase (Burdon, Thrall, & Ericson 2006). The lower the pathogen biomass will be, the higher the biomass of plants (Díaz et al. 2006).

Higher plant diversity only increases the provision of plant products but does not seem to guarantee a higher security in this provision. Our result is particularly relevant in the context of the intense debate about biodiversity effects on ecosystem stability and resilience (Ives & Carpenter 2007; Isbell, Polley, & Wilsey 2009). While previous qualitative reviews had suggested a positive role of biodiversity on reducing the temporal variance in ecosystem properties (Hooper et al. 2005; Díaz et al. 2006), and previous meta-analyses had found ambivalent results (Balvanera et al. 2006), our results clearly did not find significant effects of plant diversity on security.

Non-consistent effects among methods used here (QMA, $\mathrm{QMA_{nops}}$ and VC) were found for pest regulation. Comparable inconsistencies have been observed among previous meta-analyses, which include positive (Schmid et al. 2009a), negative (Jactel & Brockerhoff 2007) or positive and negative effects (Vehviläinen, Koricheva, & Ruohomäki 2007) of plant diversity on herbivores. Several factors may modify the effect of plant diversity at multiple trophic levels, such as the trophic distance between the level at which diversity is manipulated and the one at which the response is measured (Balvanera et al. 2006) or the identity of species that are going extinct (Cardinale et al. 2006). Given that effects in different directions are simultaneously observed, and that complex bottom-up and top-down feedback effects are also simultaneously operating, straightforward responses of manipulating diversity at a particular trophic level might not necessarily be expected.

No consistent effects of plant diversity on soil fertility regulation were found by our methods (QMA, $\mathrm{QMA_{nops}}$ and VC) and with our previous meta-analysis (Balvanera et al. 2006). Further research is needed on this topic.

The consistent effects of plant diversity on ecosystem service provision found here need to be further explored, by considering not only effects of richness, but rather incorporating those of species evenness (Wilsey & Potvin 2000) and species composition, both taxonomically and functionally (Wardle, Bonner, & Barker 2000; Kirby & Potvin 2007; Fornara & Tilman 2008). Also, further exploration is needed on the effects of the diversity of the regional species pool and the related differences in diversity of local species pools (Valone & Hoffman 2002). Further work is needed to explore whether results from the local scale can be extrapolated into meaningful predictions about how plant diversity will impact ecosystem functioning and the capacity to provide services at appropriately realistic larger scales and in natural rather than experimental ecosystems.

Overall our study allowed us to show consistently positive effects of plant diversity on the provision of services. Conservation of biodiversity, of course does not need to be reduced to its implications on ecosystem service provision, and variables such as species richness and evenness, used in the biodiversity and ecosystem functioning research, were perceived and appreciated by lay people as indicators of attractiveness in natural meadows, demonstrating that plant diversity in itself is attractive to humans (Lindemann-Matthies, Junge, & Matthies 2010). Although some have questioned the policy and conservation implications of BEF research (Srivastava & Vellend 2005), we believe that our results are consistent enough to urge for increased management efforts to protect biodiversity not only for its own sake but also in humans' and society's interest to ensure the provision and increase of ecosystem services at levels conducive to our continued well-being (Balvanera et al. 2006; Díaz et al. 2006; Bennett & Balvanera 2007; Duffy 2009).

Conclusions

We have consistently confirmed previously suggested positive effects of plant diversity on four ecosystem services, provisioning of useful plant products, erosion control, resistance to plant invasions and pathogen regulation. Nevertheless, increasing plant diversity does not seem to guarantee a higher security in the provision of plant products. No consistent effects of plant diversity on pest regulation and on soil fertility regulation could be found. Our conclusions are supported by a number of complementary analyses. Nevertheless, further analyses with other service providers are urgently needed. The paramount role of plant diversity in the provision of ecosystem services should be included into conservation planning and management. Clearly, the very least that can be concluded from the experimental results analyzed here is that a precautionary approach, aimed at avoiding further reductions of plant diversity, is justified if we want to prevent further reductions in the provision of ecosystem services. Therefore, maintaining plant diversity is crucial if the management goal is to ensure benefits for human well-being.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2010.06.009.

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Capítulo III

Plant diversity and generation of ecosystem services at the landscape scales: expert knowledge assessment*

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Summary

1. In spite of the increasing amount of experimental evidence on the importance of plant species richness for ecosystem functioning at local scales, its role on the generation of ecosystem services at scales relevant for management is still largely unknown. To foster research on this topic, we assessed expert knowledge on the role of plant diversity in the generation of services at the landscape scale.

2. We developed a survey that included three levels of organization and seven components of plant diversity; four provisioning, six regulating and four cultural services; as well as three resources and three conditions among key abiotic factors that are likely to provide a contribution to service generation equalling that of plant diversity. Eighty experts in areas of biodiversity, ecosystem functioning and services answered the survey.

3. The experts identified species diversity within a community and diversity of communities within the landscape as the most important levels of organization for service generation, both with positive effects. Composition and number of species were considered to be the most relevant components of plant diversity, the latter with a positive effect on services. Water availability was identified as the most important abiotic resource.

4. Our results suggest different approaches to management for sustaining the generation of services at the landscape scale. Provisioning services were perceived as largely influenced by abiotic resources and less so (although positively) by plant diversity. Regulating services were expected to strongly depend on both plant diversity and abiotic factors. A particularly strong positive effect of plant diversity was expected for the generation of cultural services. Some variation in answers could be attributed to expert background.

5. *Synthesis and applications.* The expert survey generated detailed information and new hypotheses on the relationship between plant diversity and services at the landscape scale. Future research is needed to test these hypotheses, yet the areas of agreement identified in this study can be used immediately, with caution, as synthetic expert knowledge at spatial scales

which are relevant for management, to guide technological and policy interventions ensuring the maintenance of biodiversity and ecosystem service delivery.

Keywords

Abiotic resources and conditions, components of diversity, cultural services, diversity-direction of effect hypotheses, levels of organization of diversity, provisioning services, regulating services, survey.

Introduction

The study of the influence of biodiversity on ecosystem functioning has developed over the past 20 years into an important area of ecological research (Naeem *et al.* 2009). Results from this research clearly point to the critical role that biodiversity plays for the generation of ecosystem services and thus human well-being. To date, qualitative (Diaz *et al.* 2006) and quantitative (Balvanera *et al.* 2006; Worm *et al.* 2006; Quijas, Schmid & Balvanera 2010) syntheses derived from experimental manipulation of biodiversity and ecosystem functioning have shown a consistently positive effect of diversity in the generation of ecosystem services for a range of organisms, habitats and services.

However, these syntheses are limited because they mostly refer to the outcomes of small-scale experiments, are confined to a limited range of ecosystem services, deal mostly with species richness and not with other components of diversity, do not address the role played by abiotic factors in such relationships, and potentially generate equivocal messages as a result of confounding effect directions from a range of ecosystem service providers and habitats. Experiments manipulating diversity have largely been developed at local (<10 ha) scales (Balvanera *et al.* 2006) and yet ecosystems are managed and services delivered at landscape (10–1,000 ha) to regional (>1, 000 ha) scales (Kremen 2005; Duffy 2009). The syntheses are also limited by their focus on only a few types of ecosystem services, mainly regulating and provisioning ones (Balvanera *et al.* 2006; Worm *et al.* 2006;

Quijas, Schmid & Balvanera 2010), cultural services being poorly described (Worm *et al.* 2006). Studies in this area only focus on the species level of organization, and on richness as the main measure of species diversity (Balvanera *et al.* 2006), thus ignoring the relative contributions of other biodiversity attributes, such as level of organization (e.g. genotype, populations, communities), species evenness, species composition, and functional diversity (Kremen 2005; Diaz *et al.* 2007; Luck *et al.* 2009). Furthermore, the relative importance of abiotic factors with respect to diversity on ecosystem functioning or services has seldom been analyzed (Diaz *et al.* 2007). Finally, a wide variety of organisms that may function as ecosystem service providers (Luck *et al.* 2009) have simultaneously been considered in syntheses (Balvanera *et al.* 2006; Worm *et al.* 2006), yet, their individual contribution to ecosystem services is likely to be different (Luck *et al.* 2009; Quijas, Schmid & Balvanera 2010).

Future research on the relationship between biodiversity, functioning and services should embrace a broader range of spatial scales, biodiversity components, and ecosystem services; include the relative roles of abiotic factors with respect to biodiversity; and dissect the roles of specific ecosystem service providers in order to be applied to management decisions. In particular, focusing on terrestrial plants as ecosystem service providers can be quite useful given their fundamental role in ecosystem functioning, their direct contribution to the generation of many ecosystem services, and the unsurprising majority of studies focussing on the relationships between their diversity and ecosystem functioning (Quijas, Schmid & Balvanera 2010; Cardinale *et al.* 2011).

Given the lack of information described above, one approach is to synthesize present understanding, define key knowledge gaps and stimulate further hypothesis testing through expert assessments (Schläpfer, Schmid & Seidl 1999). Expert elicitation, a technique used to synthesize opinions of experts, has been in use for several decades in the disciplines of economics, sociology, political science, social psychology, and public opinion research (De Vaus 2002), and more recently it is also being incorporated in studies of ecology and conservation biology (Halpern *et al.* 2007; Donlan *et al.* 2010). Expert judgment is not intended to be a substitute for scientific research, but to define the current knowledge that may not otherwise be easily accessible, illustrate the current sense of expert knowledge, reveal areas of greater or lesser agreement and help drive future applied research (Halpern *et al.* 2007; Donlan *et al.* 2010). An initial survey of expert knowledge aimed at understanding the relationship between biodiversity and its components on ecosystem processes, and the generation of ecosystem services, was conducted by Schläpfer, Schmid & Seidl (1999). In the last decade, biodiversity and ecosystem functioning research has added realism by including other components of diversity (e.g. Wilsey & Potvin 2000), increasing the spatial scale for analysis of processes related to ecosystem services (e.g. Wohl, Arora & Gladstone 2004), using more realistic extinction scenarios (e.g. Zavaleta & Hulvey 2004), simultaneously measuring multiple functions (e.g. Hector & Bagchi 2007) and incorporating natural (e.g. Fukami & Wardle 2005) and anthropogenic gradients of disturbance (e.g. Zavaleta *et al.* 2003). A new expert assessment would allow us to synthesize perceptions and advances relevant for managing both biodiversity and ecosystem services to ensure their maintenance.

In this paper, we use an expert assessment approach to synthesize current understanding of how plant diversity relates to the generation of 14 ecosystem services at the landscape spatial scale. We focus on: (*i*) direction of effect and relative importance of different levels of organization of plant diversity in the generation of ecosystem services, (*ii*) direction of effect and relative importance of different components of plant diversity in the generation of ecosystem services, and (*iii*) importance of plant diversity relative to the abiotic resources and conditions that can have direct effects on the generation of ecosystem services. We also assessed potential for biases in results given by the background of participating experts.

Materials and methods

Spatial scale

Understanding the spatial scales at which ecosystems are managed and services are delivered to people will be essential to developing landscape-level conservation and management plans (Kremen 2005). For that reason, this assessment is focused at the landscape scale, defined here as areas ranging from 10 to 1,000 ha (0.01 to 10 km^2; 24,710 to 2,471,000 acres). We used analogies to help experts visualize theses scales (e.g. the Principality of Monaco or Niagara Falls has an area of 100 ha, whilst the city of Beverly Hills has an area of 1,000 ha).

Components of the survey

A summary of the approach that we used in this survey is shown in Fig. 1. We divided the survey into five sections. The first and second sections evaluated understanding about the direction of effect (DE) and relative importance (RI) of the levels of organization (LO) of plant diversity on service generation. The third and fourth sections evaluated understanding about the DE and RI of components of plant diversity (CD) on service generation. The fifth section evaluated understanding about RI of resources and conditions (R&C). We considered four provisioning services, six regulating services and four cultural services. We did not include supporting services, as we considered them to be ecosystem processes that indirectly benefit societies by supporting one of the other three types of services. We identified three LO relevant for the generation of services and six CD. We considered three resources and three conditions that are likely to modify both plant diversity and service generation. A glossary with all definitions can be found in Appendix S1 in Supporting Information.

Identification of the relationship between diversity and services

The DE of plant diversity on the generation of ecosystem services was assessed using five types of relationships: (*i*) the more diversity, the more service (+), (*ii*) the more diversity, the less service (–), (*iii*) there is a diversity effect on the service, but it is not possible to determine its direction or the direction is unknown (1), (*iv*) no influence of diversity on the generation of the service (0), (*v*) unknown whether there is an influence of plant diversity for the generation of the service (?). For example, "higher genetic diversity provides better pest regulation" and thus the more diversity there is, the more service (+); or "a higher number of species does not influence soil fertility," thus there is no influence of diversity on the generation of service (0).

The RI of plant diversity, as well as that of R&C, on the generation of services was assessed using four categories: (1) of little importance, (2) of intermediate importance, (3) very important and (?) of unknown importance.

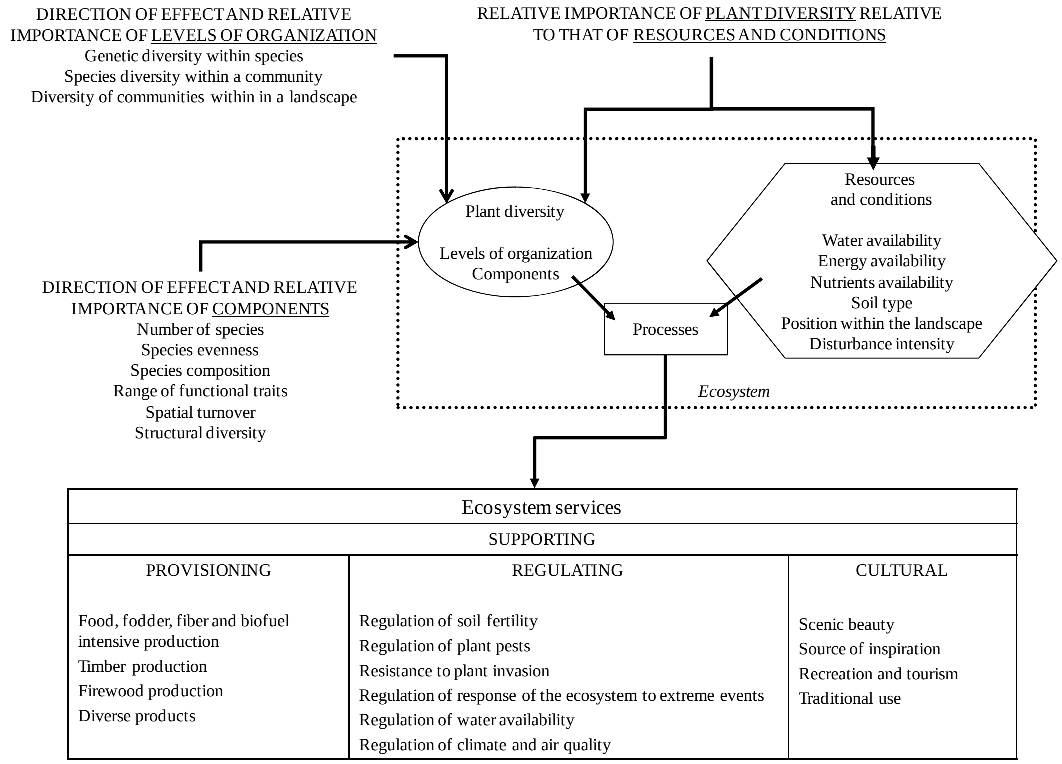


Figure 1. Framework for the design of the survey on plant diversity and the generation of ecosystem services.

Building the survey

Two drafts of the survey were developed before reaching the final version used here (for details see Appendix S2 in Supporting Information).

In the final version we included questions on the background of the expert to evaluate potential biases on the final results due to individual perspectives; the questions related to subject of expertise (e.g. population ecology, management), type of work (e.g. basic research, decision maker), type of organization (e.g. institute, environments NGOs), number of years working with plant diversity and ecosystem processes and/or services they know, and the focus ecosystems they study (e.g. tropical rainforest, grassland).

Expert selection

We defined experts as individuals who had carried out observational or experimental research on the links between plant diversity and ecosystem functioning or ecosystem services at different spatial scales. We used the contributors to the Millennium Ecosystem Assessment (MA 2005) and researchers suggested by the co-authors of this work as a source of candidates. The survey was sent by email to the 344 experts in that list for which emails could be obtained between July 2007 and March 2008; up to two reminder emails were sent. Some (56 experts) did not participate in the survey, due to time constraints (17), or to self-stated lack of expertise on plant diversity and ecosystem services (38). A total of 80 experts (23%) from 27 countries and working in 14 types of ecosystems responded to the survey (more details see Appendix S3).

Analysis

We registered the frequencies of the different types of responses and then addressed the following questions:

i. Do experts tend to recognize a particular direction of effect or relative importance of plant diversity in the generation of ecosystem services when considering all levels of organization or all components of plant diversity?

ii. What is the direction of effect and relative importance of the different levels of organization and components of plant diversity most commonly mentioned by experts when considering all services?

iii. What is the relative importance of resources and conditions with respect to plant diversity most frequently mentioned when considering all services?

iv. What is the direction of effect and relative importance of the different levels of organization most frequently recognized by experts for the generation of each of services?

v. What is the direction of effect and relative importance of the different components of plant diversity most frequently recognized by experts for the generation of each of services?

vi. What is the relative importance of resources and conditions with respect to plant diversity most frequently recognized for the generation of each of services?

vii. How does the background of experts explain the differences in how frequently they chose different direction of effect and relative importance they assigned to plant diversity and resources and conditions for the generation of services?

To test for differences in answer probabilities, we assumed as a null model that all answers to a question would be equally likely. Thus, the five possible answers (–, 1, +, 0, ?) about DE and the four possible answers (1,2,3,?) about the RI of plant diversity and R&C on the generation of services were all considered equally likely. While this may not always have been the best null model, we had no further information to develop more specific null models. Significant deviation from the expected equal answer probabilities were detected with generalized linear and $\chi 2$ tests (Sokal & Rohlf 1995; for details see Appendix S4). We used Bonferroni corrections to account for the large numbers of test performed (360 hypotheses tested; critical $P<0.00014$ for individual tests, corresponding to an overall significance level of $P<0.05$). We used adjusted residuals (residuals divided by their variance) as an a-posteriori test for identifying particular frequencies responsible for the significant χ^2 values, and to explore whether particular answer frequencies were larger (or smaller) than expected from the null model (Everitt 1992).

We assessed biases caused by different backgrounds of experts on frequencies of responses regarding the links between plant diversity and ecosystem services. We used χ^2 tests to test for independence of answers with respect to expert characteristics (e.g. five types of relationships vs. type of ecosystem). We used a Bonferroni correction on the critical *P* values as a-priori test for the numbers of test performed (25 hypotheses tested; critical $P<0.002$). Adjusted residuals were also used to identify particular frequencies that differed from the null model (calculated using the same Bonferroni correction).

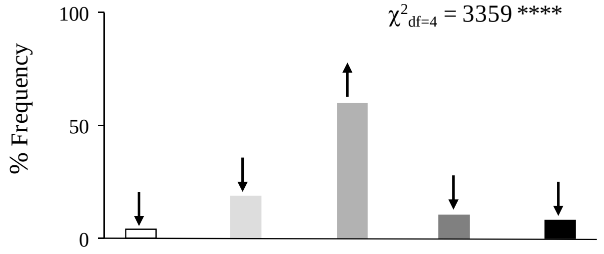
Results

We found that most experts recognized a positive effect of plant diversity on the generation of ecosystem services when all LO (Fig. 2a) and all CD (Fig. 2b) were pooled together. However, there was no consensus on the RI of plant diversity in the generation of services. We found large discrepancies between experts, with opinions for importance varying between little importance and very important often considered for levels of organization ($\chi^2 = 8.1$, $P=0.01$, df= 2). Yet, most CD were frequently considered to be of little importance ($\chi^2 = 22.8$, $P<0.0001$, df= 2).

Levels of organization

Genetic diversity within species, species diversity within a community, and the diversity of the communities in the landscape were consistently identified as having a positive effect on ecosystem service generation (genetic $\chi^2 = 601.4$, $P<0.00014$, df = 4; species $\chi^2 = 1980.1$, $P<0.00014$, df = 4; community $\chi^2 = 1609.7$, $P<0.00014$, df = 4; Table 1). However, the RI changed between LO, because plant diversity at the level of species ($\chi^2 = 594.6$, $P<0.00014$, df = 3) and communities in the landscape ($\chi^2 = 474.4$, $P<0.00014$, df = 3) levels were most often considered as very important, while diversity at the genetic ($\chi^2 = 1110.57$, $P<0.00014$, df = 3) level of organization was most frequently recognized as of little importance.

(a) Level of organization of plant diversity



(b) Components of plant diversity

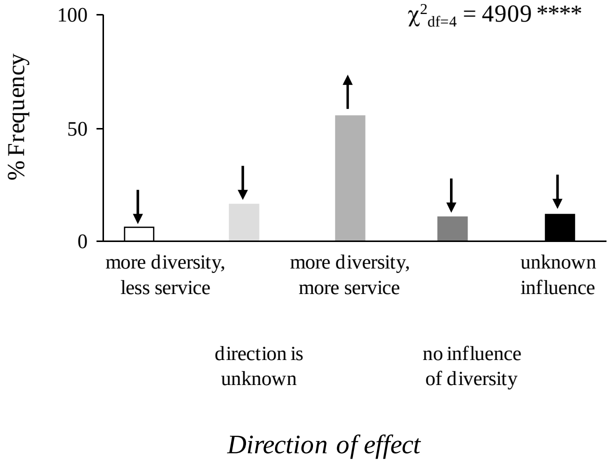


Figure 2. Total frequency of expert assessment on direction of effect of levels of organization and components of plant diversity on the generation of ecosystem services. In (a) the total frequencies of answers for each type of effect were obtained by adding up both all levels of organization and all services; in (b) the total frequencies of answers were obtained by adding up both all components and all services. Arrows indicate that frequencies were significantly higher (↑) or lower (↓) than expected from a null model of equal frequencies of all answers; **** = P<0.0001.

Components of diversity

Positive effects of different CD on service generation were reported, but their RI differed between components (Table 1). Clear positive effects were attributed to number of species ($\chi^2 = 1575.7$, $P<0.00014$, df = 4), species evenness ($\chi^2 = 395$, $P<0.00014$, df = 4), functional diversity ($\chi^2 = 661$, $P<0.00014$, df = 4), spatial turnover ($\chi^2 = 411.5$, $P<0.00014$, df = 4) and structural diversity ($\chi^2 = 1044.8$, $P<0.00014$, df = 4). While number of species was consistently considered as very important ($\chi^2 = 272$, $P<0.00014$, df = 3), plant species composition and structural diversity were thought to be of intermediate importance to very important (composition $\chi^2 = 531$, $P<0.00014$, df = 3; structural $\chi^2 = 227.7$, $P<0.00014$, df = 3). Other CD including species evenness, functional diversity and spatial turnover were rated as less important for the generation of services.

Table 1. Expert assessment of direction of effect and relative importance of levels of organization and components of plant diversity on the generation of ecosystem services. Cells with a square indicate levels of organization and components that were significantly more frequently mentioned than would be expected from a null model of equal frequencies of all answers, both for effects and relative importance; $P<0.00014$ (■); cells with no square indicate no significantly different frequencies from those expected from the null model. (--) is used to show that the direction of species composition effect on the generation of services could not be assessed (see text for details)

Attributes of plant diversity		Effects					Relative importance			
		–	1	+	0	?	1	2	3	?
Levels of organization	**Genetic** diversity within species			■	■		■			
	Species diversity within a community			■				■	■	
	Diversity of **communities** within in the landscape			■					■	
Components	Number of species			■					■	
	Species evenness			■			■			
	Species composition	--	--	--	--	--		■	■	
	Functional diversity			■			■			
	Spatial turnover			■			■			
	Structural diversity			■				■	■	

Symbols and numbers: Effects: (–) the more diversity the less service; (1) there is a diversity effect on the service, but it is not possible to determine its direction or the direction is unknown; (+) the more diversity the more service; (0) no influence of diversity on the generation of the services; (?) unknown whether there is an influence of plant diversity for the generation of services. Relative importance: (1) little importance; (2) intermediate importance; (3) very important; (?) unknown importance.

Abiotic resources and conditions

Plant diversity together with water availability were most frequently considered by experts as the most important factors for the generation of ecosystem services (plant diversity $\chi^2 = 79.7$, $P<0.00014$, df = 3; water $\chi^2 = 37.1$, $P<0.00014$, df = 3; Table 2). Disturbance intensity was identified to be of only intermediate importance; soil type and position on the landscape were rated of intermediate to little importance. Energy and nutrient availability were recorded as the least important for the generation of services.

Table 2. Expert assessment on the relative importance of plant diversity with respect to that of resources and conditions for the generation of ecosystem services. Presentation of cells follow those of Table 1; $P<0.00014$ (■)

		Relative importance			
		1	2	3	?
	Plant diversity			■	
Resources	Water availability			■	
	Energy availability	■			
	Nutrient availability	■			
Conditions	Soil type	■	■		
	Position within the landscape	■	■		
	Disturbance intensity		■		

Symbols and numbers: Relative importance: (1) little importance; (2) intermediate importance; (3) very important; (?) unknown importance.

Levels of organization and the types of ecosystem services

Experts consistently regarded species diversity within a community as the most important LO, with positive effects on provisioning services (Table 3). Genetic diversity was recognized as the least important for these services, with either positive effects or non-effects most commonly reported. Species diversity within a community and the diversity of the communities in the landscape were most often considered to be from intermediate importance to very important for the generation of regulating services; in contrast, genetic diversity was considered the least important. Positive effects of species diversity and diversity of the communities were indicated for all regulating services. Positive or non-existent effects of genetic diversity on regulating services were most often chosen (Table 3).
Experts considered plant diversity at the species and community levels of intermediate importance to very important for the generation of cultural services, and positive effects were the most frequent in both cases. Genetic diversity was recognized as the least important for cultural services, with no-effect most commonly reported (Table 3).

Table 3. Expert assessment of direction of effect and relative importance of levels of organization of plant diversity on the generation of ecosystem services. Presentation of cells follow those of Table 1; $P<0.00014$ (■)

Type	Services	Direction of effect															Relative importance											
		Genetic					Species					Community					Genetic				Species				Community			
		–	1	+	0	?	–	1	+	0	?	–	1	+	0	?	1	2	3	?	1	2	3	?	1	2	3	?
Provisioning	Food, fodder, fiber and biofuel intensive production			■					■					■			■						■		■			
	Timber production								■								■						■		■			
	Firewood production				■				■								■						■					
	Diverse products			■					■					■			■						■					
Regulating	Soil fertility								■					■			■						■					
	Plant pests			■					■					■									■					
	Resistance to plant invasion			■					■					■			■						■					
	Response of the ecosystem to extreme events			■					■					■			■					■					■	
	Water availability				■				■					■			■					■					■	
	Climate regulation and air quality				■				■					■			■					■					■	
Cultural	Scenic beauty				■				■					■			■					■					■	
	Source of inspiration				■				■					■			■					■					■	
	Recreation and tourism				■				■					■			■					■					■	
	Traditional use			■					■					■			■						■					

Symbols and numbers: Effects: (–) the more diversity the less service; (1) there is a diversity effect on the service, but it is not possible to determine its direction or the direction is unknown; (+) the more diversity the more service; (0) no influence of diversity on the generation of the services; (?) unknown whether there is an influence of plant diversity for the generation of services. Relative importance: (1) little importance; (2) intermediate importance; (3) very important; (?) unknown importance.

Components of diversity and the types of ecosystem services

Species composition, i.e. specific combination of the species or presence/absence of particular species within a plant community, was the only DC that was most frequently identified by experts as very important for provisioning services (Table 4); most of the other components of plant diversity were expected to have positive effects of little importance on provisioning services.

For regulating services, species composition and number of species were considered to be the most important CD; positive effects were reported for the generation of soil fertility, regulation of plant pests and invasion resistance (Table 4). The functional diversity was considered important with for the regulation of the response of the ecosystem to extreme events. Positive effects of functional diversity and structural diversity were identified for water related services and for climate regulation and air quality.

Species composition was most often considered as the most important CD for the generation of various cultural services. Structural diversity was identified as important for scenic beauty, and number of species was important for traditional use. Most of the CD were identified as having positive effects on the generation of all cultural services, except for functional diversity, which was considered to have no effects on these services (Table 4).

Abiotic resources and conditions and the types of ecosystem services

The relative importance of R&C differed markedly among types of services (Table 5). Water, energy and nutrient availability were considered most important for the majority of provisioning services. Plant diversity was most important for three regulating services, water availability for one service, nutrient availability, soil type position within the landscape for one service and disturbance intensity for two services. In the case of cultural services, only water availability was identified as important for the generation of recreation and tourism services; in all other cases only plant diversity was considered important.

Table 4. Expert assessment of direction of effects and relative importance of components of plant diversity on the generation of ecosystem services. Presentation of cells as Table 1; $P<0.00014$ (■)

Type	Services	Direction of effects																									Relative importance																							
		Number of species					Species evenness					Functional diversity					Spatial turnover					Structural diversity					Number of species				Species evenness				Species composition				Functional diversity				Spatial turnover				Structural diversity			
		–	1	+	0	?	–	1	+	0	?	–	1	+	0	?	–	1	+	0	?	–	1	+	0	?	1	2	3	?	1	2	3	?	1	2	3	?	1	2	3	?	1	2	3	?	1	2	3	?
Provisioning	Food, fodder, fiber and biofuel intensive production			■																																		■						■							
	Timber production																					■					■				■						■		■				■				■			
	Firewood production								■															■							■						■		■				■				■			
	Diverse products			■					■					■					■					■					■								■													
Regulating	Soil fertility			■					■					■										■													■													
	Plant pests			■					■					■					■					■					■								■													
	Resistance to plant invasion			■					■					■					■					■					■								■													
	Response of the ecosystem to extreme events			■					■					■					■					■							■										■									
	Water availability			■										■										■							■																			
	Climate regulation and air quality													■										■			■				■																			
Cultural	Scenic beauty			■					■						■				■					■							■						■			■									■	
	Source of inspiration			■											■				■					■							■								■											
	Recreation and tourism			■					■						■				■					■							■						■		■											
	Traditional use			■					■					■					■					■					■								■													

Symbols and numbers: Effects: (–) the more diversity the less service; (1) there is a diversity effect on the service, but it is not possible to determine its direction or the direction is unknown; (+) the more diversity the more service; (0) no influence of diversity on the generation of the services; (?) unknown whether there is an influence of plant diversity for the generation of services. Relative importance: (1) little importance; (2) intermediate importance; (3) very important; (?) unknown importance.

Table 5. Expert assessment on the relative importance of plant diversity with respect to that of abiotic resources and conditions for the generation of ecosystem services. Presentation of cells as Table 1; $P<0.00014$ (■)

Type	Services	Plant diversity				Resources												Conditions											
						Water availability				Energy availability				Nutrients availability				Soil type				Position within the landscape				Disturbance intensity			
		1	2	3	?	1	2	3	?	1	2	3	?	1	2	3	?	1	2	3	?	1	2	3	?	1	2	3	?
Provisioning	Food, fodder, fiber and biofuel intensive production	■						■				■				■													
	Timber production	■						■				■				■				■									
	Firewood production	■						■				■				■													
	Diverse products			■																									
Regulating	Soil fertility		■													■				■									
	Plant pests			■		■				■								■				■							
	Resistance to plant invasion			■																		■						■	
	Response of the ecosystem to extreme events			■																								■	
	Water availability							■																■					
	Climate regulation and air quality																					■							
	Scenic beauty			■						■				■				■											
	Source of inspiration			■						■				■				■											
	Recreation and tourism			■				■		■				■				■											
	Traditional use			■						■																			

Symbols and numbers: Relative importance: (1) little importance; (2) intermediate importance; (3) very important; (?) unknown importance.

Biases given by expert background

Biases associated with the background of experts were found in the frequencies of responses for direction of effects (DE) and relative importance (RI) of plant diversity on service generation. When pooling together all LO we found an effect of the type of organization ($\chi^2 = 54.6$, $P<0.002$, df= 12) and of the focus ecosystem that scientists studied ($\chi^2 = 205.5$, $P<0.002$, df= 52): experts working for NGOs indicated that plant diversity had no effects on ecosystem services more frequently than expected from a null model, while those working in agroecosystems more frequently chose an unknown influence. The RI of plant biodiversity on ecosystem service provision was influenced by the focus ecosystem ($\chi^2 = 104.5$, $P<0.002$, df= 39); experts working in agroecosystems and successional forest chose an unknown relative importance of plant diversity more frequently. When pooling together all CD, we found that subject of expertise ($\chi^2 = 347$, $P<0.002$, df= 24), type of organization ($\chi^2 = 203.3$, $P<0.002$, df= 12), years of experience ($\chi^2 = 87.8$, P<0.002, df= 12) and focus ecosystem ($\chi^2 = 516.6$, $P<0.002$, df= 52) influenced expert assessments: plant and community ecologists identified a positive relationship between plant diversity and service generation more frequently, while managers, individuals working for NGOs and governmental agencies, experts with less experience (<10 years) and those focusing on agroecosystems and successional forests tended to report more no-effects and unknown relationships. Responses to the RI of plant diversity were biased by subject of expertise ($\chi^2 = 120.3$, $P<0.002$, df= 18) and focus ecosystem ($\chi^2 = 103.8$, $P<0.002$, df= 39); experts studying population ecology and agroecosystems tended to choose the unknown importance option more frequently than expected. Also, respondents working in agroecosystems reported unknown importance of plant diversity relative to R&C on service generation more frequently ($\chi^2 = 72.2$, $P<0.002$, df= 39). For more details see Appendix S5.

Discussion

Overarching patterns

Our work synthesized perceptions of experts on the relationships between plant diversity and ecosystem services at the landscape scale. The assessment showed that when all the services were pooled together a positive effect of plant diversity on service provision was consistently found. The generality of this positive effect is consistent with previous publications on the contribution of diversity to a stable supply of ecosystem services as spatial and temporal variability increases, which typically occurs over larger areas, such as the ones addressed here (Loreau, Mouquet & Gonzalez 2003; Diaz *et al.* 2006).

However, there was no consensus on the relative importance of plant diversity on service provision. The relative importance given to diversity changed among services. This lack of consensus may derive from different underlying mechanisms, the effect of context or just the scarcity of information in this topic.

Consistent with previous qualitative reviews (Kremen 2005; Diaz *et al.* 2006), experts consistently identified diversity of species within a community and diversity of communities within a landscape as the most important levels of organization for service generation. In both cases a positive relationship was suggested. Composition and number of species were considered to be the most relevant components of plant diversity. However, experts interviewed saw little importance for the role played by genetic diversity in the provision of services, despite the growing evidence of its role in generating useful plant products such as food, fodder and fibre (Jackson, Pascual & Hodgkin 2007), regulation of plant pests (Schweitzer *et al.* 2005) and resistance to plant invasion (Barberi *et al.* 2010) at the landscape scale. Our results reflected consistency only for what appear to be the more widely known levels of organization and components of plant diversity among ecologists (Hooper *et al.* 2005).

Patterns for different types of ecosystem services

Positive relationships between plant diversity and the generation of provisioning services at the landscape scale were consistently reported, thus suggesting that experts expected clear local synergy between the maintenance of biodiversity (in conserved habitats or agroecosystems) and obtaining provisioning services to satisfy human needs. The role of species evenness and functional diversity on the generation of provisioning services (e.g. food, fodder, fibre and intensive biofuel production) was not recognized. This is partially consistent with the growing evidence critical role that agrobiodiversity plays in much of the world's food supply (Perfecto & Vandermeer 2010).

Positive effects of plant diversity were consistently recognized for some regulating services, and not for others. We recognized two main groups: those with answer consistency and those with no consistency. The first group corresponds to services that have been widely studied at the local scale and studied less at the landscape scale (e.g. soil fertility, plant pest, resistance to plant invasion; Landis *et al.* 2005; Vacher *et al.* 2008). The second group, showing a lack of consistency for the questions on direction of effect and relative importance, correspond to services for which these links have not been documented (e.g. water amount, quality and temporal variability). Although there is a growing amount of evidence on the links between plant diversity and regulating services or the processes that underpin them (e.g. Quétier *et al.* 2007; more detailed references in Appendix S6), and the importance of functional diversity on regulating services at landscape scales (e.g. maintenance of soil fertility, landslide and avalanche risk; Diaz *et al.* 2007; Lavorel *et al.* 2011). The lack of consistency in these factors identified in the current study suggests either a lack of understanding of the ecological processes associated to service generation, a lack of clear patterns emerging from such literature, or a lack of awareness of a larger set of biophysical literature outside the field of ecology.

Finally, experts consistently recognized a positive effect of plant diversity on the generation of cultural services. This is surprising given ecologists' limited understanding of these services (Chan *et al.* 2011), although the role of functional diversity at the landscape scale has been shown for these services (Diaz *et al.* 2007; Lavorel *et al.* 2011). The consensus may reflect connections between cultural diversity and biodiversity which are widely known in the fields of economic botany, indigenous use of native plants, and anthropology and cultural services (e.g. cultural heritage, land stewardship; Quétier *et al.* 2007).

Relative importance of abiotic resources and conditions

The relative importance of resources and conditions with respect to plant diversity on service provision at the landscape scale varied greatly among types of services. Provisioning services were perceived to be largely influenced by abiotic resources and little influenced (although positively) by plant diversity; regulating services were thought to depend on both plant diversity and abiotic resources and conditions; abiotic factors were not considered relevant for cultural services. These results differ from previous syntheses (Loreau *et al.* 2001; Hooper *et al.* 2005; Balvanera *et al.* 2006) and may indicate that experts assumed a greater influence of abiotic factors among than within sites, thus increasing the relative importance of resources and conditions at the larger landscape scale (Loreau, Mouquet & Gonzalez 2003). Further research is needed to fully understand how resources and conditions are related to biodiversity and service provision as spatial and temporal scale increase.

Limitations of assessment: representativeness and biases of experts and data analyses

The assessment was aimed at identifying people who have carried out research on plant diversity and ecosystem services, and is thus not based on a random sample of people. The percentage of experts that responded to the survey (23%) is similar to that reported by other expert opinion studies on biodiversity (Schläpfer, Schmid & Seidl 1999; Halpern *et al.* 2007). The majority of experts worked in community and ecosystem ecology at research institutes, and had more than 10 years of experience with plant diversity or ecosystem processes/services at the time of the survey. Analyzing the characteristics that described the experts in this study (see Appendix S3) showed that they have thought deeply about the subject and were thus likely to provide authoritative estimates on plant diversity and ecosystem services. Furthermore, their understanding of the topic was very likely to have included experience beyond their particular research publications.

Some biases emerged from expert background. As explained above, experts working in management, in NGOs or governmental agencies, those focusing on transformed ecosystem (e.g. cropland, pasture, exotic pine and eucalyptus plantations, irrigated rice fields, secondary tropical wet forest, savanna transition) and those with less experience (<10 years) tended to report no influence of plant diversity on service generation (nature of effects and relative importance) more frequently. This suggests that experts dealing with real-world conditions are either more skeptical of emerging research findings derived from the experimental literature, are less aware of them, or that information relevant to their needs is lacking; for instance, a rigorous meta-analysis of the direction of effect of diversity in agricultural environments has only been recently published (Letourneau *et al.* 2011).

The future will usher in new questions on biodiversity and ecosystem services and allow access to new empirical data or additional expert opinion. Given the broad reach of the internet, web-based expert opinion surveys are a strategic way to aggregate information that can help set priorities for conservation and management action plans and related research (Donlan *et al.* 2010). Priority setting for maintenance of biodiversity and management of ecosystem services at the landscape scale cannot wait for exhaustive empirical research. Instead, survey instruments can be easily replicable and quickly updated to include new sources of information, control for expert bias and refine the results from direction of effect and relative importance of plant diversity on services generation.

The statistical methods used here were very useful to address the questions posed. The Bonferroni adjustments may have increased the probability of not rejecting some null hypothesis when it would been appropriate to do so (Moran 2003). However, changes in the observed patterns with this correction were only found for the most complex assessments of the effects on individual ecosystem services (Tables 4 and 5) and so the adjustments helped us to more clearly identify the major inconsistencies among experts (Appendix S5). The use of generalized mixed effect models with individual experts as a random factor and expert background categories as fixed contrasts within this random factor would have been an alternative analysis possibility (De Vaus 2002). Due to the complexity of the design we used the described χ^2 tests without random factors instead.

Future research: main questions and management implications

The results of our expert knowledge assessment can provide different hypotheses about the relationships between plant diversity and services generation that could be tested further. Future research should focus more on the relative importance of plant diversity on services, rather than the direction of its effects, which are better known.

Plant genetic diversity effects seem to differ between ecosystem services types. Also, the relative role of plant diversity on service provision may change across types of ecosystems. The role of components of plant diversity such as functional diversity may change across different types of regulating and cultural services. Finally, exploring the relative role of plant diversity with respect to that of abiotic resources and conditions for different types of ecosystem services is particularly relevant for management. This set of hypotheses should help to identify unexamined research questions that would lead to a novel approach to observational and experimental studies for the foundation of rigorous and science-based evidence for the management, conservation and sustainable use of biodiversity and ecosystem services at the landscape scale.

Our approach and results can be used in a number of ways to inform and aid management decisions. This expert assessment can identify themes of agreement that may be used with caution as a synthesis of expert knowledge to guide technological and policy interventions. It also highlights themes for which closer communication between scientists and managers is needed.

Conclusions

Our survey revealed the attributes of plant diversity which, in the eyes of the interviewed experts, are most likely to have effects on the generation of services at landscape scales. Expert assessment identified diversity of species within a community and diversity of communities within a landscape as the most important levels of organization for service generation with positive effects; the same can be said for composition and number of species among the components of plant diversity. Water availability was perceived to be the most important abiotic resource for service generation at the landscape scale; but this was not the case for all services. Provisioning services were thought to be largely influenced by abiotic resources and little influenced (although positively) by plant diversity. Sustaining the generation of regulating services was expected to depend on both plant diversity and abiotic resources and conditions. A very important positive effect was attributed to plant diversity for the generation of cultural services. Most experts know and seem to trust the results of observational and experimental research showing that plant diversity increases ecosystem functions; this pattern was true even for experts carrying out more real-world work, who were among the most skeptical about the existence of such links. Key areas of future research to guide ecosystem management include the role of plant genetic diversity and that of abiotic factors on landscape (i.e. management-relevant) scales. Overall, the experts interviewed agreed that, at the landscape scale, the importance of maintaining plant diversity is crucial if the management goal is to ensure and sustain provision of ecosystem services for human well-being.

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Supporting Information in Anexo 2

Additional Supporting Information may be found in the online version of this article
Appendix S1. Glossary of terms used in this survey.
Appendix S2. Phases of building the survey assessment.
Appendix S3. Background experts that answered the survey on the relationship between plant diversity and ecosystem services.
Appendix S4. Direction of effect and relative importance of levels of organization, components of plant diversity, abiotic resources and conditions.
Appendix S5. Biases associated with background experts that were found on the frequencies for direction of effects and relative importance of plant diversity on service generation.
Appendix S6. Publications found in a search of the ISI Web of Knowledge about relationship between plant diversity and ecosystem services.

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Capítulo IV

Modelación y mapeo de la diversidad vegetal dentro de una cuenca hidrológica

Modeling and mapping plant diversity within a Mexican watershed

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Resumen

La modelación y mapeo de la diversidad vegetal es una herramienta ampliamente utilizada para guiar la toma de decisiones relacionadas con la identificación de áreas prioritarias para conservación. A la fecha, los modelos se han concentrado en la riqueza específica de árboles, con escasa información sobre otras formas de vida y otros índices de diversidad. En este trabajo analizamos la distribución espacial de distintas formas de vida e índices de diversidad a partir de su cuantificación local y modelación en una cuenca hidrológica situada en la costa del Pacífico Mexicano. Se cuantificó la diversidad vegetal en 50 sitios contrastantes, con respecto a sus condiciones ambientales e historia de manejo de la cuenca. En cada sitio se establecieron cuadrantes anidados, identificando todos los individuos herbáceos y leñosos. Se calculó la riqueza específica para cuatro formas de vida, así como cuatro índices de diversidad para todas las especies. Para todos estos se describieron los patrones espaciales en toda la cuenca a partir de modelos predictivos usando análisis de regresión múltiple con base en variables derivadas de cartografía digital y percepción remota y los datos de campo. Se compararon los patrones espaciales y se identificaron las áreas de mayor concentración de diversidad (hotspots). La capacidad predictiva de los modelos fue variable, siendo el valor más bajo para la riqueza de hierbas ($R^2 = 0.30$) y el más alto para la riqueza de árboles ($R^2 = 0.88$). Las variables predictivas más importantes fueron el índice de vegetación normalizado para la época de lluvias y la cobertura de selva baja. La capacidad predictiva de los modelos fue variable, mostrando relaciones significativas entre los datos observados y modelados para solo tres de los ocho modelos. Los patrones espaciales de diversidad difirieron entre las distintas formas de vida e índices, aunque se detectaron varias áreas de altos valores de diversidad para todos los índices. Los resultados muestran que la selección de la forma de vida e índice de diversidad pueden afectar la exactitud y predicción de las áreas prioritarias de conservación. La producción y comparación de patrones espaciales para distintos estimadores de la diversidad son una

herramienta poderosa para la identificación de áreas prioritarias para la conservación.

Palabras claves

Índice de Simpson, riqueza específica de especies, índice de Chao 1, índice Alfa de Fisher, validación de modelos, regresión múltiple, Criterio de Información Akaike.

Introducción

La actual pérdida de biodiversidad originada por la acelerada degradación y transformación de los ecosistemas, destaca la urgencia de generar estrategias para su conservación (Rockstrom *et al.* 2009). En este sentido, el conocimiento de la distribución geográfica de la biodiversidad ha sido una estrategia útil para guiar la toma de decisiones en la identificación de áreas prioritarias de conservación (Foody 2008; Gillespie *et al.* 2008). Para generar la información espacial de la biodiversidad en áreas escasamente exploradas o no cuantificadas se han utilizado modelos empíricos predictivos que relacionan datos de las especies y variables biofísicas, los cuales son proyectados con ayuda de algún Sistema de Información Geográfica a un mapa digital (Mateo *et al.* 2011; Foody 2008). La solidez y realismo de los mapas depende en gran medida del conjunto de datos y el método de modelado geográfico (Guisan & Zimmermann 2000; Guisan & Thuiller 2005).

Los modelos predictivos de los patrones espaciales de la diversidad se basan en datos de campo así como información cartográfica o derivada de percepción remota. Los datos de campo, sobre todo aquellos que reflejan las abundancias relativas de las especies, son una fuente de información que permite construir modelos que reflejan la respuesta de las especies a las condiciones biofísicas predominantes así como las condiciones de disturbio (Guisan & Thuiller 2005). Sin embargo, los datos de campo no están exentos de sesgos asociados al esfuerzo de muestreo o condiciones de la observación

(Gotelli & Colwell 2001). El uso de variables biofísicas predictivas derivadas de información cartográfica y percepción remota permiten escalar los datos de campo a regiones más amplias. En particular es relevante incorporar aquellas variables que reflejen el desempeño temporal de las especies vegetales (principalmente en ambientes estacionales), los factores biofísicos que afectan directamente a la diversidad, así como aquellas que permitan evaluar las perturbaciones antropogénicas relevantes a las especies estudiadas (Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Gillespie *et al.* 2008).

La modelación de la distribución geográfica de las especies está sustentada en el concepto de nicho ecológico (Vandermeer 1972, Soberón & Peterson 2005). El nicho ecológico es un concepto abstracto que agrupa en un solo término descriptivo todas las condiciones biofísicas necesarias para mantener una población viable de un organismo. El nicho ecológico comprende dos componentes, el nicho fundamental, que es el hipervolumen n-dimensional donde cada punto corresponde a un estado en el medio ambiente que permite que una población o especie exista indefinidamente; y el nicho efectivo o realizado, que es la porción del hipervolumen que es ocupada por una población o especie, cuando esta ha caído en competencia con otras poblaciones o especies (Hutchinson 1957, 1978). Dentro del contexto de la modelación, un punto a debate se ha generado al tratar de definir que componente del nicho esta siendo representado (Araújo & Guisan 2006). Algunos autores señalan que los modelos que consideran al conjunto de puntos de presencia de una especie puede aproximar al nicho fundamental (Soberón & Peterson 2005). Otros autores han considerado que los modelos proporcionan una representación espacial del nicho realizado, por que las distribuciones observadas son ya restringidas por las interacciones bióticas (principalmente la competencia), la dispersión, la dinámica poblacional y las condiciones biofísicas examinadas (Guisan & Zimmermann 2000; Guisan & Thuiller 2005). Sin duda, el nicho ecológico se ha convertido en un concepto tanto teórico como metodológico que ha trascendido el ámbito de la ecología, por su utilidad para generar mapas de distribución espacial e identificar áreas importantes de conservación (Guisan & Zimmermann 2000, Díaz Porras 2006).

La teoría de nicho ecológico permitió estudiar la relación entre los organismos y su ambiente y de cómo éstos interactúan para estructurar las comunidades, tanto ecológica como geográficamente (Díaz Porras 2006). La integración de la teoría de la competencia como fuerza motora en la estructuración del nicho efectivo o realizado de las especies o las poblaciones (Hutchinson 1978), ayudo a explicar de manera un tanto más sencilla la dinámica de los nichos. Dos especies con requerimientos ambientales similares, pueden ocasionar una disminución poblacional en cualquiera de éstas, por lo que es comprensible que especies así, no puedan ocupar el mismo nicho ecológico, por lo que su área de distribución y abundancia de las especies se ve afectada (Vázquez 2005). Así, los patrones espaciales de las comunidades son el resultado de los patrones individuales de las especies o poblaciones, pudiendo variar uno de otro independientemente pero compartiendo o repartiendo el gradiente ambiental. En este sentido, los índices de diversidad son una herramienta conceptual que permite considerar tanto las diferencias espaciales de las especies individuales como las diferencias de la estructura horizontal de las comunidades vegetales (Austin 2002; Yue *et al.* 2007). Si bien, la teórica ecológica que sostiene el cálculo de los índices ha permitido su uso para representar espacialmente a la diversidad vegetal (Magurran 2004), los modelos de distintos índices enfrentan el reto de comparar los patrones espaciales entre índices y discutir si las diferencias espaciales se deben al número y abundancia de los individuos contados, al esfuerzo de muestreo, y/o la disponibilidad de condiciones abióticas para el crecimiento de las especies (Gotelli & Colwell 2001; Magurran 2004).

La identificación de variables predictivas que definen los patrones espaciales para las distintas formas de vida y de los distintos índices de diversidad permitirá una mejor planeación de la conservación de las distintas facetas de la diversidad. Se sabe que los distintos tipos de organismos responden de forma diferencial antes las condiciones biofísicas o antropogénicas (Whittaker *et al.* 2001; Christensen & Heilmann-Clausen 2009). La distribución espacial de especies leñosas está fuertemente determinado por variables climáticas, de productividad y heterogeneidad ambiental a escalas regionales, pero también a variables edáficas y a interacciones bióticas que operan a escalas locales (Pausas & Austin 2001; Whittaker *et al.* 2001; Field *et al.* 2009). En cambio, la distribución espacial de especies herbáceas a escala local y de paisaje ha sido más frecuentemente relacionada con la microtopografía y la fertilidad del suelo (Christensen & Heilmann-Clausen 2009; McEwan & Muller 2011; Vockenhuber *et al.* 2011). Las perturbaciones antropocéntricas también definen los patrones espaciales de especies herbáceas y leñosas (Schnitzer & Bongers 2002; Luck *et al.* 2007), aunque pocos trabajos de modelación han incorporado este tipo de variables predictivas (Cayuela *et al.* 2006; Christensen & Heilmann-Clausen 2009; Feilhauer & Schmidtlein 2009).

La modelación de los índices de diversidad ha permitido la identificación de las variables predictivas biofísicas y antropogénicas que definen sus patrones espaciales. Para los índices de diversidad, los patrones espaciales de la riqueza de especies a escala regional están determinados por variables climáticas, topográficas, de productividad y heterogeneidad ambiental (Gould 2000; Luoto *et al.* 2002; Dogan & Dogan 2006; Wohlgemuth *et al.* 2008; Feilhauer & Schmidtlein 2009; Altamirano *et al.* 2010). Para el índice de Alpha de Fisher, los patrones espaciales están determinados por variables climáticas, heterogeneidad ambiental y disturbio (Cayuela *et al.* 2006). En cambio, la distribución espacial del índice de dominancia de Simpson a escala regional ha sido más frecuentemente relacionada con variables de clima y topografía (Dogan & Dogan 2006). Las variables relacionadas con las perturbaciones antropocéntricas tendrán que ser incorporadas en la modelación de los índices por su potencial efecto en la estructura horizontal de las comunidades vegetales, componente que definen en parte la distribución espacial de los índices de diversidad (Austin 2002; Yue *et al.* 2007).

Las concentraciones de alta diversidad o hotspots permiten diseñar estrategias de conservación. La identificación espacial de hotspots es a partir de los patrones fragmentados de mapas individuales de hotspots, o por la sobreposición de varios modelos e identificando las concentraciones de hotspots dentro de un área. Los hotspots identificados por sobreposición representan áreas potencialmente más factibles para orientar los esfuerzos de conservación (Parviainen *et al.* 2009). Además, este último modo de identificación de hotspots tiene mejor control de formas de vida o índices de diversidad poco modelados y/o mapas de predicción poco aceptables (Gioia & Pigott 2000, Parviainen *et al.* 2009). De los distintos índices existentes, la riqueza de árboles o de todas las plantas, son los más usados para detectar concentraciones de hotspots (Gould 2000; Luoto *et al.* 2002; Cayuela *et al.* 2006; Dogan & Dogan 2006; Feilhauer & Schmidtlein 2009; Altamirano *et al.* 2010; Parviainen *et al.* 2009). Es posible que la sobreposición de los mapas de hotspots de riqueza de distintas formas de vida o los hotspots de distintos índices de diversidad permita la identificación de áreas prioritarias para la conservación de la diversidad vegetal. Sin embargo, esta cuestión no ha sido evaluada.

En este estudio analizamos la distribución espacial de distintas formas de vida y de distintos índices de la diversidad vegetal a partir de su cuantificación local y modelación en una cuenca hidrológica. La cuantificación local abarcó el gradiente climático así como el mosaico de tipos de cobertura y uso del suelo que han resultado de la historia de manejo. Los objetivos específicos son: i) la comparación de las variables predictivas para las distintas formas de vida y los distintos índices de diversidad, ii) la evaluación de la capacidad predictiva y confiabilidad predictiva de los distintos modelos obtenidos, y iii) la comparación de los patrones espaciales de diversidad para las distintas formas de vida y los distintos índices de diversidad y la identificación de áreas particularmente diversas. El trabajo se desarrollo en la cuenca del Río Cuitzmala, en la costa del estado de Jalisco, la cual es característica del gradiente biofísico y de manejo que se da a lo largo de la Costa del Pacífico Mexicano y representa además una zona para la cual se cuenta con amplio conocimiento sobre la estructura y funcionamiento de los ecosistemas y el manejo que de este hacen las poblaciones locales (Maass *et al*, 2003; Maass *et al*. 2005).

Métodos

Área de estudio

El estudio se realizó en la Cuenca del Río Cuitzmala, en la costa del Pacífico Mexicano. La cuenca tiene una superficie de 1,089 km^2, un gradiente de altitud que abarca de los 0 a 1,730 m.s.n.m. La cuenca presenta de 21 diferentes tipos de cobertura de vegetación y uso de suelo (TCUS) de acuerdo al Inventario Nacional Forestal (Martínez-Trinidad 2007) y la caracterización por parte del Centro de Investigaciones en Geografía Ambiental, UNAM (Larrazábal *et al.* 2008). Además de la elevada heterogeneidad ambiental, la cuenca está siendo sometida a procesos de transformación antropogénica del paisaje, con transformaciones a pastizal y cultivo, que ocupan cerca del 30% de su superficie (Maass *et al*. 2003; Maass *et al*. 2005).

Selección de sitios de muestreo

Para poder abarcar la elevada heterogeneidad biofísica así como la historia de manejo de la cuenca se ubicaron 50 sitios de muestreo con criterios jerárquicos de selección. Los criterios fueron: *i*) el gradiente altitudinal, *ii*) las distintas unidades morfoedafológicas, *iii*) el TCUS y *iv*) la exposición de ladera. El gradiente de altitud está relacionado con cambios en precipitación y la temperatura, los cuales determinan los gradientes de riqueza de especies por las variaciones en las condiciones microambientales (Deng *et al*. 2007; Field *et al*. 2009). El gradiente altitudinal se reclasifico en seis rangos, de 300 metros cada uno, a partir del nivel del mar. Las unidades morfoedafológicas representan factores que influyen en las tasas de crecimiento y vigor reproductivo de la vegetación, así como en la disponibilidad de agua en el suelo. Se utilizó la caracterización territorial de la cuenca realizada por Martínez-Trinidad (2007), basada en datos de relieve, clima, geología, pendientes y edafología. El muestreo se enfocó en las 4 unidades morfoedafológicas dominantes (montaña de granito, lomerío de granito, montaña volcano clástica y montaña caliza) que ocuparon el 86% de la superficie de la cuenca. El TCUS es el resultado de la historia de uso del suelo en la región. El muestreo se enfocó en los cuatro principales TCUS, que en contribución decreciente a la superficie total de la cuenca son selva mediana, selva baja, bosque de encino y pastizal (Martínez-Trinidad 2007; Larrazábal *et al.* 2008). La exposición de ladera determina diferencias en la cantidad de insolación total anual, con impactos en el microclima y el tiempo de residencia y el contenido de agua en el suelo (Galicia *et al.* 1999). Se ubicaron un mismo número de sitios en laderas de exposición norte y sur.

Censos de vegetación

Los censos de vegetación estuvieron diseñados para abarcar los principales estratos y formas de vida de las comunidades vegetales. Decidimos usar tamaños de cuadro anidados unos dentro de otros debido a que son logísticamente más factibles. El tamaño de cuadro y anidamiento para optimizar el análisis de las distintas formas de vida vegetales (Stohlgren *et al.* 1997; Turner *et al.* 2001). Además, este diseño ha mostrado ser adecuado para extrapolar valores locales de diversidad a toda una región (Turner *et al.* 2001). Todos los individuos leñosos se censaron en cuadrantes anidados de 400 m^2, 100 m^2 y 25 m^2, donde los criterios de diámetro a la altura del pecho (DAP) fueron $\geq$5 cm, $\geq$ 2.5 cm y $\leq$ 2.5, respectivamente. Todos los individuos herbáceos con menos de un metro de altura se censaron en cuatro cuadros de 1 m^2 dentro del cuadro de 25 m^2. Para los individuos censados se registró forma de vida, el diámetro a la altura del pecho (leñosas) o el porcentaje de cobertura (hierbas) e y la identidad taxonómica. Los censos se realizaron en los meses de septiembre a noviembre del 2007 para facilitar la identificación del material botánico. La identificación taxonómica se hizo en campo, en laboratorio y por cotejo de ejemplares de herbario. Se cuenta con una colección de referencia de los ejemplares en el Centro de Investigaciones en Ecosistemas, UNAM.

Estimación local de diversidad vegetal

La estimación de la diversidad vegetal dentro de la cuenca considero índices que abarcan tanto la identidad como la abundancia relativa de las especies (Magurran 2004). La riqueza específica, índice que considera solo la identidad de las especies, se calculo para cuatro formas de vida (hierbas, liana, arbustos y árboles). Para el total de especies, se calcularon los índices de Alpha de Fisher, Chao 1 y dominancia de Simpson. La riqueza de especies es un índice fácil de calcular e interpretar y ampliamente utilizado; el Alpha de Fisher es un índice que es poco sensible a la frecuencia de especies raras; el índice Chao1 estima la riqueza total, considerando aquellas que no pudieron ser detectadas, a partir de los patrones de rareza; el índice de Simpson refleja los patrones de dominancia (Gotelli & Cowell 2001; Magurran 2004; Colwell 2009). Otros aspectos conceptuales y estadísticos fueron considerados durante la estimación de estos índices (mayores detalles se muestran en la Tabla S1 del Material Suplementario). Los índices fueron obtenidos en el programa StimateS 8 (Colwell 2006), programa que controla los efectos del tamaño de muestra a través de la técnica de la rarificación (Gotelli & Cowell 2001; Cowell e*t al.* 2004).

Variables predictivas de diversidad vegetal y fuentes de información

La modelación de los patrones espaciales de las especies vegetales se basó en variables independientes que están estrechamente relacionadas con el desempeño de las plantas vasculares, restringiéndose a las que estuvieron disponibles para toda el área de estudio. Se identificaron una serie de variables topográficas, de perturbación antropogénica, hidrológicas y de biomasa vegetal

(Tabla 1) que describen tanto gradientes de recursos relacionados con la materia y la energía consumida por la plantas (p. ej. nutrimentos, agua, luz), como gradientes indirectos asociados a la disponibilidad de recursos (p.ej. pendiente, exposición, elevación, posición topográfica, tipo de hábitat, geología) y con la historia de manejo (p. ej. suelo de uso agrícola o ganadero) Guisan & Zimmermann 2000; Guisan & Thuiller 2005). Las variables se obtuvieron de la cartografía digital, imágenes de percepción remota y los sistemas de información geográfica (SIG). Los detalles metodológicos para la obtención de los valores por variable predictiva se muestran en el Tabla S2.

Variables topográficas

La topografía está asociada con cambios en condiciones biofísicas incluyendo los patrones de precipitación y temperatura, así como condiciones microclimáticas, y del suelo. Las variables predictivas para describir las variaciones topográficas fueron la radiación total anual, la exposición, la pendiente y la altitud (Tabla 1). La radiación total anual determina la demanda evapotranspirativa afectando a su vez la capacidad de retención y de disponibilidad de agua del suelo (Galicia *et al.* 1999). La exposición de la ladera determina diferencias en la cantidad de insolación total anual con efectos en el microclima y potenciales de evapotranspiración, el tiempo de residencia y el contenido de agua en el suelo, modificando las características de la vegetación asociada a las laderas (Galicia *et al.* 1999). La pendiente del terreno afecta el movimiento superficial y subterráneo del agua, la capacidad de infiltración y el efecto de la erosión hídrica (Galicia *et al.* 1999). La altitud está relacionada con la precipitación y la temperatura, determina variaciones en las condiciones ambientales a cortas distancias a través de los gradientes (Deng *et al.* 2007).

Tabla 1. Variables predictivas para la generación de los modelos de la diversidad vegetal en la Cuenca del Río Cuitzmala. Los valores son para 50 sitios de muestreo. Las variables en negritas fueron usadas en las regresiones múltiples para obtener los modelos predictivos de la diversidad vegetal. n= número de variable; MDE= modelo digital de elevación del terreno, NDVI = Índice de vegetación de diferencia normalizada, NDII= Índice de diferencia infrarroja normalizado. Las imágenes SPOT para la época seca y de lluvias fueron de mayo y septiembre del 2007, respectivamente.

n	Nombres y unidades de medida	Código en modelos predictivos	Derivación (resolución)
Topográficas			
1	**Radiación total anual (Watt hora/m^2)**	Radiación	MDE (10x10m)
2	**Exposición (grados)**	Exposición	
3	Pendiente (grados)	Pendiente	
4	**Altitud (metros)**	Altitud	
Perturbación antropogénica			
5	**Distancia euclidiana a la carretera (m)**	Dist. Euc. Carretera	MDE (10x10m)
6	**Distancia de recorrido a la carretera (m)**	Dist. Carretera	
7	**Distancia de recorrido a los pueblos (m)**	Dist. Pueblos	
8	**Distancia de recorrido a los pueblos con más de 300 habitantes (m)**	Dist. Pueblos +300 hab.	
Hidrológicas			
9	**Distancia a cualquier cauce del rio (m)**	Dist. Cauces	MDE (10x10m)
10	**Distancia al cauce principal (m)**	Dist. Cauce Principal	
11	**Índice topográfico de humedad relativa (m)**	TRMI	
12	Índice topográfico de humedad relativa modificado (m)	TRMIm	
Biomasa vegetal			
13	**NDVI para lluvias círculo 50 m**	$\text{NDVI}_{\text{lluvias}}$ 50m	Imagen SPOT (20x20m)
14	NDVI para lluvias dona 250 m	$\text{NDVI}_{\text{lluvias}}$ 250m	
15	**NDVI para lluvias dona 500 m**	$\text{NDVI}_{\text{lluvias}}$ 500m	
16	**NDII para lluvias círculo 50 m**	$\text{NDII}_{\text{lluvias}}$ 50m	
17	NDII para lluvias dona 250 m	$\text{NDII}_{\text{lluvias}}$ 250m	
18	NDII para lluvias dona 500 m	$\text{NDII}_{\text{lluvias}}$ 500m	
19	**NDVI para secas círculo 50 m**	$\text{NDVI}_{\text{secas}}$ 50m	Imagen SPOT (5x5m)
20	NDVI para secas dona 250 m	$\text{NDVI}_{\text{secas}}$ 250m	
21	**NDVI para secas dona 500 m**	$\text{NDVI}_{\text{secas}}$ 500m	
22	**NDII para secas círculo 50 m**	$\text{NDII}_{\text{secas}}$ 50m	
23	NDII para secas dona 250 m	$\text{NDII}_{\text{secas}}$ 250m	
24	NDII para secas dona 500 m	$\text{NDII}_{\text{secas}}$ 500m	
25	**Porcentaje cobertura del dosel círculo 50 m**	% dosel 50m	Imagen SPOT (5x5m)
26	Porcentaje cobertura del dosel dona 250 m	% dosel 250m	
27	**Porcentaje cobertura del dosel dona 500 m**	% dosel 500m	
28	**Bosque de encino**	BE	Imagen SPOT (5x5m)
29	**Pastizal**	P	
30	**Selva baja**	SB	
31	**Selva mediana**	SM	

Variables de perturbación antropogénica

La perturbación antropogénica influye fuertemente en los patrones de diversidad de especies debido a sus efectos en características del disturbio, en la disponibilidad de recursos, y la presencia de especies invasoras (Luck *et al.* 2007; Christensen & Heilmann-Clausen 2009). Las variables predictivas para describir la perturbación antropogénica fueron la distancia euclidiana a la carretera, la distancia de recorrido a la carretera, la distancia de recorrido a los pueblos y la distancia de recorrido a los pueblos con más de 300 habitantes (Tabla 1). La distancia euclidiana a la carretera indica el trayecto en línea recta de los sitios de muestreo a la carretera más cercana, como indicador de la accesibilidad de los pobladores para generar impactos en las comunidades vegetales. La distancia de recorrido, considerando la pendiente del terreno, es el trayecto de los sitios de muestreo a la carretera o pueblo más cercano, como indicador de la accesibilidad de los pobladores para generar zonas degradadas o en constante transformación (Christensen & Heilmann-Clausen 2009). La distancia de recorrido a los pueblos con más de 300 habitantes es el trayecto de los sitios de muestreo a una de las cuatro más importantes localidades dentro de la cuenca, como indicador de la accesibilidad de los pobladores para generar impactos en las comunidades vegetales (Christensen & Heilmann-Clausen 2009; Maass *et al.* 2003).

Variables hidrológicas

El agua es el principal factor limitante para la producción de biomasa dentro del área de estudio. Las variables hidrológicas consideradas para describir la disponibilidad de este recurso en los sitios de muestreo fueron la distancia a cualquier cauce del río, la distancia al cauce principal, el índice topográfico de humedad relativa (TRMI) y el índice topográfico de humedad relativa modificado (TRMIm) (Tabla 1). La distancia a cualquier cauce del río indica la posición del sitio de muestre con respecto a los cauces y zonas de mayor escorrentía. La distancia al cauce principal indica la accesibilidad de la vegetación de los sitios de muestreo al agua superficial y subterránea del cauce del Río Cuitzmala. El índice topográfico de humedad relativa (TRMI) indica la disponibilidad de humedad relativa en el suelo en los sitios de muestreo (Parker 1982). El TRMI modificado indica la disponibilidad de humedad en el suelo, ajustado por las condiciones de exposición, ángulo de la pendiente y posición en el paisaje (Manis *et al.* 2002).

Variables de biomasa vegetal

La cantidad de biomasa depende de la diversidad biológica (Cardinale et al 2011) y por otro lado la productividad (tasa de conversión de recursos a biomasa por unidad de área y de tiempo) es un predictor de los niveles de diversidad vegetal (Mittelbach *et al.* 2001). Las variables de biomasa fueron índices espectrales, el porcentaje de cobertura del dosel y los tipos de cobertura y uso del suelo (Tabla 1). Los índices espectrales derivados de las imágenes satelitales están fuertemente correlacionados con la productividad primaria neta y la tasa evapontraspirativa a escalas locales, regionales y globales (Pausas *et al.* 2003; Levin *et al.* 2007). Los índices espectrales utilizados fueron el índice de vegetación de diferencia normalizada (NDVI), que refleja la cantidad de biomasa fotosintéticamente activa y esta correlacionado con el área foliar y la productividad primaria neta (Deng *et al.* 2007; Levin *et al.* 2007); y el índice de diferencia infrarroja normalizado (NDII) que refleja el contenido de humedad en la vegetación (Hernández-Stefanoni & Dupuy 2007; Altamirano *et al.* 2010). Debido a la fuerte estacionalidad en la disponibilidad de agua en la zona de estudio (García-Oliva *et al.* 2002) y a la presencia de vegetación caducifolia como la selva baja y algunos elementos de la selva mediana, ambos índices fueron obtenidos para la época seca (mayo) y de lluvias (septiembre). La cobertura del dosel es un indicador de la presencia de individuos arbóreos (Turner *et al.* 2003). Finalmente, los tipos de cobertura y usos del suelo (TCUS) reflejan las respuestas de la vegetación a las condiciones biofísicas así como los procesos de transformación a los que han sido sujetos (Turner *et al.* 2001). Se consideraron los cuatro principales TCUS dentro de la cuenca: la selva mediana, la selva baja, el bosque de encino y los pastizales.

Efecto de la escala espacial

Distintos procesos que determinan la diversidad vegetal operan a distintas escalas: en particular, los patrones de dispersión de las especies vegetales dependen del tipo dispersión y del vector involucrado (Grubb 1977; Field *et al.* 2009). Para explorar como la escala espacial afecta la capacidad de distintas variables predictoras de biomasa para predecir la diversidad calculamos las variables de biomasa vegetal (NDVI, NDII, cobertura del dosel) a tres escalas espaciales, es decir, a 50 m, 250m y 500 m (ver Tabla S2 para detalles metodológicos de su cálculo).

Combinación de los TCUS

La cobertura del suelo y su uso están correlacionada con la riqueza de especies vegetales en condiciones de limitada variación climática a escala regional (Turner *et al.* 2001; Kerr & Cihlar 2004). Diversos trabajos han mostrado que la combinación de TCUS son las variables predictoras más importantes para modelos predictivos de diversidad (Luoto *et al.* 2002; Wohlgemuth *et al.* 2008; Field *et al.* 2009). Para explorar si los TCUS incrementan la capacidad predictiva de los modelos se obtuvieron 17 combinaciones de TCUS (Tabla S3), mismas que se ingresaron al generar los modelos predictivos.

Modelos predictivos de diversidad vegetal

Se utilizaron regresiones múltiples para correlacionar los valores locales de diversidad vegetal y las variables predictivas obtenidas de la cartografía digital e imágenes de la percepción remota. Para las 31 variables predictivas, se realizo un análisis de correlación para evitar el uso de variables colineares, excluyendo las variables altamente correlacionadas ($|r| > 0.76$). Un total de 21 variables fueron incluidas en el análisis (Tabla 1).

Las ocho variables de respuesta de la diversidad mostraron una distribución normal.

Para construir los modelos de regresiones múltiples se consideraron todas las posibles combinaciones de las variables predictivas (un total de 9,246 modelos por cada forma de vida e índice de diversidad; Burnham & Anderson 2002); no fueron consideradas interacciones entre variables ni parámetros cuadráticos. Todos los análisis fueron realizados en el paquete estadístico JMP 8.0 (SAS 2008).

La selección del mejor modelo predictivo de diversidad vegetal se llevó a cabo en cuatro pasos. En el primer paso usamos el *Akaike Information Criterion* de segundo orden, usando la corrección para tamaños de muestra pequeños (AICc, por sus siglas en inglés), para elegir los 15 modelos con el AICc más bajo. En el segundo paso calculamos el Δi de cada modelo, que es la diferencia entre el AICci de cada modelo i y el mínimo AICc; seleccionamos sólo los modelos con $\Delta i < 2$. En el tercer paso, elegimos los modelos con los más altos valores del coeficiente de determinación (R^2). En el cuarto paso, seleccionamos el mejor modelo para maximizar el poder predictivo así como la inclusión de las variables independientes que más frecuentemente aparecieron como relevantes a los distintos modelos y cuya capacidad predictiva individual fuera mayor; estas variables son aquellas con mayor peso Akaike (*wi.*), que es la suma de los valores *wi* de cada variable para todos los modelos *i* (Burnham & Anderson 2002).

Evaluación de la confiabilidad predictiva de los modelos

La confiabilidad predictiva de los modelos de la diversidad vegetal fue evaluada usando regresiones lineares entre los valores observados y los valores modelados (Guisan & Zimmermann 2000). La construcción de los modelos predictivos contempló la exclusión de 20 de los 50 sitios de muestreo para así contar con datos independientes pero comparables para hacer esta evaluación. Los 20 sitios excluidos fueron obtenidos al azar a partir de un muestreo estructurado para representar de forma proporcional con el número de puntos de muestreo para los distintos rangos de altitud y los TCUS, y seleccionado aquel conjunto de puntos aleatorios que abarcara toda la cuenca. Los modelos predictivos de la diversidad fueron construidos con los 30 sitios restantes.

El valor de R^2 fue utilizado para medir la confiabilidad predictiva, a partir del porcentaje de varianza explicado por la asociación linear entre los datos observados (d_{obs}) y los datos modelados (d_{mod}). Otro método de validación consistió en comparaciones cualitativas entre el rango de valores observados en campo con respecto al rango de valores modelados y mostrados en los mapas.

Mapas de diversidad vegetal

El mejor modelo predictivo para cada forma de vida e índice de diversidad se utilizo para extrapolar los valores locales de la diversidad vegetal a toda la cuenca. La generación de los mapas de diversidad vegetal se basó en la homogenización del tamaño de gradilla (30x30m) de las variables predictivas. Este tamaño de gradilla *i)* reduce el cociente entre el tamaño del sitio de muestreo (400 m^2) y de pixel (900 m^2) (Cayuela *et al.* 2006), *ii)* aumenta la resolución espacial de los mapas finales (Guisan & Zimmermann 2000) y *iii)* disminuye la incertidumbre que se incorpora al momento de la extrapolación (Guisan & Zimmermann 2000; Dungan *et al.* 2002). La generación y procesamiento de los mapas se realizo en ArcGIS/Arcinfo 9.2 (ESRI 2006).

Identificación de patrones espaciales de diversidad vegetal

Para ilustrar las implicaciones de manejo y conservación de la distribución espacial de la diversidad vegetal analizamos los patrones generales de distribución de la diversidad y comparamos los resultados obtenidos para las distintas formas de vida e índices. Se compararon los patrones de riqueza para las distintas formas de vida, y los distintos índices de diversidad para todas las especies. Los mapas individuales fueron clasificados en tres categorías de riqueza o diversidad, utilizando la clasificación breaks (Jenks) como método natural y más parsimonioso de agrupamiento de los datos (ESRI 2006).

Para evaluar la existencia de áreas de mayor concentración diversidad (hotspots) se generaron mapas síntesis. Se realizo el reescalamiento de los valores de cada gradilla de los mapas individuales en dos clases relativas: sin valor (0), la cual corresponde a las dos primeras categorías de riqueza o diversidad de los mapas originales; y con valor (1) que corresponde a la categoría con los mayores valores de riqueza o diversidad. Se generaron tres mapas síntesis: i) la suma de los valores de riqueza por celda considerando las cuatro formas de vida, ii) la suma de los valores de los cuatro índices de diversidad, y iii) la suma de los valores de las cuatro formas de vida y los cuatro índices de diversidad. Los dos primero mapas presentan una escala de valores de uno a cuatro, mientras que el tercer mapa una escala uno a ocho.

Resultados

Cuantificación local de diversidad vegetal

Un total de 4,198 individuos pertenecientes a 557 especies y 65 morfo especies de 93 familias fueron registradas en los 50 sitios de muestreo (Tabla S4). Del número total de especies identificadas el 29% fueron hierbas, 15% lianas, 22% arbustos y 34% árboles.

Variables predictivas de la diversidad vegetal

Las variables predictivas relevantes para los modelos variaron entre formas de vida e índices de diversidad (Fig. 1). La riqueza de hierbas y árboles fueron explicadas por la cobertura de selva baja; la cobertura conjunta de selva baja y selva mediana fue la variable más relevante para la riqueza de lianas y la riqueza de arbustos fue explicada por la exposición de las laderas. Para todas las especies vegetales, la predicción de la riqueza especifica y el índice de

Simpson fueron explicados por la cobertura conjunta de pastizal y bosque de encino; la cobertura de selva baja fue la variable más relevante en la predicción de la diversidad de Alpha de Fisher; el índice de Chao 1 fue explicado por el índice de vegetación normalizado para la época de lluvias a la escala espacial de 500 m ($NDVI_{lluvias}$ 500 m).

Modelos predictivos: riqueza de formas de vida

La capacidad de los modelos para predecir los patrones espaciales de riqueza varío ampliamente entre las formas de vida (Tabla 2). La menor capacidad predictiva fue para la riqueza de hierbas ($R^2 = 0.30$), y la mayor fue para la riqueza de árboles ($R^2 = 0.88$).

La confiabilidad predictiva de los modelos de riqueza varío ampliamente entre formas de vida. Para las lianas, la relación entre los datos observados (d_{obs}) y los modelados (d_{mod}) fue significativa ($F=5.2$, $P<0.05$., $R^2 = 0.23$); se obtuvieron relaciones no significativas entre d_{obs} y d_{mod} para la riqueza de hierbas, arbustos y árboles. Las comparaciones cualitativas entre el rango de valores observados en campo (d_{obs}) y los valores modelados (d_{mod}) muestra que la riqueza de hierbas ($d_{mod}=18.5 > d_{obs}=15$), lianas ($d_{mod}=12.5 > d_{obs}=8$) y arbustos ($d_{mod}=17.1 > d_{obs}=10$) fue sobrestimada por los modelos, mientras que la riqueza de árboles ($d_{mod}=16.5 < d_{obs}=27$) fue subestimada.

Tabla 2. Modelos de regresión para evaluar la contribución de las variables cartográficas y de percepción remota a la riqueza de distintas formas de vida y distintos índices de diversidad para todas las plantas en la Cuenca del Río Cuitzmala, México. $P< 0.05$ (*); $P< 0.01$ (**); $P<0.001$ (***), $P<0.0001$ (****). Wi_{mod} = Peso Akaike de todo el modelo, Wi_{par} = Peso Akaike de cada parámetro del modelo. En negritas la variable que explica el mayor porcentaje de varianza para cada modelo. Dist = distancia, NDVI = Indice de vegetación normalizado, SB = Selva baja caducifolia, SM = Selva mediana subperenifolia, P = Pastizal, BE = Bosque de encino.

Diversidad vegetal	Wi_{mod}	F	R^2	P modelo	Parámetros del modelo	Coeficientes	Wi_{par}
Riqueza de hierbas	0.06	2.69	0.30	*	Intercepto	10.79022	
					Dist. Pueblos +300 hab	0.00014452	0.36
					Dist. Cauce Principal	-0.0002453	0.72
					NDVI$_{lluvias}$ 50m	-8.2125829	0.42
					SB	-0.9557103	0.42
Riqueza de lianas	0.11	6.90	0.53	***	Intercepto	5.08942791	
					Dist. Pueblos +300 hab.	0.00017836	1
					Dist. Cauce Principal	-0.0001945	0.97
					NDVI$_{lluvias}$ 50m	-6.8651095	1
					SB+SM	-1.0581819	0.49
Riqueza de arbustos	0.07	9.85	0.79	****	Intercepto	9.31469574	
					Radiación	-6.60E-06	1
					Exposición	0.0095053	1
					Dist. Pueblos	-0.0001242	1
					% dosel 50m	0.03671661	1
					% dosel 500m	0.03627381	1
					NDVI$_{secas}$ 50m	-20.443736	1
					NDII$_{secas}$ 50m	11.9811636	1
					NDVI$_{lluvias}$ 500m	14.2943684	1
Riqueza de árboles	0.06	26.96	0.88	****	Intercepto	6.09782755	
					Dist. Carretera	-0.0002898	0.24
					Dist. Pueblos	0.00039571	0.84
					NDVI$_{lluvias}$ 500m	12.5782224	0.70
					P	-2.7107096	0.41
					SM	-2.8951351	0.66
					SB	-5.7948871	0.87
Especies totales– Riqueza específica	0.90	20.51	0.81	****	Intercepto	21.8646717	
					Radiación	-1.25E-05	0.86
					% dosel 50m	0.08811185	1
					NDVI$_{lluvias}$ 500m	38.6086044	1
					P+BE	-4.0362303	0.48
					Selva baja	-2.8851416	0.79
Especies totales – Alpha de Fisher	0.13	17.14	0.78	****	Intercepto	18.9186901	
					Radiación	-1.21E-05	0.84
					NDII$_{secas}$ 50m	23.8585588	1
					NDVI$_{lluvias}$ 500m	34.3960049	1
					SM	-2.9237745	0.74
					SB	-6.0801358	0.79
Especies totales – Chao 1	0.07	13.26	0.68	****	Intercepto	44.98356	
					NDVI$_{secas}$ 500m	-91.0229	0.48
					NDII$_{secas}$ 50m	43.24969	0.81
					NDVI$_{lluvias}$ 500m	81.939	1
					P+BE	-7.93523	0.53
Especies totales – Índice de Simpson	0.06	14.02	0.82	****	Intercepto	-6.7935851	
					Altitud	-0.010957	0.24
					Exposición	0.01989503	1
					Dist. Pueblos	0.00034975	1
					Dist. Cauces	0.00105235	0.24
					% dosel 50mts	0.12242934	1
					NDVI$_{lluvias}$ 500m	28.146269	1
					P+BE	-2.3262766	0.47

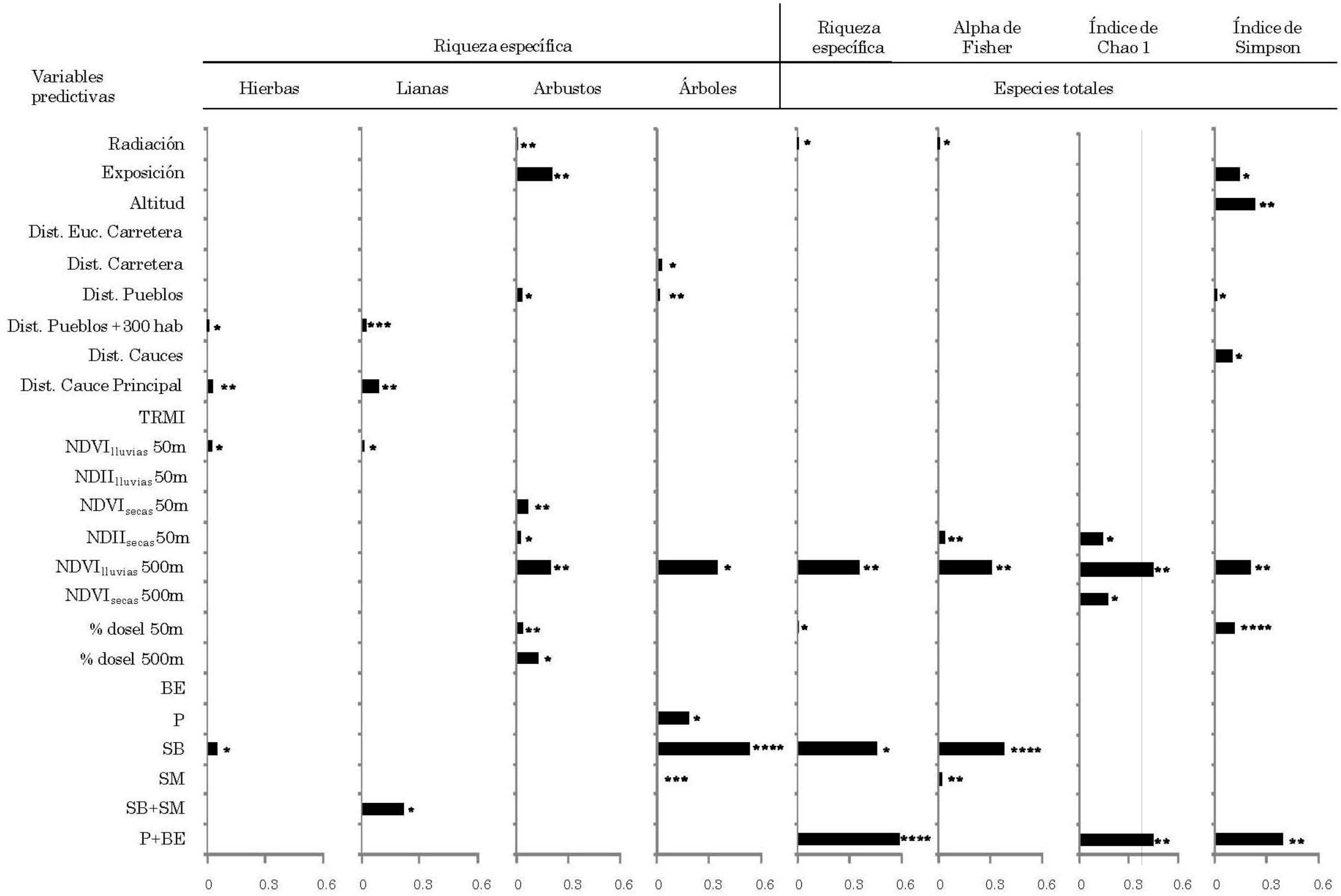

Figura 1. Proporción de la varianza de la riqueza de distintas formas de vida y de distintos índices de diversidad para todas las plantas explicada (eje x) por variables cartográficas y de percepción remota (eje y); $P < 0.05$ (*); $P < 0.01$ (**); $P<0.001$ (***), $P<0.0001$. (****).

Modelos predictivos: índices de diversidad

La capacidad de los modelos para predecir los patrones espaciales del número total de especies vegetales varío entre índices de diversidad (Tabla 2). La menor capacidad predictiva fue para el índice de Chao1 ($R^2 = 0.68$), mientras que la mayor capacidad predictiva fue para el índice de dominancia de Simpson ($R^2 = 0.82$).

La confiabilidad predictiva de los modelos para el total de especies varío entre los índices de diversidad. La relación entre los datos observados (d_{obs}) y los modelados (d_{mod}) fue significativa para la riqueza específica ($F=7.2$, $P<0.05$., $R^2 = 0.28$) y para el índice de Chao 1 ($F=4.2$, $P<0.05$., $R^2 = 0.19$); se obtuvieron relaciones relaciones no significativas entre d_{obs} y d_{mod} para Alpha de Fisher e índice de Simpson. Las comparaciones cualitativas entre el rango de valores observados en campo (d_{obs}) y los valores modelados (d_{mod}) muestran que la diversidad de Alpha de Fisher ($d_{mod}=34 > d_{obs}=30.3$) y los el índice de Simpson ($d_{mod}=38.8 > d_{obs}=31.4$) fue sobrestimados por los modelos, mientras que la riqueza específica ($d_{mod}=46 > d_{obs}=39.1$) y índice de Chao 1 ($d_{mod}=68.5 > d_{obs}=90.2$) fueron subestimados.

Áreas prioritarias para la conservación

Los patrones espaciales de riqueza observada variaron entre formas de vida (Fig. 2). El mapa de hierbas muestra que las zonas de mayor riqueza se concentran en la parte media de la cuenca, especialmente en el extremo sureste del parteaguas (Fig 2a). El mapa de lianas muestra áreas de mayor riqueza en la parte media de la cuenca, principalmente en el extremo sureste (Fig. 2b). Para los arbustos, el mapa muestra la mayor riqueza en una extensa área de la parte baja de la cuenca, una menor cantidad de fragmentos aislados y dispersos se presentan en la parte media y alta (Fig. 2c). El mapa de árboles muestra fragmentos de alta riqueza dispersos a lo largo del todo el parte aguas de la cuenca, principalmente en el extremo sureste y noroeste de la parte media (Fig. 2d).

Los patrones espaciales obtenidos para el número total de especies variaron de acuerdo al índice de diversidad considerado (Fig. 2). El mapa de riqueza observada muestra que las zonas con el mayor número de especies vegetales se concentran en la parte baja, principalmente en el extremo sureste, así como en la parte media de la cuenca (Fig. 2e). El mapa de Alpha de Fisher muestra que las áreas con una mayor riqueza real se concentra en toda la parte alta de la cuenca y pequeños fragmentos aislados en la parte baja de la cuenca, principalmente en el extremo sureste del parte aguas (Fig. 2f). El mapa del índice de Chao 1 muestra que las áreas de mayor diversidad potencial se presentan en extensas áreas de la parte baja y media de la cuenca (Fig. 2g). El mapa del índice de dominancia de Simpson muestra que la parte alta de la cuenca presenta los valores más bajos del índice (aquellos con mayor dominancia), mientras que la parte baja de la cuenca presenta extensas áreas con altos valores del índice (aquellas con mayor equitatividad, Fig. 2h).

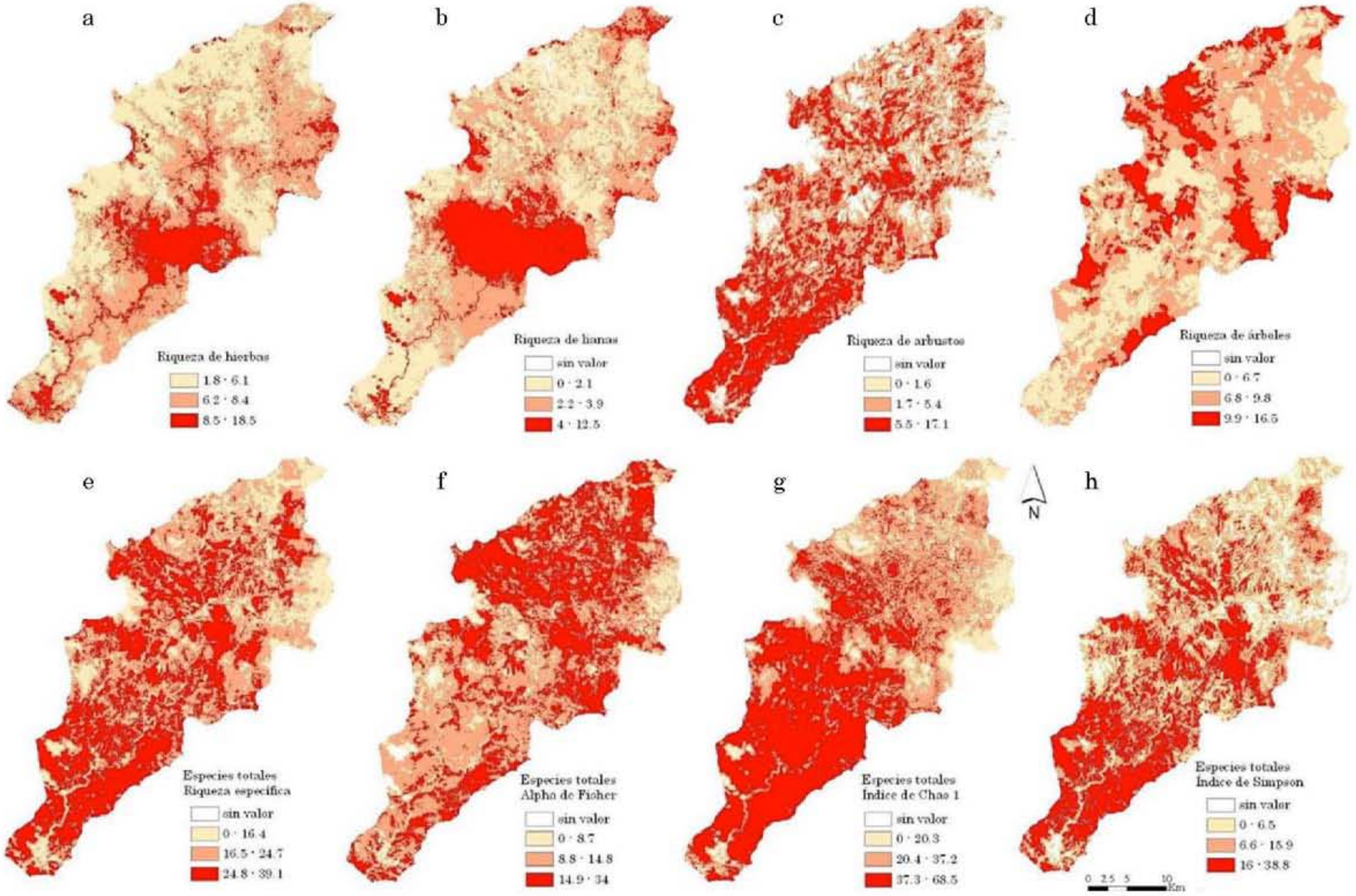

Figura 2. Mapas predictivos para la riqueza observada de cuatro formas de vida (a, b, c, d) y cuatro índices de diversidad (e, f, g, h) dentro de la Cuenca del Río Cuixmala.

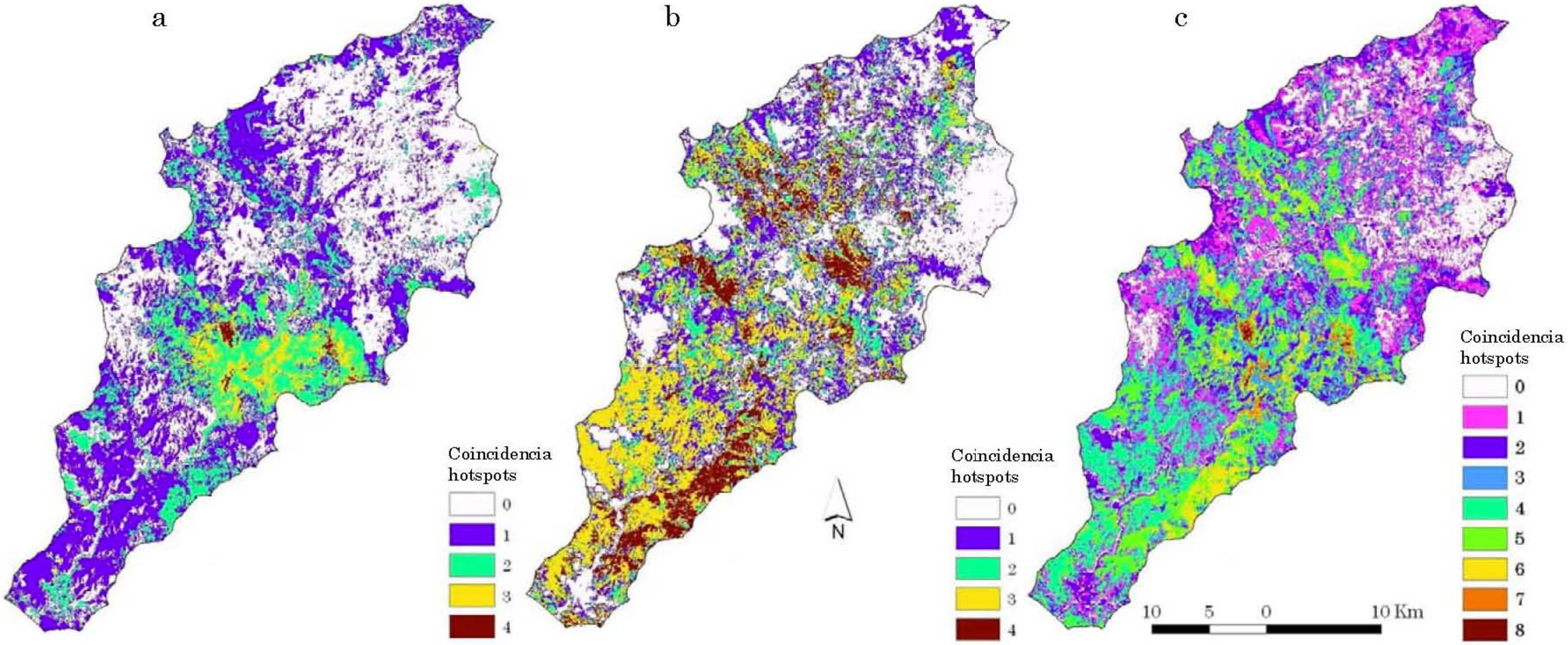

Figura 3. Mapas síntesis que muestran la coincidencia espacial de las áreas de hotspots de diversidad para las formas de vida (a), para los índices de diversidad (b) y para ambos (c) dentro de la Cuenca del Río Cuitzmala. Zonas sin hotspot indicado por cero en a, b, c; máxima coincidencia espacial de hotspots indicado por cuatro en a y b, y ocho en c.

Discusión

Variables predictivas de diversidad vegetal

Este trabajo permitió identificar las distintas variables cartográficas y de percepción remota que son las mejores indicadoras de la diversidad vegetal para este caso de estudio. Las variables relacionadas con la biomasa vegetal, derivadas de la percepción remota fueron las que mejor predijeron los patrones espaciales de la diversidad vegetal a escala regional. El índice de vegetación de diferencia normalizada (NDVI) y su variación estacional explican una elevada proporción de la varianza en la mayoría de los modelos. Considerando que el NDVI es un estimador de la cantidad de biomasa fotosintéticamente activa (González-Espinosa *et al.* 2004; Cayuela *et al.* 2006) y un estimador de productividad primaria, nuestros resultados coinciden con los trabajos que muestran relaciones positivas entre productividad y riqueza (Waide *et al.* 1999; Mittelbach *et al.* 2001); las regiones con reducida biomasa pueden reflejar zonas en donde los factores biofísicos o el manejo están reduciendo la cantidad de biomasa así como la cantidad de especies que pueden ahí coexistir. Nuestros resultados coinciden con estudios previos que han encontrado al NDVI como predictor relevante de diversidad de especies en bosques tropicales (Tuomisto *et al.* 2003; Cayuela *et al.* 2006; Hernández-Stefanoni & Dupuy 2007).

La relevancia del tipo de cobertura para la modelación de la diversidad se mostró a través de la elevada frecuencia en la que aparece en los mejores modelos y la elevada varianza que explican en la mayoría de los modelos. Llama la atención la elevada frecuencia de relaciones negativas entre la cobertura de selva baja y la diversidad vegetal, es decir, la presencia de este tipo de cobertura se traduce en una menor diversidad de especies. Esto es contrario a lo reportado por Lott & Atkinson (2002) que muestran que la gran extensión de las selva bajas de esta región (cerca del 30% en la cuenca y concentrada en la parte baja) presentan una alta diversidad y elevado índice de endemismos. Esto puede deberse a la moderada exactitud del mapa de TCUS así como a deficiencias de cobertura de la variabilidad en nuestro muestreo.

La comparación de los ocho modelos de la diversidad vegetal permitió identificar variables predictivas que permiten discernir su importancia por forma de vida e índice. Para la mayoría de las formas de vida modeladas, la distancia a los pueblos fue la variable independiente más importante, excepto para el caso de los arbustos. Las relaciones positivas de la distancia a los pueblos y la riqueza de hierbas, lianas y árboles muestra un efecto positivo de los pobladores y sus asentamientos sobre la diversidad (Luck 2007; Christensen & Heilmann-Clausen 2009). En cambio, el efecto negativo de los pueblos sobre la riqueza de arbustos indica que esta forma de vida potencialmente puede estar siendo usada por los pobladores. Para los índices de diversidad, las variables de biomasa vegetal y la escala espacial fueron las más importantes. La alta frecuencia de relaciones positivas del NDVI en un área de 500m y los índices de diversidad muestra que los cambios espaciales del paisaje circundante son importante para definir la diversidad total de las especies vegetales, relaciones espaciales poco documentadas hasta el momento (Cayuela *et al.* 2006; Levin *et al.* 2007).

Los patrones espaciales y sus implicaciones en la conservación

El análisis de los patrones espaciales de distintas formas de vida e indicadores de diversidad permite identificar áreas prioritarias para la conservación. Emergen dos patrones consistentes: (1) la baja diversidad de especies en la parte alta de la cuenca es visible en la mayoría de los mapas y (2) un cinturón de alta diversidad que va desde del extremo sureste de la parte baja hasta el extremo noreste de la parte media de la cuenca. El bajo número de especies de hierbas, lianas y árboles, baja diversidad de Chao 1 y baja dominancia de Simpson en la parte alta de la cuenca coincide con una amplia área cubierta de pastizales cultivados e inducidos para la ganadería así como una mayor frecuencia de poblaciones y extensión de carreteras. En esta zona las actividades antrópicas han contribuido a reducciones importantes en la diversidad. El hecho de que los arbustos sí presenten elevados niveles de riqueza en esta región puede responder al hecho de que estas formas de vida se desarrollan rápidamente después de los disturbios, contando en muchos casos con elevadas tasas de crecimiento (Schnitzer & Bongers 2002).

El cinturón de alta diversidad corresponde con las zonas en donde la selva baja y la selva mediana, las más diversas, están bastante bien conservadas. Los valores de alta riqueza de lianas y arbustos, así como los altos valores de los índices de riqueza específica, Chao 1 y Simpson, son medidas que no están presentes en un mapa de cobertura y que muestran los atributos de la comunidades vegetales que definen la importancia de esta zona, por ello la importancia de generar mapas individuales de las distintas facetas de la diversidad, combinarlos y sintetizarlos. Además, nuestros resultados muestran que el uso de índices que solo consideran la identidad de las especies no son suficientes para detectar las zonas de alta diversidad, es importante considerar índices que muestren los patrones de rareza y dominancia.

Importancia de los modelos y mapas para la conservación de la biodiversidad en la región

La modelación de la diversidad vegetal ha sido una estrategia útil para delimitar áreas valiosas para su conservación y dar continuidad a los esfuerzos que actualmente se realizan en áreas contiguas a la cuenca. La mayoría de los modelos de formas de vida e índices predicen varias ubicaciones de hotspots en forma esporádica en toda el área de estudio, y por lo tanto los mapas individuales de distribución de hotspots fueron marcadamente irregulares o fragmentados, y con diferencias notables en la superficie que abarcan (entre el 5 y 32%). Sin embargo, los patrones de los hotspots se vuelven muchos más claros cuando todos los mapas individuales de la diversidad se combinaron o sintetizaron. Los hotspots identificados de esta manera representan áreas potencialmente más factibles para orientar los esfuerzos de conservación (Parviainen *et al.* 2009).

La mayor concentración de hotspots dentro de la cuenca se encuentra en zonas en donde la selva baja y la selva mediana están bastante bien conservadas, bajo un ritmo lento de transformación, escasa presencia de poblaciones y carreteras. Esta zona se encuentra continúa a la Reserva de la Biosfera Chamela-Cuitzmala, por lo que el planteamiento de la conservación de esta zona daría continuidad a los beneficios ecológicos y sociales que brinda el área natural protegida. Actualmente, no existen políticas públicas en materia ambiental o de conservación aplicadas en la región (Maass *et al.* 2005; Castillo *et al.* 2009), en las cuales se puedan incorporar resultados de este tipo de trabajos.

Aspectos metodológicos que limitan el alcance de los modelos y mapas predictivos

La baja a moderada confiabilidad predictiva de la mayoría de los modelos de la diversidad vegetal puede deberse a una serie de dificultades metodológicas. Primero, los modelos podrían ser mejorados al incrementar el tamaño de los cuadros de muestreo. Field *et al.* (2009) muestran que la varianza explicada tiende a incrementar con el tamaño de los cuadros muestreados en el campo. Para nuestro trabajo, dimos prioridad a un mayor número de sitios para cubrir el gradiente ambiental y de manejo de toda la cuenca, a costa del tamaño de cuadro. Segundo, las predicciones de los modelos podrían haber sido mejoradas al usar mapas biofísicos de entrada de alta exactitud y resolución. Para este trabajo, el mapa de TCUS muestra una moderada confiabilidad (Kappa Cohen (κ) = 0.48; Fielding & Bell 1997); sin embargo, los modelos se desarrollaron en terrenos con una alta heterogeneidad espacial, donde la vegetación está distribuida en mosaicos con bruscas transiciones de un tipo de vegetación a otro. Tercero, los modelos podrían mejorar si se incorporan otras variables biofísicas relevantes para la diversidad vegetal y para ciertas formas de vida en particular. Se ha mostrado que variables indicadoras de aspectos edáficos y nutrientes, tales como la estructura y textura del suelo, medidas de niveles de nutrimentos, capacidad de retención de agua del suelo, entre otras, están altamente correlacionadas con la riqueza de especies hierbas en áreas pequeñas, pero que explican significativamente patrones espaciales en áreas mayores a 1000 km^2 (Guisan & Zimmerman 2000; Field *et al.* 2009). Sin embargo no se cuentan con mapas de esta naturaleza para la región.

Aportes a la teoría de los modelos y mapas para fomentar futuras investigaciones

Este trabajo nos permite avanzar en el modelaje de la biodiversidad con algunos aprendizajes relevantes. La primera es la importancia que tienen las variables indicadores de perturbación antrópica, que no han sido incorporados frecuentemente en estos procesos. La segunda es que las distintas formas de vida responden a distintas variables ambientales y presentan distintos patrones espaciales por lo que la incorporación de distintas formas de vida será importante para poder asegurar el mantenimiento de la biodiversidad en su conjunto. Lo mismo se puede decir para los índices de diversidad. Las diferencias en capacidad y confiabilidad predictiva de los modelos indican que una estrategia que diversifique las formas de vida e índices utilizados podrá generar mayor confiabilidad para la identificación de las zonas de mayor diversidad.

Conclusiones

En nuestro trabajo encontramos que las variables de biomasa vegetal fueron las mejores predictoras de los patrones espaciales de la diversidad vegetal dentro de la cuenca del Río Cuitzmala. También se indica la importancia de incorporar variables estimadoras del disturbio antrópico.

Los resultados muestran que distintas formas de vida responden a distintas variables biofísicas y presentan distintos patrones espaciales, generados de modelos con capacidad y confiabilidad predictiva distinta. Todo esto señala la importancia de abarcar un abanico de formas de vida y de índices de diversidad para la mejor identificación de áreas prioritarias para la conservación.

Nuestro resultados muestran una zona de baja diversidad en la parte alta de la cuenca y un cinturón de alta diversidad que va desde del extremo sureste de la parte baja hasta el extremo noreste de la parte media de la cuenca. El primer patrón corresponde con las zonas más perturbadas mientras que el segundo a las zonas mejor conservadas. La identificación de las zonas de alta diversidad fue resultado de los mapas obtenidos para las distintas formas de vida y los distintos índices de diversidad. De esta forma fue posible resumir las distintas facetas de la diversidad e identificar las zonas en donde la diversidad es consistentemente más elevada.

En el futuro será necesario desarrollar estudios dirigidos a la identificación de patrones espaciales de especies endémicas, amenazadas o con alto valor de uso o manejo por las comunidades locales, generando los criterios y medidas de conservación específicas. También será necesario consultar a los distintos actores de la región para desarrollar en conjunto estrategias adecuadas para el mantenimiento de la elevada diversidad que la cuenca alberga.

Información complementaria en Anexo 3

Tabla S1. Métodos y aspectos conceptuales de los índices de diversidad utilizados en la modelación y mapeo.
Tabla S2. Métodos para obtener las variables predictivas utilizadas en la generación de los modelos predictivos de la diversidad vegetal.
Tabla S3. Combinación de los TCUS ingresados en las regresiones múltiples para obtener los modelos predictivos de la diversidad vegetal.
Tabla S4. Lista de especies vegetales registradas en el área de estudio.

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Discusión general y conclusiones

Presentación

En este proyecto de tesis se utilizaron distintos enfoques para analizar la relación de la diversidad vegetal y la generación de servicios ecosistémicos a distintas escalas espaciales. En esta discusión general se enfatizan los resultados más sobresalientes; estos se ponen en contexto con respecto al estado del conocimiento y la teoría general sobre la relación biodiversidad y servicios para cada escala espacial, las cuales fueron revisadas en el capítulo I. Esta discusión pretende mostrar la utilidad de los enfoques y herramientas desarrolladas en este proyecto doctoral para cubrir los huecos en el conocimiento detectados durante la revisión cualitativa de la literatura.

Esta reflexión permite también identificar algunas de las preguntas más relevantes que se originan a partir de las evaluaciones que se llevaron a cabo para cada escala espacial. Se discuten las posibles implicaciones de los resultados obtenidos a la luz de la conservación de la diversidad y de los servicios, con énfasis en el efecto del manejo sobre ambos. Finalmente, se discute cómo todo lo anterior contribuye al entendimiento de los vínculos entre la diversidad vegetal, los servicios ecosistémicos, y los componentes del bienestar humano.

Contribuciones al conocimiento y preguntas relevantes que fomentan la investigación futura

Escala local

Llevé a cabo una síntesis del conocimiento sobre el efecto de la riqueza de especies sobre los servicios ecosistémicos. Al enfocarme únicamente en las plantas terrestres proporcione una propuesta explícita sobre cómo traducir los estudios de biodiversidad y funcionamiento del ecosistema en conocimiento sobre el efecto de la biodiversidad en la generación de servicios ecosistémicos.

A la fecha, el principal énfasis en la literatura ha sido sobre los vínculos entre la biodiversidad (riqueza fundamentalmente) y las funciones de los ecosistemas (Cardinale *et al.* 2006; Schmid *et al.* 2009; Cardinale *et al.* 2011). Sólo dos trabajos hicieron un vínculos hacia los servicios que son relevantes para la sociedad (Balvanera *et al.* 2006; Worm *et al.* 2006). Sin embargo, en estos trabajos la equivalencia entre funciones y servicios no es explícita y presenta limitaciones. En particular, al mezclar los efectos de distintos tipos de proveedores de servicios se confunden muchas funciones que pueden tener efectos muy distintos sobre los servicios.

La aportación de esta tesis fue hacer explícitos los vínculos entre unidades proveedoras de servicios, las funciones y los servicios, para de ahí generar una nueva síntesis más robusta. Pudimos reducir la incertidumbre en la asignación de las funciones a servicios a través de un análisis sistemático de las variables medidas en los estudios experimentales, su correspondencia con las propiedades y los ecosistemas y luego con los servicios asociados.

El uso del marco conceptual de proveedor de servicios ecosistémicos (Capítulo I) fue particularmente útil en este trabajo porque permitió entender la complejidad de las relaciones entre el nivel de organización biológica, tipos de ecosistemas, las propiedades y procesos ecosistémicos y la generación de los servicios. Las implicaciones de este esfuerzo de traducción confirmo cuantitativamente lo que previos trabajos habían sugerido, es decir, el efecto positivo de la diversidad vegetal sobre la generación de los servicios.

Dos preguntas relevantes surgen para avanzar en el conocimiento de la biodiversidad y los servicios a escala local. ¿Es posible generar un marco conceptual y metodológico para hacer la traducción explícita entre los indicadores medidos en campo y en los experimentos, las propiedades del ecosistema y los servicios para todas las distintas unidades proveedoras de servicios, los distintos niveles de organización y los distintos tipos de diversidad? Se cuenta ya con algunos ejercicios similares de traducción de las funciones a servicios para explorar los efectos de otras unidades proveedoras de servicios (grupos de microorganismos del suelo, Barrios 2007; invertebrados de aguas subterráneas, Boulton *et al.* 2008; microbios, Ducklow 2008) y para otros tipos de diversidad (diversidad funcional, de Bello *et al.* 2010). Sin embargo, estos trabajos solo se han quedado en la evaluación cualitativa del efecto. Además, varios de estos trabajos presentan dificultades en diferenciar las propiedades, de los procesos, de las funciones y de los servicios, aspectos de la traducción que aún requieren de un mayor esfuerzo (de Groot *et al.* 2010).

¿Cuál es el papel relativo que desempeña la diversidad vegetal con respecto a otros factores en la generación de los servicios, mas no en las funciones? Paquette & Messier (2011) mostraron que es posible cuantificar el efecto relativo que tienen las condiciones abióticas con respeto a la riqueza de especies y a la diversidad funcional sobre la generación de un servicio (madera) en diferentes tipos de ecosistemas a través de modelos de ecuaciones estructurales. Un meta-análisis reciente mostró que el cambio en riqueza tiene efectos sobre el funcionamiento de los ecosistemas comparables con los del cambio climático, o los niveles elevados de nitrógeno (Hooper *et al.* 2012).

Escala de paisaje

A escala de paisaje hicimos una evaluación de las opiniones de los expertos sobre la relación entre la diversidad vegetal y la generación de servicios. Este trabajo permitió generar información detallada acerca de las relaciones esperadas para una amplia gama de servicios, niveles de organización e indicadores de diversidad, así como acerca de la importancia relativa de la diversidad con respecto a otras condiciones del ecosistema.

El trabajo permitió generar nuevas hipótesis sobre la relación entre la diversidad y los servicios a escalas de paisaje que podrán ser evaluadas en el futuro. Una pregunta central gira alrededor del desarrollo de herramientas para evaluar la importancia relativa de la diversidad en la generación de los servicios, y ya no solamente la magnitud y dirección de los efectos.

Los resultados de este trabajo destacan la clara y diferencial importancia de la diversidad con respecto a las condiciones abióticas en la generación de los distintos tipos de servicios. Diverso trabajos indicaban la importancia de evaluar los factores ambientales claves que afectan la generación de servicios sobre el espacio y tiempo (Kremen 2005; Diaz *et al.* 2007). Además, la alta variabilidad de condiciones abióticas que pueden encontrarse dentro de los paisajes hace poco fiable que este tipo de variables puedan ser controladas en estudios experimentales u observacionales.

Este trabajo confirma la necesidad de incluir tanto condiciones y recursos como los atributos de la diversidad vegetal, como variables explicativas para describir que describan los patrones espaciales de generación de los servicios ecosistémicos. Este tipo de modelación ya ha sido realizado recientemente (Lavorel *et al.* 2011).

Los resultados de este trabajo también sugieren la necesidad de explorar los mecanismos y procesos fundamentales que controlan la entrega de la generación de los servicios en el paisaje. Estos mecanismos están apenas siendo explorados (Philpott *et al.* 2009; Lavorel *et al.* 2011; Lavorel & Grigulis 2012).

En este trabajo también encontramos que la relación entre diversidad vegetal y servicios cambia entre servicios. Los expertos perciben consistentemente un efecto positivo de la diversidad sobre los servicios de provisión (p.ej. producción de alimentos, madera, leña y productos diversos) y los servicios culturales (p. ej. belleza escénica, fuente de inspiración, recreación y turismo, uso tradicional. Para los servicios de regulación, los expertos perciben un efecto positivo de la diversidad sobre la fertilidad del suelo, regulación de plagas, resistencia a plantas invasoras y respuesta de los ecosistemas a eventos extremos; mientras que hay un falta de consistencia del efecto de la diversidad sobre la regulación de la disponibilidad de agua y regulación del clima y calidad del aire. Si bien aún quedan por comprobarse las percepciones de los expertos, llama la atención la diferencia entre los patrones observados a escala local, en el capítulo II, y los observados a escala de paisaje, en el capítulo III. El efecto positivo de la diversidad sobre la producción de alimentos y la regulación de especies invasoras se mantiene entre escalas. En cambio, el efecto negativo y sin efecto de la diversidad sobre la regulación de la fertilidad del suelo y la regulación de las plagas, respectivamente, cuantificado a escala local, los expertos perciben un efecto positivo de la diversidad sobre ambos servicios a escala regional.

¿Las relaciones entre la diversidad y los servicios cambian entre escalas espaciales? Y de ser así ¿a qué se pueden deber estos cambios? Los resultados de esta tesis sugieren que sí son distintos los patrones. Es posible que las diferencias se deban a sesgos en las percepciones de los expertos. Sin embargo es mucho más probable que distintos mecanismos de mantenimiento de la diversidad, de la generación de servicios ecosistémicos y efectos del manejo estén operando diferencialmente a distintas escalas.

Escala regional

A escala regional se modelaron los patrones espaciales de la diversidad en una cuenta hidrológica, para en un futuro poderlos relacionar con los patrones espaciales de los servicios ecosistémicos en la misma región (Fig. 1). Los resultados muestran que distintas formas de vida y distintos índices de diversidad responden de forma distinta a las condiciones ambientales y por lo tanto requieren de distintos estimadores para ser modelados. Esto es importante debido a que se utilizan generalmente el mismo tipo de variables para modelar la diversidad, sin enfatizar estas diferencias (Dogan & Dogan 2006; Hernández-Stefanoni & Dupuy 2007).

Los patrones espaciales de la diversidad vegetal difirieron entre las distintas formas de vida e índices. Esto significa que las prioridades de conservación cambian entre formas de vida e índices y es necesario tomar esto en cuenta para la planeación de la conservación.

Este trabajo permitirá la exploración de las relaciones espaciales de la diversidad vegetal y los servicios a escala regional. Se ha mostrado que las áreas con altos valores de biodiversidad no son necesariamente coinciden con las áreas que más generan servicios (Chan *et al.* 2006; Naidoo *et al.* 2008; Anderson *et al.* 2009). Recientemente, se ha encontrado que si el análisis espacial se enfoca en unidades proveedoras de servicios, hay una alta coincidencia de que las zonas de mayor generación de servicios, son las zonas de mayor riqueza y diversidad funcional vegetal (Egoh *et al.* 2009; Lavorel *et al.* 2011). Más relevante aún es si el análisis funcional y espacial de la diversidad y los servicios se enfoca no solo en las plantas terrestres, como unidad proveedora, sino en su forma de vida y descriptores de su diversidad.

En el futuro, será necesario poder explorar más a fondo las relaciones funcionales y espaciales de la diversidad y los servicios a escala regional. La exploración de estos ha enfatizado la congruencia espacial (Chan *et al.* 2006; Egoh *et al.* 2009), más que sus relaciones funcionales (Anderson *et al.* 2009; Lavorel *et al.* 2011).

En un futuro próximo será posible evaluar las relaciones funcionales y espaciales entre componentes específicos de la diversidad vegetal y los servicios ecosistémicos. Esto será posible debido a los modelos para los patrones espaciales de la diversidad generados en esta tesis (capítulo IV), y a aquellos generados para los servicios ecosistémicos en para la misma cuenca (Martínez-Harms 2010).

Las preguntas que surgen son ¿Las áreas más diversas son también las más críticas para la generación de servicios individuales o para la combinación de servicios? ¿Se conserva el efecto positivo de la diversidad sobre los servicios obtenido a escala local y de paisaje?

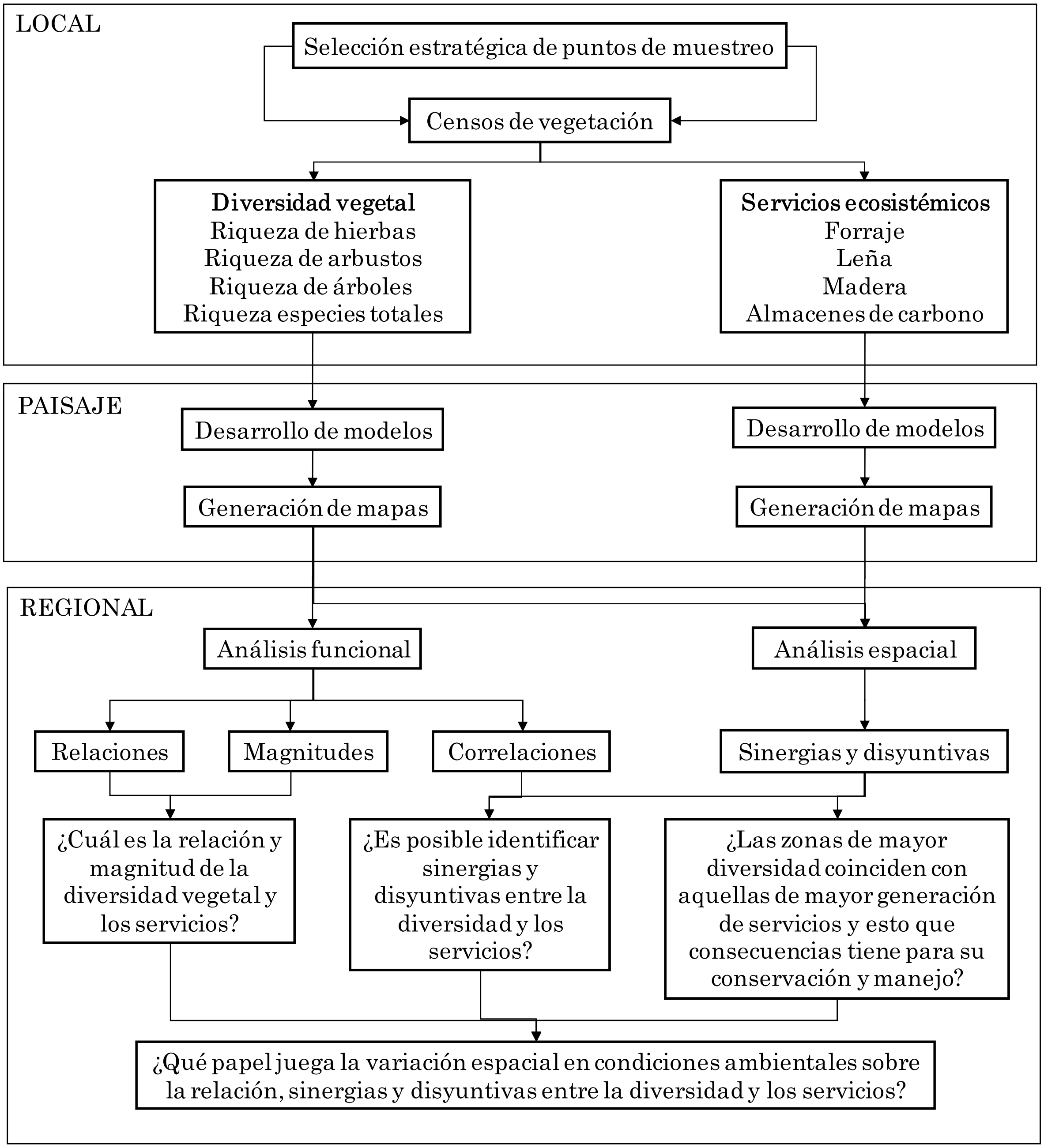

Figura 1. Sistematización de los métodos y evaluaciones a diferentes escalas espaciales para el análisis de la relación entre la diversidad vegetal y los servicios ecosistémicos.

Implicaciones para la conservación y el manejo

El papel fundamental que la diversidad vegetal juega en la generación de servicios ecosistémicos debe ser explícitamente incorporado a la planificación de la conservación de la biodiversidad y al manejo de ecosistemas para fomentar la generación de distintos servicios. A escala local, el análisis de los estudios experimentales puede tomarse como base para un principio precautorio, es decir, destinado a evitar una mayor reducción de la diversidad vegetal y evitar la reducción en la generación de servicios. A escala de paisaje, es necesario considerar diferentes enfoques de manejo para la generación sustentable de servicios, en función de la importancia relativa de la diversidad vegetal con respecto a las condiciones abióticas. A escala regional, la modelación mostró que la selección de la forma de vida e índice de diversidad pueden afectar la identificación de las áreas prioritarias de conservación, y podría también afectar la generación de servicios (Chan *et al.* 2006; Egoh *et al.* 2009; Lavorel *et al.* 2011). La evaluación funcional y espacial de la diversidad y los servicios permitirá no solo plantear estrategias adecuadas para el mantenimiento de la elevada diversidad y los servicios asociados dentro de la región de estudio, sino que permitirá avanzar en los aprendizajes de la relación.

Diversidad vegetal y servicios ecosistémicos: vinculación con el bienestar humano

El entendimiento de los vínculos entre la biodiversidad y el bienestar humano requiere vincular los servicios ecosistémicos con el componente social de los sistemas. Considerar todas las partes de los sistemas socio-ecológicos, requieren por supuesto entender la relación de la diversidad y los servicios, pero es también importante considerar el contexto social y político dentro del cual la biodiversidad está cambiando y los distintos servicios son promovidos o disminuidos (Fisher *et al.* 2009; Raudsepp-Hearne *et al.* 2010).

En el futuro, los estudios sobre la biodiversidad y los servicios tendrán que considerar los componente ecológico y social de los sistemas, la escala institucional y espacial a la cual los distintos beneficiarios perciben a los servicios (MA 2003; Hein *et al.* 2006; Fisher *et al.* 2009) y el valor que estos les da (Chan *et al.* 2011; Lamarque *et al.* 2011) por sus importantes consecuencias que estos elementos tienen en la formulación o implementación de planes de conservación y manejo.

Conclusiones

La revisión cualitativa de la literatura mostró la importancia que tiene la biodiversidad en la generación de servicios ecosistémicos; estos sin embargo son complejos, y cambian entre escalas espaciales.

El meta-análisis de estudios experimentales mostró que al enfocarse exclusivamente en la diversidad vegetal es posible identificar claramente los vínculos entre funciones y servicios ecosistémicos, y que en general hay un efecto positivo de la diversidad vegetal y los servicios a escala local; sin embargo, es necesario en el futuro cuantificar servicios y no tanto funciones.

La percepción de expertos mostró que en general existe una relación positiva entre la diversidad vegetal y los servicios ecosistémicos a escala de paisaje, pero que estas tendencias cambian entre servicios y están influenciadas por el papel que juegan las condiciones del ecosistema; este capítulo generó nuevas hipótesis que podrán ser probadas en el futuro.

La modelación de la diversidad vegetal mostró que los patrones espaciales de diversidad difirieron entre las distintas formas de vida e índices, lo que muestra que la identificación de áreas prioritarias para la conservación y en un futuro cercano la evaluación de la relación espacial y funcional entre la diversidad y los servicios deben tomar en cuenta distintas formas de vida e índices de diversidad.

Los distintos enfoques de análisis muestran la importancia de mantener la diversidad vegetal para garantizar y aumentar la generación de servicios ecosistémicos que benefician el bienestar humano.

En el futuro, será necesaria la integración de los acercamientos y resultados obtenidos a distintas escalas para así poder informar a tomadores de decisiones y diseñadores de políticas sobre los efectos de los cambios en la diversidad sobre el bienestar humano.

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Anexos

Anexo 1. Material suplementario del capítulo II

Appendix A. Supplementary data

Table 1. Number of papers and measurements in database of Schmid et al. (2009b) that were used for Balvanera et al. (2006) and this manuscript. The number of papers and measurements used for meta-analysis of this manuscript were 43% and 26% of Schmid's database, respectively, while for vote-counting these numbers were 60% and 47%, respectively.

	Schmid et al. (2009b) *Ecological Archives* E090-059-D1	Balvanera et al. (2006)	This manuscript	
			Meta-analysis	For vote counting
Papers considered	137	103	59	82
Shared* papers		56		
Records considered	761	446	197	361
Shared* records		186		

* Shared between Balvanera et al. (2006) the meta-analysis of this manuscript

Anexo 2. Material suplementario del capítulo III

Appendix S1. Glossary of terms used in this survey.

The ecosystem services
Food, fodder, fiber and biofuel intensive production: products from plants within human dominated systems (agricultural, pastoral and agro-pastoral systems).
Timber production: solid and fibrous parts of trunks in trees with a diameter at breast height ≥ 30 cm, which are used as construction material or for the manufacturing industry.
Firewood production: wild plant materials used as fuel.
Diverse products: wild plants or their parts extracted from natural to semi-natural ecosystems with present uses as non-timber forest products or future potential uses.
Regulation of soil fertility: regulation of the amount and availability of nutrients (NPK) for the establishment and growth of plants.
Regulation of plant pests: regulation of the populations of herbivores, fungal and microbial pathogens that attack plants in agricultural, pastoral or forestry systems.
Resistance to plant invasion: inhibition of the establishment, growth, survival, and reproduction of invasive species, defined as plants that are established beyond their distribution range.
Regulation of response of the ecosystem to extreme events: regulation of the impacts of an extreme event (e.g. intense rains, strong winds, drought, extremely high or low temperatures, fires and tropical cyclones) on the ecosystem and of its consequences on human settlements within the ecosystem.
Regulation of water availability: regulation of amount, quality and temporal variability of freshwater considering the complex interactions between climate, water cycle components, vegetation and soil characteristics that occur at multiple spatial and temporal scales.
Regulation of climate and air quality: the influence of functional composition of vegetation and size and spatial arrangement of landscape units over large areas, modify albedo, heat absorption, movement of air masses of different temperature and moisture at the local, regional, and global scales.
Scenic beauty: important source of aesthetic pleasure.
Source of inspiration: source of inspiration for artistic, cultural and spirituals expressions.
Recreation and tourism: place where people can rest, relax, refresh and enjoy.
Recreation and tourism: is the incorporation of places or products following in traditional rituals and customs that bond human communities.

The levels of organization of plant diversity
Genetic diversity within species: variation between individuals of the same population in their genetic (and phenotypic) characteristics.

Species diversity within a community: variation of the characteristics of the species that coexist in a same community included the variation between ecotypes and varieties of crops.
Diversity of **communities** within in the landscape: variation in characteristics of the communities (or associations of species) that are found within a same landscape unit.

The <u>components</u> of plant diversity
Number of species: amount of species within a plant community.
Evenness species: similarity in the relative contribution of the species of a community to the relative abundance, relative biomass, or relative cover within a plant community.
Species composition: specific combination of the species or presence/absence of particular species within a plant community.
Functional diversity: expressed as range of variation for different functional traits between groups of species and therefore different effects on the functioning of the ecosystem.
Spatial turnover: changes in the composition of species along space within a plant community.
Structural diversity: variation in plant height, architecture, strata (stratum) quantity, location and position of plants or their parts within a plant community.

The <u>resources and conditions</u>
Water availability: total amount of available water for plants for a given area as rain, snow, hail, fog or dew within a given period time.
Energy availability: total amount of energy used for plants in metabolic activities associated with photosynthesis.
Nutrient availability: amount and availability of inorganic nutrients (NPK), necessary for plant growth.
Soil type: physical and structural characteristics of soil that determine its capacity to support plant development.
Position within the landscape: localization occupied by vegetation unit in the relief (e.g. ridge, slope, piedmont).
Disturbance intensity: intensity (measurement of impact), frequency (number of times it happens for a given time), magnitude (affected area) and duration (time of permanence) of the disturbance.

Appendix S2. Phases of building the survey assessment.

A first version of the survey considered 15 ecosystem services, five levels of organization and six components of plant diversity, and six resources/conditions. This first version was applied to 15 graduate students. As a result of this pilot we reduced the amount of services to reduce fatigue effects during interviews, and deleted aspects that were not relevant at the landscape scale (e.g. biome level of organization). A second version of the survey considered 11 services, five levels of organization and six components of plant diversity, and six resources/conditions.

The second version was applied to 10 researchers at the National University of Mexico. Their suggestions to improve the final version of the survey included further explaining the concepts used in each of the steps of the survey, providing more detailed instructions for completing the tables, and including only resources and conditions with potential importance for generation of services at the landscape scale (e.g. evapotranspiration and temperature are probably not so relevant at the landscape scale).

Appendix S3. Background experts that answered the survey on the relationship between plant diversity and ecosystem services.

Table S1. Categories of background experts. With the exception of years of working with plant diversity or ecosystem processes/services, experts could indicate more than one area of study, type of work and organization, and focus ecosystem in which they work.

Background category	Background subcategory	Percentage of expert who belong to the subcategory
Subject to expertise	Plant diversity	21%
	Population ecology	4%
	Community ecology	49%
	Ecosystem ecology	33%
	Management	23%
	Landscape	8%
	Others	15%
Type of work	Basic research	46%
	Applied research	50%
	Decision maker	4%
Type of organization	Institute	93%
	Environmental NGOs	3%
	Governmental agencies	5%
	Other	1%
Years working with plant diversity or ecosystem processes/services	1-10	33%
	11-20	34%
	21-30	23%
	>31	11%
Focus ecosystem	Tropical rain forest	30%
	Temperate forest	20%
	Tropical dry forest	15%
	Grassland	15%
	Agroecosystem	15%
	Desert	14%
	Savanna	8%
	Shrubland	5%
	Coastal	4%
	Wetland	4%
	Succesional forest	4%
	Cloud forest	3%
	Alpine	1%
	Others	5%

Appendix S4. Direction of effect and relative importance of levels of organization, components of plant diversity, abiotic resources and conditions.

We registered the frequencies of the different types of responses and then addressed the following question: How do type of service, type of plant diversity attribute, type of abiotic resources and conditions and interactions among these factors explain differences in how frequently experts chose different types of effects and what relative importance they assigned to plant diversity for the generation of services?

We evaluated the significant differences in the frequencies for direction of effects and relative importance of plant diversity, and abiotic resources and conditions on the generation of services with generalized linear models. Significant effects of type of services (e.g. services × direction of effect), of type of plant diversity attribute (e.g. level or organization × direction of effect), of the type of resources and conditions (e.g. resources/conditions × relative importance) and interactions among these factors (e.g. services × level of organization × direction of effect), on the frequencies of the different types of effect or relative importance were identified. All generalized linear models assumed a Poisson distribution and a log link function within S-Plus (Crawley, 2002).

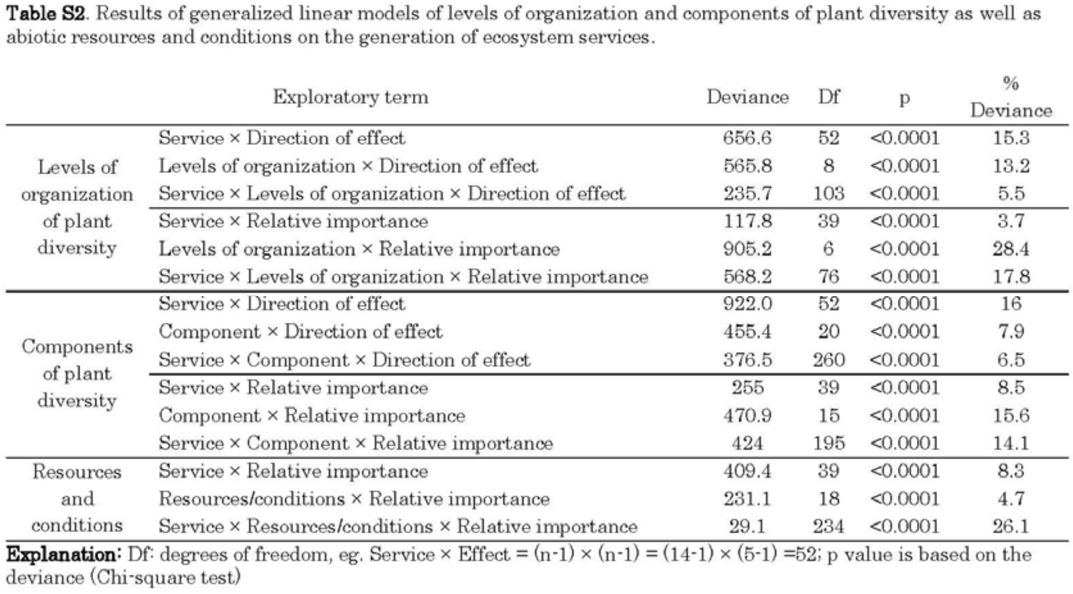

Table S2. Results of generalized linear models of levels of organization and components of plant diversity as well as abiotic resources and conditions on the generation of ecosystem services.

	Exploratory term	Deviance	Df	p	% Deviance
Levels of organization of plant diversity	Service × Direction of effect	656.6	52	<0.0001	15.3
	Levels of organization × Direction of effect	565.8	8	<0.0001	13.2
	Service × Levels of organization × Direction of effect	235.7	103	<0.0001	5.5
	Service × Relative importance	117.8	39	<0.0001	3.7
	Levels of organization × Relative importance	905.2	6	<0.0001	28.4
	Service × Levels of organization × Relative importance	568.2	76	<0.0001	17.8
Components of plant diversity	Service × Direction of effect	922.0	52	<0.0001	16
	Component × Direction of effect	455.4	20	<0.0001	7.9
	Service × Component × Direction of effect	376.5	260	<0.0001	6.5
	Service × Relative importance	255	39	<0.0001	8.5
	Component × Relative importance	470.9	15	<0.0001	15.6
	Service × Component × Relative importance	424	195	<0.0001	14.1
Resources and conditions	Service × Relative importance	409.4	39	<0.0001	8.3
	Resources/conditions × Relative importance	231.1	18	<0.0001	4.7
	Service × Resources/conditions × Relative importance	29.1	234	<0.0001	26.1

Explanation: Df: degrees of freedom, eg. Service × Effect = (n-1) × (n-1) = (14-1) × (5-1) =52; p value is based on the deviance (Chi-square test)

The results showed significant differences in expert assessments were consistently found in the generalized linear model for direction of effect and relative importance of plant diversity, as well as abiotic factors on the generation of services (Table S2). Experts recognized that the direction of effect and relative importance of plant diversity on the generation of services varied among services, between levels of organization and components, and among combinations of particular services and particular plant diversity attributes. Similarly, variation in the frequencies of the relative importance of different abiotic resources and conditions were found among services, among resources/conditions and among combinations of resources/conditions and services.

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Appendix S5. Biases associated with background experts that were found on the frequencies for direction of effects and relative importance of plant diversity on service generation.

Table S3. Biases given by expert´s background. The columns identify the background of experts while rows identify the different sections of the questionnaire. The degree of significance of a χ^2 test to explore for independence of answers with respect to expert characteristics (e.g. five types of relations vs. type of ecosystem).In bold the responses that were significantly more frequent than those expected by null model indicating both the category of expert and the response they prefer; in italic the responses that were significantly less frequent.

Exploratory term in the survey	Background category
Direction of effect of levels of organization of plant diversity	χ^2 = 54.6, P<0.05, df= 12; environmental NGOs **(0)**
	χ^2 = 44.8, P<0.05, df= 12; < 10 years expertise *(1)*
	χ^2 = 205.5, P<0.05, df= 52; agroecosystem **(?)**; wetland **(-)**
Relative importance of levels of organization of plant diversity	χ^2 = 44.8, P<0.05, df= 12; 21 to 30 years expertise **(2)**
	χ^2 = 104.5, P<0.05, df= 39; agroecosystem **(?)**; successional forest **(2)**
Direction of effect of components of plant diversity	χ^2 = 346.9, P<0.05, df= 24; plant diversity **(+)**, *(1), (?)*; population ecology **(?)**; community ecology *(0)*, **(+)**; management **(–)**, *(1)*, **(?)**
	χ^2 = 203.3, P<0.05, df= 12; institute *(0)*; environmental NGOs **(0)**, *(–)*; governmental **(0)**, *(?)*
	χ^2 = 87.8, P<0.05, df= 12; <10 years expertise **(0)**; 11 to 20 years expertise *(0)*; 21 to 30 years expertise **(1)**; > 31 years expertise *(1)*
	χ^2 = 516.6, P<0.05, df= 52; temperate forest *(?)*; tropical dry forest *(?)*; agroecosystem *(+)*, **(?)**; desert *(?)*; savanna **(?)**; coastal vegetation *(0)*, **(+)**, **(?)**; wetland **(-)**; successional forest *(0)*, **(?)**; cloud forest **(?)**
Relative importance of components of plant diversity	χ^2 = 120.3, P<0.05, df= 18; population ecology **(?)**
	χ^2 = 103.8, P<0.05, df= 39; agroecosystem **(?)**
Relative importance of plant diversity with respect to that of resources and conditions	χ^2 = 72.2, P<0.05, df= 39; agroecosystem **(?)**

Symbols and numbers: Effects: (–) the more diversity the less service; (1) there is a diversity effect on the service, but it is not possible to determine its direction or the direction is unknown; (+) the more diversity the more service; (0) no influence of diversity on the generation of the services; (?) unknown whether there is an influence of plant diversity for the generation of services. Relative importance: (1) little importance; (2) intermediate importance; (3) very important; (?) unknown importance.

Appendix S6. Publications found in a search of the ISI Web of Knowledge about relationship between plant diversity and ecosystem services

Table S4.1. Publications found in a search of ISI Web of Science and Biological Abstracts for October 2010 for each component of the survey. A search of the ISI Web of Knowledge (http://www.isiknowledge.com) for papers using the specific search terms (in italic) for each component of the survey as a topic yielded a total number of publications (number in this column) in the last 20 years. These articles are not exhaustive of what has been published but they do allow us to assess the relative amount of research on the different topics. We excluded all articles which did not study ecosystem services. The relevant publications considered only studies which solely provide conceptual work or qualitative assessment about relationship, or any case study in a specified area. Some articles appeared in several categories.

Component survey		Search terms	Total number of publications	Number of publications relevant to this survey
Levels of organization of plant diversity	Genetic	*genetic diversity* and *plant* and *ecosystem services* and *landscape*	3	2
	Species	*species diversity* and *plant* and *ecosystem services* and *landscape*	44	6
	Community	*community diversity* and *plant* and *ecosystem services* and *landscape*	28	2
Components of plant diversity	Number of species	*species number* or *species richness* and *plant* and *ecosystem services* and *landscape*	32	1
	Evenness between species	*evenness* or *dominance index* or *Simpson index* and *plant* and *ecosystem services* and *landscape*	2	1
	Composition	*composition* and *plant* and *ecosystem services* and *landscape*	22	2
	Range of functional traits	*functional traits* or *functional diversity* or *functional types* or *functional group* and *plant* and *ecosystem services* and *landscape*	16	4
	Spatial turnover	*spatial turnover* or *beta diversity* and *plant* and *ecosystem services* and *landscape*	3	1
	Structural diversity	*structural diversity* and *plant* and *ecosystem services* and *landscape*	6	1
Resources and conditions	Water availability	*water* and *diversity* and *plant* and *ecosystem services* and *landscape*	7	1
	Energy availability	*energy* and *diversity* and *plant* and *ecosystem services* and *landscape*	6	0
	Nutrient availability	*nutrient* and *diversity* and *plant* and *ecosystem services* and *landscape*	2	0
	Soil type	*soil type* and *diversity* and *plant* and *ecosystem services* and *landscape*	1	0
	Position in the landscape	*relief position* or *ridge* or *slope* or *piedmont* and *diversity* and *plant* and *ecosystem services* and *landscape*	0	0
	Disturbance intensity	*disturbance* and *diversity* and *plant* and *ecosystem services* and *landscape*	14	2
Ecosystem services	Food/fodder/fiber/biofuel intensive production	*diversity* and *plant* and *food* or *fodder* or *fiber* or *biofuel* and *landscape*	110	3
	Timber production	*diversity* and *plant* and *timber* and *landscape*	33	1
	Firewood production	*diversity* and *plant* and *fuel* and *landscape*	13	0
	Diverse products	*diversity* and *plant* and *non-timber forest products* and *landscape*	0	0
	Soil fertility	*diversity* and *plant* and *soil fertility* and *landscape*	38	1
	Plant pests	*diversity* and *plant* and *herbivores* or *fungal* or *microbial pathogen* or *pest* and *landscape*	144	10
	Resistance to plant invasion	*diversity* and *plant* and *invasive species* and *landscape*	101	15
	Response of the ecosystem to extreme events	*diversity* and *plant* and *extreme events* or *hurricane* or *flood* or *fire* or *avalanche* or *natural hazard* or *tropical cyclone* and *landscape*	196	5
	Water availability	*diversity* and *plant* and *water amount* or *water quality* or *water temporality* and *landscape*	51	3
	Climate regulation and air quality	*diversity* and *plant* and *climate regulation* or *air quality* and *landscape*	7	0
	Scenic beauty	*diversity* and *plant* and *scenic beauty* and *landscape*	4	2
	Source of inspiration	*diversity* and *plant* and *inspiration* and *landscape*	0	0
	Recreation and tourism	*diversity* and *plant* and *recreation* or *tourism* and *landscape*	29	3
	Traditional use	*diversity* and *plant* and *traditional use* or *ritual* or *customs* and *landscape*	48	3

Table S4.2. Publications found in a search of ISI Web of Science and Biological Abstracts for October 2010 for plant diversity and resources and conditions for each ecosystem services. Details as Table S4.1.

Type	Ecosystem services	Search terms	Total number of publications	Number of publications relevant to this survey
Provisioning	Food/fodder/fiber/ biofuel intensive production	*diversity* and *plant* and *food* or *fodder* or *fiber* or *biofuel* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	36	0
	Timber production	*diversity* and *plant* and *timber* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	15	0
	Firewood production	*diversity* and *plant* and *fuel* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	3	0
	Diverse products	*diversity* and *plant* and *non-timber forest products* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	0	0
Regulating	Soil fertility	*diversity* and *plant* and *soil fertility* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	30	1
	Plant pests	*diversity* and *plant* and *herbivores* or *fungal* or *microbial pathogen* or *pest* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	48	1
	Resistance to plant invasion	*diversity* and *plant* and *invasive species* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	47	5
	Response of the ecosystem to extreme events	*diversity* and *plant* and *extreme events* or *hurricane* or *flood* or *fire* or *avalanche* or *natural hazard* or *tropical cyclone* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	119	3
	Water availability	*diversity* and *plant* and *water amount* or *water quality* or *water temporality* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	52	4
	Climate regulation and air quality	*diversity* and *plant* and *climate regulation* or *air quality* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	5	1
Cultural	Scenic beauty	*diversity* and *plant* and *scenic beauty* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	1	0
	Source of inspiration	*diversity* and *plant* and *inspiration* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	0	0
	Recreation and tourism	*diversity* and *plant* and *recreation* or *tourism* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	12	1
	Traditional use	*diversity* and *plant* and *traditional use* or *ritual* or *customs* and *landscape* and *water* or *energy* or *nutrient* or *soil type* or *relief position* or *ridge* or *slope* or *piedmont* or *disturbance*	22	5

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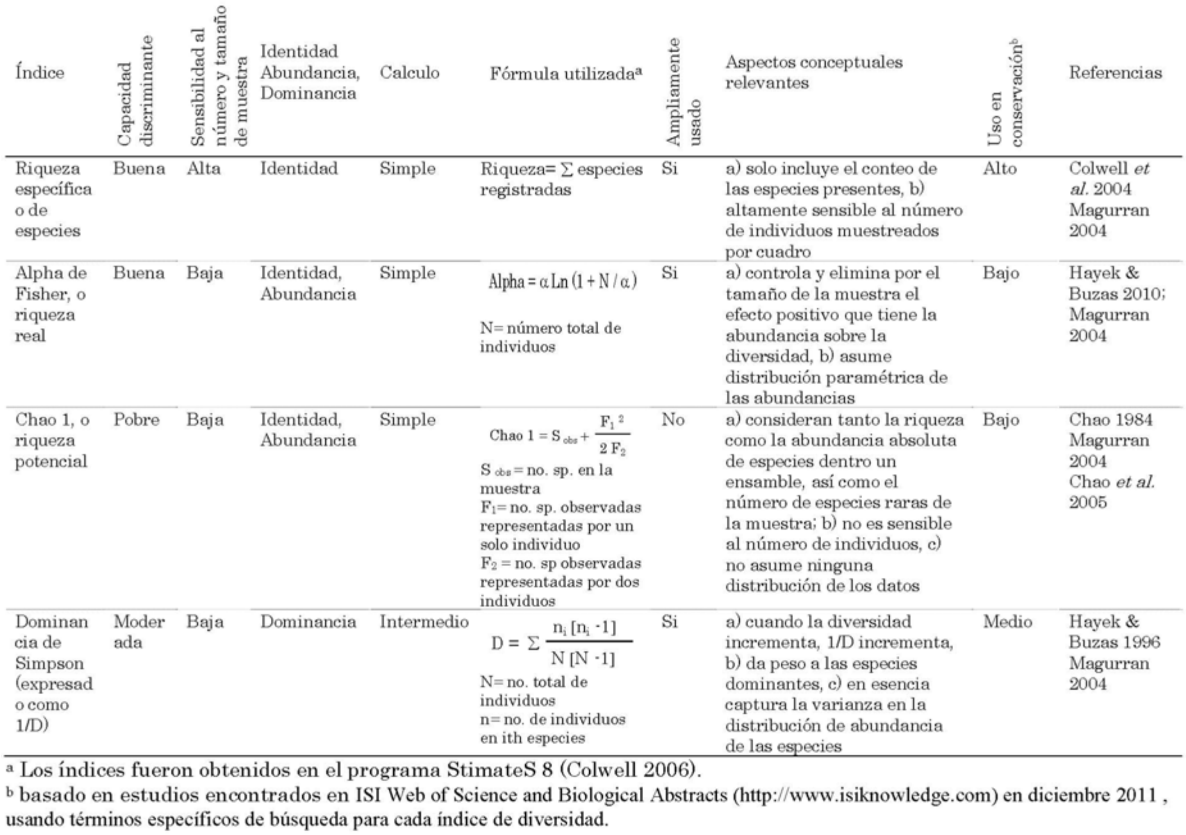
Anexo 3. Material suplementario del capítulo IV

Tabla S1. Métodos y aspectos conceptuales de los índices de diversidad utilizados en la modelación y mapeo.



Índice	Capacidad discriminante	Sensibilidad al número y tamaño de muestra	Identidad Abundancia, Dominancia	Calculo	Fórmula utilizada[a]	Ampliamente usado	Aspectos conceptuales relevantes	Uso en conservación[b]	Referencias
Riqueza específica o de especies	Buena	Alta	Identidad	Simple	Riqueza= $\sum$ especies registradas	Si	a) solo incluye el conteo de las especies presentes, b) altamente sensible al número de individuos muestreados por cuadro	Alto	Colwell *et al.* 2004 Magurran 2004
Alpha de Fisher, o riqueza real	Buena	Baja	Identidad, Abundancia	Simple	$\text{Alpha} = \alpha \operatorname{Ln}(1 + N/\alpha)$ N= número total de individuos	Si	a) controla y elimina por el tamaño de la muestra el efecto positivo que tiene la abundancia sobre la diversidad, b) asume distribución paramétrica de las abundancias	Bajo	Hayek & Buzas 2010; Magurran 2004
Chao 1, o riqueza potencial	Pobre	Baja	Identidad, Abundancia	Simple	$\text{Chao 1} = S_{obs} + \frac{F_1^{\,2}}{2F_2}$ S_{obs}= no. sp. en la muestra F_1= no. sp. observadas representadas por un solo individuo F_2 = no. sp observadas representadas por dos individuos	No	a) consideran tanto la riqueza como la abundancia absoluta de especies dentro un ensamble, así como el número de especies raras de la muestra; b) no es sensible al número de individuos, c) no asume ninguna distribución de los datos	Bajo	Chao 1984 Magurran 2004 Chao *et al.* 2005
Dominancia de Simpson (expresado como 1/D)	Moderada	Baja	Dominancia	Intermedio	$D = \Sigma \frac{n_i\,[n_i - 1]}{N\,[N - 1]}$ N= no. total de individuos n= no. de individuos en ith especies	Si	a) cuando la diversidad incrementa, 1/D incrementa, b) da peso a las especies dominantes, c) en esencia captura la varianza en la distribución de abundancia de las especies	Medio	Hayek & Buzas 1996 Magurran 2004

[a] Los índices fueron obtenidos en el programa StimateS 8 (Colwell 2006).

[b] basado en estudios encontrados en ISI Web of Science and Biological Abstracts (http://www.isiknowledge.com) en diciembre 2011 , usando términos específicos de búsqueda para cada índice de diversidad.

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Tabla S2. Métodos para obtener las variables predictivas utilizadas en la generación de los modelos de la diversidad vegetal en la Cuenca del Río Cuitzmala.[a] Todas las variables explicativas fueron homogenizadas a tamaño de gradilla de 900 m^2. [b] El procesamiento y análisis de la cartografía digital y las imágenes de percepción remota fueron realizados en ArcGIS/Arcinfo 9.2 (ESRI 2006). Las imagenes SPOT para la época seca y de lluvias fueron de mayo y septiembre del 2007, respectivamente.

n	Código en modelos predictivos	Desarrollo metodológico [a,b]	Derivación (resolución)
Topográficas			
1	Radiación	Se derivaron del modelo digital de elevación de terreno (MDE)	MDE (10x10m)
2	Exposición		
3	Pendiente		
4	Altitud		
Perturbación antropogénica			
5	Dist. Euc. Carretera	Se derivo de la distancia lineal de los sitios de muestreo a la carretera	MDE (10x10m)
6	Dist. Carretera	Se derivo de la distancia con pendiente del terreno de los sitios de muestreo a la carretera	
7	Dist. Pueblos	Se derivo de la distancia con pendiente del terreno de los sitios de muestreo al pueblo más cercano	
8	Dist. Pueblos +300 hab.	Se derivo de la distancia con pendiente del terreno de los sitios de muestreo al pueblo más cercano y con más de 300 habitantes	
Hidrológicas			
9	Dist. Cauces	Se derivo de la distancia con pendiente del terreno de los sitios de muestreo al cauce más cercano	
10	Dist. Cauce Principal	Se derivo de la distancia con pendiente del terreno de los sitios de muestreo al cauce del río Cuixmala	
11	TRMI	Se calculo a partir de cuatro elementos derivados del DEM: la posición topográfica, la exposición, la forma y ángulo de la pendiente	
12	TRMIm	Se recalculo el valor de TRMI, al incorporar ajustes en la exposición, ángulo de la pendiente y posición del relieve	
Biomasa vegetal			
13	NDVI$_{\text{lluvias}}$ 50m	Se cálculo el NDVII utilizando las bandas visibles (rojas) y las bandas del infrarrojo cercano de la imagen satelital. Se cálculo el NDII utilizando las bandas del infrarrojo cercano y el infrarrojo medio de la imagen satelital. La obtención del círculo de 50 m, donas de 250m y 500 m se detalla en las variables de porcentaje de cobertura del dosel.	Imagen SPOT (20x20m)
14	NDVI$_{\text{lluvias}}$ 250m		
15	NDVI$_{\text{lluvias}}$ 500m		
16	NDII$_{\text{lluvias}}$ 50m		
17	NDII$_{\text{lluvias}}$ 250m		
18	NDII$_{\text{lluvias}}$ 500m		
19	NDVI$_{\text{secas}}$ 50m		Imagen SPOT (5x5m)
20	NDVI$_{\text{secas}}$ 250m		
21	NDVI$_{\text{secas}}$ 500m		
22	NDII$_{\text{secas}}$ 50m		
23	NDII$_{\text{secas}}$ 250m		
24	NDII$_{\text{secas}}$ 500m		
25	% dosel 50m	En torno al punto central de los sitios de muestreo, se generaron buffers circulares de 50, 250 y 500 m^2 de perímetro. Al buffer circular de 250m^2 se le resto el buffer de 50m^2 y al de 500m^2 se le resto el de 250m^2. El resultado fue la obtención de un círculo de 50 m, donas de 250m y 500 m.	Imagen SPOT (5x5m)
26	% dosel 250m		
27	% dosel 500m		
28	BE	Se obtuvo un mapa de mapa de tipos de cobertura y uso de suelo a partir de la clasificación visual y supervisada de la imagen SPOT de la época de secas, con 2 verificaciones de campo.	Imagen SPOT (5x5m)
29	P		
30	SB		
31	SM		

Tabla S3. Combinaciones de los tipos de coberturas y usos del suelo (TCUS) ingresadas en las regresiones múltiples para obtener los modelos predictivos de la diversidad vegetal. No= número de combinación; P= pastizal, BE= Bosque de encino, SB= selva baja, SM= selva mediana.

No	TCUS no ingresada al modelo	TCUS ingresada al modelo	Supuesto de la combinación
1	P,BE,SM,SB		La cobertura vegetal no es importante para predecir la diversidad
2	BE,SM,SB	P	Solo la cobertura de P es importante para predecir la diversidad
3	P,SM,SB	BE	Solo la cobertura de BE es importante para predecir la diversidad
4	P,BE,SB	SM	Solo la cobertura de SM es importante para predecir la diversidad
5	P,BE,SM	SB	Solo la cobertura de SB es importante para predecir la diversidad
6	P	SM,SB,BE	La cobertura de SM, SB y BE son importantes para predecir la diversidad
7	SM	P,SB,BE	La cobertura de P, SB y BE son importantes para predecir la diversidad
8	SB	P,SM,BE	La cobertura de P, SM y BE son importantes para predecir la diversidad
9	BE	P,SM,SB	La cobertura de P, SM y SB son importantes para predecir la diversidad
10		P,BE,SM,SB	La cobertura por separado de P, BE, SB y SM son importantes predictores de la diversidad
11	P,SM	BE+SB	La cobertura conjunta de BE y SB son mejores predictores de la diversidad, más que el BE separado de la SB
12	P,SB	BE+SM	La cobertura conjunta de BE y SM son mejores predictores de la diversidad, más que el BE separado de la SM
13	P,BE	SB+SM	La cobertura conjunta de SB y SM son mejores predictores de la diversidad, más que la SB separado de la SM
14	SM,SB	P+BE	La cobertura conjunta de P y BE son mejores predictores de la diversidad, más que el P separado del BE
15	SM,BE	P+SB	La cobertura conjunta de P y SB son mejores predictores de la diversidad, más que el P separado de la SB
16	SB,BE	P+SM	La cobertura conjunta de P y SM son mejores predictores de la diversidad, más que el P separado de la SM
17		P+BE+SM+SB	La cobertura en conjunto de P, BE, SB y SM son mejores predictores de la diversidad, más que cada tipo de cobertura por separado

Tabla S4. Lista de especies vegetales registradas en el área de estudio. Los ejemplares fueron cotejados en el herbario de la Estación de Biología de Chamela, UNAM y el herbario del Centro Universitario de la Costa Sur, UdeG.

Hierbas

Especie	Familia
Acalypha	Euphorbiaceae
Acalypha alopecuroidea	Euphorbiaceae
Acalypha microphylla	Euphorbiaceae
Acalypha ostryifolia	Euphorbiaceae
Acalypha vagans	Euphorbiaceae
Adiantum amplum	Adiantaceae
Adiantum lunulatum	Adiantaceae
Adiantum patens	Adiantaceae
Adiantum poiretii	Adiantaceae
Adiantum princeps	Adiantaceae
Aeschynomene	Fabaceae
Ageratum corymbosum	Asteraceae
Amaranthus	Amaranthaceae
Andropogon gayamus	Poaceae
Anemia jaliscana	Schizaceae
Anoda	Malvaceae
Aristida	Poaceae
Axonopus compressus	Poaceae
Ayenia	Sterculiaceae
Ayenia filiformis	Sterculiaceae
Baltimora geminata	Asteraceae
Bidens	Asteraceae
Calathea soconuscum	Maranthaceae
Canavalia	Fabaceae
Carminatia recondita	Asteraceae
Chamaecrista nictitans	Caesalpinaceae
Chamaecrista punctulata	Caesalpinaceae
Chamaesyce	Euphorbiaceae
Chamaesyce hyssopifolia	Euphorbiaceae
Coccocypselum hirsutum	Rubiaceae
Commelina	Commelinaceae
Commelina coelestis	Commelinaceae
Commelina erecta	Commelinaceae
Commelina leiocarpa	Commelinaceae
Commelina rufipes	Commelinaceae
Corchorus	Tiliaceae
Cracca	Fabaceae
Crotalaria incana	Fabaceae
Cuphea leptopoda	Lythraceae
Cynanchum	Asclepiadaceae
Cyperus hermaphroditus	Cyperaceae
Delilia	Asteraceae
Iresine	Amaranthaceae
Iresine diffusa	Amaranthaceae
Jarilla heterophylla	Caricaceae
Lagascea	Asteraceae
Lagrezia	Amaranthaceae
Lasiacis divaricata	Poaceae
Lasiacis oaxacensis	Poaceae
Lasiacis procerrima	Poaceae
Lasiacis ruscifolia	Poaceae
Lithachne pauciflora	Poaceae
Mandevilla subsagittata	Asclepiadaceae
Maranta arundinacea	Maranthaceae
Melampodium	Asteraceae
Melampodium divaricatum	Asteraceae
Melampodium gracile	Asteraceae
Milleria quinqueflora	Asteraceae
Mimosa affinis	Mimosaceae
Monniera trifolia	Rutaceae
Muhlenbergia speciosa	Poaceae
Olyra latifolia	Poaceae
Oplismenus	Poaceae
Oplismenus burmannii	Poaceae
Panicum hirticaule	Poaceae
Panicum maximun	Poaceae
Paspalum	Poaceae
Paspalum denticulatum	Poaceae
Paspalum paniculatum	Poaceae
Perymenium	Asteraceae
Perymenium buphthalmoides	Asteraceae
Pisoniella arborescens	Nyctaginaceae
Polyanthes geminiflora	Liliaceae
Priva	Verbenaceae
Pseuderanthemum alatum	Acanthaceae
Ruellia	Acanthaceae
Russelia	Scrophulariaceae
Salvia	Lamiaceae
Schrankia distachya	Mimosaceae
Senecio	Asteraceae
Senna	Caesalpinaceae
Senna obtusifolia	Caesalpinaceae
Sida acuta	Malvaceae
Sida glabra	Malvaceae

Desmodium	Fabaceae	*Sida linifolia*	Malvaceae
Desmodium angustifolium	Fabaceae	*Solanum*	Solanaceae
Desmodium aparines	Fabaceae	*Spermacoce*	Rubiaceae
Desmodium barbatum	Fabaceae	*Spermacoce confusa*	Rubiaceae
Desmodium glabrum	Fabaceae	*Spermacoce verticillata*	Rubiaceae
Desmodium intortum	Fabaceae	*Stevia latifolia*	Asteraceae
Dicliptera	Acanthaceae	*Stylosanthes*	Fabaceae
Dicliptera resupinata	Acanthaceae	*Stylosanthes guianensis*	Fabaceae
Dicliptera thaspinoides	Acanthaceae	*Tagetes lunulata*	Asteraceae
Digitaria horizontalis	Poaceae	*Talinum paniculatum*	Portulacaceae
Dorstenia	Moraceae	*Talinum triangulare*	Portulacaceae
Dorstenia drakena	Moraceae	*Tephrosia*	Fabaceae
Elytraria imbricata	Acanthaceae	*Tephrosia diversifolia*	Fabaceae
Eriosema diffusum	Fabaceae	*Tetramerium*	Acanthaceae
Eriosema pulchellum	Fabaceae	*Tinantia erecta*	Commelinaceae
Eupatorium	Asteraceae	*Tinantia glabra*	Commelinaceae
Eupatorium geminatum	Asteraceae	*Trixis*	Asteraceae
Eupatorium quadrangulare	Asteraceae	*Urochloa fasciculata*	Poaceae
Eupatorium sagittatum	Asteraceae	*Valeriana palmeri*	Valerianaceae
Euphorbia	Euphorbiaceae	*Valeriana urticifolia*	Valerianaceae
Euphorbia francoana	Euphorbiaceae	*Verbena*	Verbenaceae
Euphorbia graminea	Euphorbiaceae	*Verbesina montanoifolia*	Asteraceae
Florestina pedata	Asteraceae	*Xanthosoma*	Araceae
Gesner	Scrophulariaceae	*Zinnia flavicoma*	Asteraceae
Henrya insularis	Acanthaceae	*Zornia diphylla*	Fabaceae
Hyptis suaveolens	Lamiaceae		

Lianas

Especie	Familia	Especie	Familia
Adenocalymma inundatum	Bignoniaceae	*Ipomoea nil*	Convolvulaceae
Amphilophium paniculatum	Bignoniaceae	*Ipomoea triloba*	Convolvulaceae
Antigonon flavescens	Polygonaceae	*Iresine interrupta*	Amaranthaceae
Aristolochia foetida	Aristolochiaceae	*Liabum caducifolium*	Asteraceae
Aristolochia taliscana	Aristolochiaceae	*Liabum simile*	Asteraceae
Arrabidaea patellifera	Bignoniaceae	*Mandevilla andrieuxii*	Asclepiadaceae
Arrabidaea viscida	Bignoniaceae	*Marsdenia*	Asclepiadaceae
Byttneria aculeata	Sterculiaceae	*Marsdenia astephanoides*	Asclepiadaceae
Byttneria catalpifolia	Sterculiaceae	*Matelea*	Asclepiadaceae
Calopogonium caeruleum	Fabaceae	*Matelea chrysantha*	Asclepiadaceae
Calopogonium mucunoides	Fabaceae	*Matelea pavonni*	Asclepiadaceae
Canavalia acuminata	Fabaceae	*Melloa quadrivalvis*	Bignoniaceae
Canavalia villosa	Fabaceae	*Melothria pendula*	Cucurbitaceae
Cardiospermum halicacabum	Sapindaceae	*Nissolia*	Fabaceae
Centrosema sagittatum	Fabaceae	*Nissolia fruticosa*	Fabaceae
Cissampelos pareira	Menispermaceae	*Nissolia fruticosa*	Fabaceae

Cissus sicyoides	Vitaceae
Clitoria	Fabaceae
Clytostoma	Bignoniaceae
Clytostoma binatum	Bignoniaceae
Cologania	Fabaceae
Cologania procumbens	Fabaceae
Combretum	Combretaceae
Combretum fruticosum	Combretaceae
Cucurbita moschata	Cucurbitaceae
Cyclanthera tamnoides	Cucurbitaceae
Dioscorea	Dioscoreaceae
Dioscorea chamela	Dioscoreaceae
Dioscorea convolvulacea	Dioscoreaceae
Dioscorea jaliscana	Dioscoreaceae
Dioscorea plumifera	Dioscoreaceae
Doyerea emetocathartica	Cucurbitaceae
Echinopepon racemosus	Cucurbitaceae
Entada polystachya	Mimosaceae
Forsteronia spicata	Apocynaceae
Galactia	Fabaceae
Gaudichaudia mcvaughii	Malpighiaceae
Gouania rosei	Rhamnaceae
Gouania stipularis	Rhamnaceae
Heteropterys laurifolia	Malpighiaceae
Heteropterys palmeri	Malpighiaceae
Hippocratea celastroides	Hippocrataceae
Hiraea reclinata	Malpighiaceae
Ipomoea batatoides	Convolvulaceae
Ipomoea decasperma	Convolvulaceae
Ipomoea hederifolia	Convolvulaceae
Ipomoea meyeri	Convolvulaceae
Ipomoea minutiflora	Convolvulaceae
Nissolia leyogine	Fabaceae
Passiflora filipes	Passifloraceae
Passiflora goniosperma	Passifloraceae
Passiflora jorullensis	Passifloraceae
Paullinia cururu	Sapindaceae
Paullinia sessiliflora	Sapindaceae
Phaseolus	Fabaceae
Phaseolus coccineus	Fabaceae
Phaseolus jaliscanus	Fabaceae
Phaseolus leptostachyus	Fabaceae
Phaseolus lunatus	Fabaceae
Phaseolus vulgaris	Fabaceae
Pithecoctenium crucigerum	Bignoniaceae
Poiretia punctata	Fabaceae
Pristimera celastroides	Hippocrataceae
Rhynchosia minima	Fabaceae
Rhynchosia precatoria	Fabaceae
Rhynchosia tarphantha	Fabaceae
Rourea glabra	Ochnaceae
Semialarium mexicanum	Hippocrataceae
Serjania	Sapindaceae
Serjania brachycarpa	Sapindaceae
Serjania psilophylla	Sapindaceae
Sicyos barbatus	Cucurbitaceae
Smilax moranensis	Smilacaceae
Solanum refractum	Solanaceae
Strychnos	Loganiaceae
Teramnus	Fabaceae
Teramnus uncinatus	Fabaceae
Tetrapterys	Malpighiaceae
Tragia pacifica	Euphorbiaceae
Vigna linearis	Fabaceae

Arbustos

Especie	Familia
Abutilon	Malvaceae
Abutilon barrancae	Malvaceae
Abutilon reventum	Malvaceae
Acacia farnesiana	Mimosaceae
Acacia pennatula	Mimosaceae
Acalypha	Euphorbiaceae
Acalypha alopecuroidea	Euphorbiaceae
Acalypha cincta	Euphorbiaceae
Acalypha langiana	Euphorbiaceae
Acalypha schiedeana	Euphorbiaceae
Aeschynomene	Fabaceae
Aeschynomene amorphoides	Fabaceae

Especie	Familia
Henrya tuberculosperma	Acanthaceae
Hochreutinera amplexifolia	Malvaceae
Jatropha platyphylla	Euphorbiaceae
Justicia	Acanthaceae
Justicia candicans	Acanthaceae
Justicia caudata	Acanthaceae
Justicia pringlei	Acanthaceae
Karwinskia latifolia	Rhamnaceae
Lasianthaea	Asteraceae
Lasianthaea ceanothifolia	Asteraceae
Lasianthaea fruticosa	Asteraceae
Lasianthaea helianthoides	Asteraceae

Aphelandra	Acanthaceae
Ardisia revoluta	Myrsinaceae
Argythamnia lottiae	Euphorbiaceae
Ateleia	Fabaceae
Bauhinia	Caesalpinaceae
Bauhinia ungulata	Caesalpinaceae
Befaria glauca	Ericaceae
Bouvardia cordiflora	Rubiaceae
Brongniartia	Fabaceae
Caesalpinia	Caesalpinaceae
Calea urticifolia	Asteraceae
Calliandra	Mimosaceae
Calliandra anomala	Mimosaceae
Calliandra formosa	Mimosaceae
Calliandra marginata	Mimosaceae
Capsicum	Solanaceae
Carlowrightia	Acanthaceae
Chamaecrista	Caesalpinaceae
Clethra	Clethraceae
Clidemia	Melastomataceae
Comocladia engleriana	Anacardiaceae
Conostegia xalapensis	Melastomataceae
Coursetia caribaea	Fabaceae
Cracca berenicea	Fabaceae
Cracca mollis	Fabaceae
Croton roxanae	Euphorbiaceae
Croton suberosus	Euphorbiaceae
Decachaeta haenkeana	Asteraceae
Desmodium cinereum	Fabaceae
Diospyros	Ebenaceae
Diospyros aequoris	Ebenaceae
Erythrina	Fabaceae
Erythroxylum havanense	Erythroxylaceae
Erythroxylum mexicanum	Erythroxylaceae
Esenbeckia	Rutaceae
Eugenia	Myrtaceae
Eugenia capuli	Myrtaceae
Eupatorium collinum	Asteraceae
Eupatorium glaberrimum	Asteraceae
Eupatorium odoratum	Asteraceae
Eupatorium petiolare	Asteraceae
Fuchsia	Onagraceae
Guettarda	Rubiaceae
Hamelia patens	Rubiaceae
Heimia salicifolia	Lythraceae
Helicteres baruensis	Sterculiaceae
Heliocarpus americanus	Tiliaceae
Malpighia	Malpighiaceae
Mexianthus mexicanus	Asteraceae
Miconia glaberrima	Melastomataceae
Mimosa	Mimosaceae
Mimosa quadrivalvis	Mimosaceae
Peniocereus	Cactaceae
Perymenium alticola	Asteraceae
Perymenium uxoris	Asteraceae
Phyllanthus	Euphorbiaceae
Phyllanthus acuminatus	Euphorbiaceae
Physodium adenodes	Sterculiaceae
Piper abalienatum	Piperaceae
Piper jaliscanum	Piperaceae
Piper pseudofuligineum	Piperaceae
Piper rosei	Piperaceae
Piper tuberculatum	Piperaceae
Pisonia aculeata	Nyctaginaceae
Pouzolzia palmeri	Urticaceae
Psychotria horizontalis	Rubiaceae
Randia	Rubiaceae
Randia aculeata	Rubiaceae
Randia armata	Rubiaceae
Randia laevigata	Rubiaceae
Randia tetracantha	Rubiaceae
Ruellia foetida	Acanthaceae
Ruellia inundata	Acanthaceae
Salvia	Lamiaceae
Salvia brachyodonta	Lamiaceae
Salvia carnea	Lamiaceae
Salvia longistyla	Lamiaceae
Sapranthus	Annonaceae
Schrankia jaliscensis	Mimosaceae
Securidaca	Polygalaceae
Senecio megaphyllus	Asteraceae
Senna	Caesalpinaceae
Senna hirsuta	Caesalpinaceae
Senna pallida	Caesalpinaceae
Solanum	Solanaceae
Solanum aphyodendron	Solanaceae
Stemmadenia donnell-smithii	Apocynaceae
Stenocereus	Cactaceae
Tabernaemontana amygdalifolia	Apocynaceae
Tephrosia	Fabaceae
Triumfetta semitriloba	Tiliaceae
Verbesina	Asteraceae
Verbesina sphaerocephala	Asteraceae
Wedelia acapulcensis	Asteraceae

Heliocarpus palmeri	Tiliaceae	*Zamia loddigesii*	Zamiaceae
Henrya	Acanthaceae		

Árboles

Especie	Familia	Especie	Familia
Acacia glomerosa	Mimosaceae	*Hybiscus*	Tiliaceae
Acacia hindsii	Mimosaceae	*Inga*	Mimosaceae
Acacia picachensis	Mimosaceae	*Ipomoea*	Convolvulaceae
Acrocomia mexicana	Arecaceae	*Ipomoea wolcottiana*	Convolvulaceae
Aeschynomene	Fabaceae	*Jacaratia*	Caricaceae
Albizia occidentalis	Mimosaceae	*Jacaratia mexicana*	Caricaceae
Albizia tomentosa	Mimosaceae	*Jacquinia pungens*	Theophrastaceae
Allosidastrum hilarianum	Malvaceae	*Jatropha chamelensis*	Euphorbiaceae
Alvaradoa amorphoides	Simaroubaceae	*Jatropha malacophylla*	Euphorbiaceae
Amphipterygium adstringens	Julianaceae	*Lasiocarpus ferrugineus*	Malpighiaceae
Andira inermis	Fabaceae	*Leucaena*	Mimosaceae
Annona	Annonaceae	*Leucaena esculenta*	Mimosaceae
Annona glabra	Annonaceae	*Leucaena lanceolata*	Mimosaceae
Annona palmeri	Annonaceae	*Leucaena leucocephala*	Mimosaceae
Annona purpurea	Annonaceae	*Licaria nayaritensis*	Lauraceae
Annona reticulata	Annonaceae	*Lippia umbellata*	Verbenaceae
Annona squamosa	Annonaceae	*Litsea glaucescens*	Lauraceae
Aphananthe monoica	Ulmaceae	*Lonchocarpus*	Fabaceae
Apoplanesia paniculata	Fabaceae	*Lonchocarpus cochleatus*	Fabaceae
Astronium graveolens	Anacardiaceae	*Lonchocarpus eriocarinalis*	Fabaceae
Ateleia pterocarpa	Fabaceae	*Lonchocarpus guatemalensis*	Fabaceae
Ayenia	Sterculiaceae	*Lonchocarpus lanceolatus*	Fabaceae
Ayenia wrightii	Sterculiaceae	*Lonchocarpus minor*	Fabaceae
Bauhinia divaricata	Caesalpinaceae	*Lonchocarpus mutans*	Fabaceae
Brahea	Arecaceae	*Lonchocarpus*	Fabaceae
Brosimum alicastrum	Moraceae	*Luehea candida*	Tiliaceae
Bunchosia	Malpighiaceae	*Lysiloma acapulcense*	Mimosaceae
Bunchosia palmeri	Malpighiaceae	*Lysiloma microphyllum*	Mimosaceae
Bursera	Burseraceae	*Malpighia ovata*	Malpighiaceae
Bursera arborea	Burseraceae	*Megastigma*	Rutaceae
Bursera bipinnata	Burseraceae	*Mimosa arenosa*	Mimosaceae
Bursera cinerea	Burseraceae	*Monniera trifolia*	Rutaceae
Bursera excelsa	Burseraceae	*Morus*	Moraceae
Bursera heteresthes	Burseraceae	*Myrospermum frutescens*	Fabaceae
Bursera instabilis	Burseraceae	*Myroxylon balsamum*	Fabaceae
Bursera roseana	Burseraceae	*Nectandra*	Lauraceae
Bursera simaruba	Burseraceae	*Opuntia*	Cactaceae
Byrsonima crassifolia	Malpighiaceae	*Opuntia excelsa*	Cactaceae
Caesalpinea eriostachys	Caesalpinaceae	*Oxandra lanceolata*	Annonaceae
Caesalpinia caladenia	Caesalpinaceae	*Pachycereus*	Cactaceae
Caesalpinia eriostachys	Caesalpinaceae	*Persea hintonii*	Lauraceae
Capparis incana	Capparaceae	*Phyllanthus mocinianus*	Euphorbiaceae
Capparis indica	Capparaceae	*Piptadenia constricta*	Mimosaceae
Capparis verrucosa	Capparaceae	*Piranhea mexicana*	Euphorbiaceae

Casearia	Flacourtiaceae
Casearia corymbosa	Flacourtiaceae
Casearia sylvestris	Flacourtiaceae
Casearia tremula	Flacourtiaceae
Cecropia obtusifolia	Cecropiaceae
Ceiba	Bombacaceae
Ceiba acuminata	Bombacaceae
Ceiba aesculifolia	Bombacaceae
Chiococca	Rubiaceae
Chloroleucon mangense	Mimosaceae
Cnidoscolus spinosus	Euphorbiaceae
Coccoloba	Polygonaceae
Coccoloba liebmannii	Polygonaceae
Cochlospermum vitifolium	Cochlospermaceae
Colubrina	Rhamnaceae
Colubrina triflora	Rhamnaceae
Comocladia engleriana	Anacardiaceae
Conzattia multiflora	Caesalpinaceae
Cordia	Boraginaceae
Cordia alliodora	Boraginaceae
Cordia dentata	Boraginaceae
Cordia prunifolia	Boraginaceae
Cordia salvadorensis	Boraginaceae
Cordia sebestena	Boraginaceae
Couepia polyandra	Chrysobalanaceae
Croton	Euphorbiaceae
Croton schiedeanus	Euphorbiaceae
Cupania glabra	Sapindaceae
Curatella americana	Dilleniaceae
Dalbergia congestiflora	Fabaceae
Daphnopsis	Thymelaeaceae
Erythrina	Fabaceae
Erythrina lanata	Fabaceae
Erythroxylum	Erythroxylaceae
Esenbeckia berlandieri	Rutaceae
Eupatorium areolare	Asteraceae
Exostema caribaeum	Rubiaceae
Exostema mexicanum	Rubiaceae
Ficus insipida	Moraceae
Ficus microchlamys	Moraceae
Ficus padifolia	Moraceae
Ficus pertusa	Moraceae
Forchammeria pallida	Capparaceae
Forchhammeria pallida	Capparaceae
Guaiacum coulteri	Zygophyllaceae
Guapira macrocarpa	Nyctaginaceae
Guarea	Meliaceae
Guarea glabra	Meliaceae
Guazuma ulmifolia	Sterculiaceae
Piscidia	Fabaceae
Piscidia carthagenensis	Fabaceae
Pithecellobium dulce	Mimosaceae
Platymiscium lasiocarpum	Fabaceae
Plumeria rubra	Apocynaceae
Poeppigia procera	Caesalpinaceae
Pouteria mammosa	Sapotaceae
Prockia crucis	Flacourtiaceae
Pseudobombax ellipticoideum	Bombacaceae
Psidium	Myrtaceae
Psidium sartorianum	Myrtaceae
Psidium sartorium	Myrtaceae
Pterocarpus	Fabaceae
Pterocarpus orbiculatus	Fabaceae
Quercus	Fagaceae
Quercus aristata	Fagaceae
Quercus glaucescens	Fagaceae
Quercus magnoliifolia	Fagaceae
Quercus martinezii	Fagaceae
Quercus peduncularis	Fagaceae
Quercus resinosa	Fagaceae
Quercus rugosa	Fagaceae
Randia thurberi	Rubiaceae
Recchia mexicana	Simaroubaceae
Ruprechtia fusca	Polygonaceae
Samyda	Flacourtiaceae
Samyda mexicana	Flacourtiaceae
Sapium	Euphorbiaceae
Sapium pedicellatum	Euphorbiaceae
Sapranthus violaceus	Annonaceae
Senna atomaria	Caesalpinaceae
Sideroxylon	Sapotaceae
Sideroxylon capiri	Sapotaceae
Sideroxylon cartilaguneum	Sapotaceae
Spondias purpurea	Anacardiaceae
Stemmadenia	Apocynaceae
Stemmadenia grandiflora	Apocynaceae
Styrax	Styracaceae
Swartzia simplex	Fabaceae
Synardisia	Myrsinaceae
Tabebuia impetiginosa	Bignoniaceae
Tabebuia rosea	Bignoniaceae
Talipariti tiliaceum	Malvaceae
Thouinia paucidentata	Sapindaceae
Thouinia serrata	Sapindaceae
Thouinidium decandrum	Sapindaceae
Trema micrantha	Ulmaceae
Trichilia trifolia	Meliaceae
Trichospermum insigne	Tiliaceae

Guettarda elliptica	Rubiaceae	*Urea caracasana*	Urticaceae
Gyrocarpus jatrophifolius	Hernandiaceae	*Urera*	Urticaceae
Haematoxylon brasiletto	Caesalpinaceae	*Urera pacifica*	Urticaceae
Helicteres	Sterculiaceae	*Vitex hemsleyi*	Verbenaceae
Heliocarpus	Tiliaceae	*Willardia mexicana*	Fabaceae
Heliocarpus occidentalis	Tiliaceae	*Xylosma intermedium*	Flacourtiaceae
Heliocarpus pallidus	Tiliaceae	*Zanthoxylum arborescens*	Rutaceae
Hippomane mancinella	Euphorbiaceae	*Zanthoxylum caribaeum*	Rutaceae
Hura polyandra	Euphorbiaceae	*Zanthoxylum fagara*	Rutaceae
Hybanthus mexicanus	Violaceae	*Zanthoxylum mollissimum*	Rutaceae