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Plant diversity enhances provision of ecosystem services: A new synthesis

Sandra Quijas[a,*], Bernhard Schmid[b], Patricia Balvanera[a]

[a]*Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Apdo. Postal 27-3, Sta. Ma. de Guido, Morelia, Michoacán 58090, Mexico*
[b]*Institute of Evolutionary Biology and Environmental Studies, Universität Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland*

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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

*Corresponding author. Tel.: +52 55 56 23 27 07; fax: +52 55 56 27 19.
E-mail address: squijas@oikos.unam.mx (S. Quijas).

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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.

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

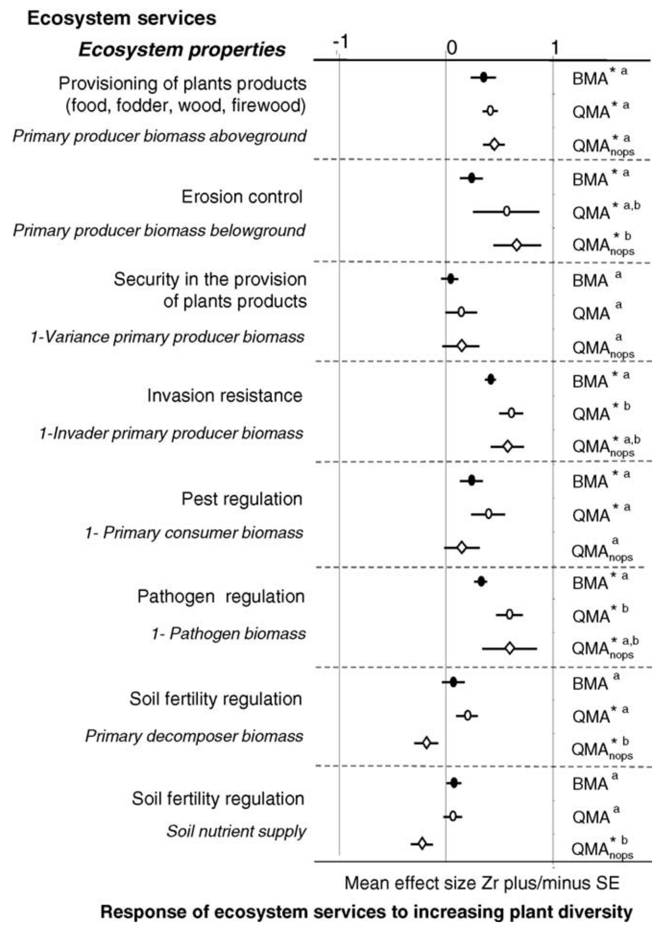

Fig. 1. Magnitude and direction of plant diversity effects on ecosystem services comparing a more comprehensive meta-analysis (Balvanera et al. 2006; BMA, solid circles) and the present meta-analysis, which was restricted to studies manipulating plant diversity in terrestrial ecosystems. Ecosystem properties 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.

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 ($\mathbf{QMA_{nops}}$)

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 ($\mathbf{QMA_{nops}}$) 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.

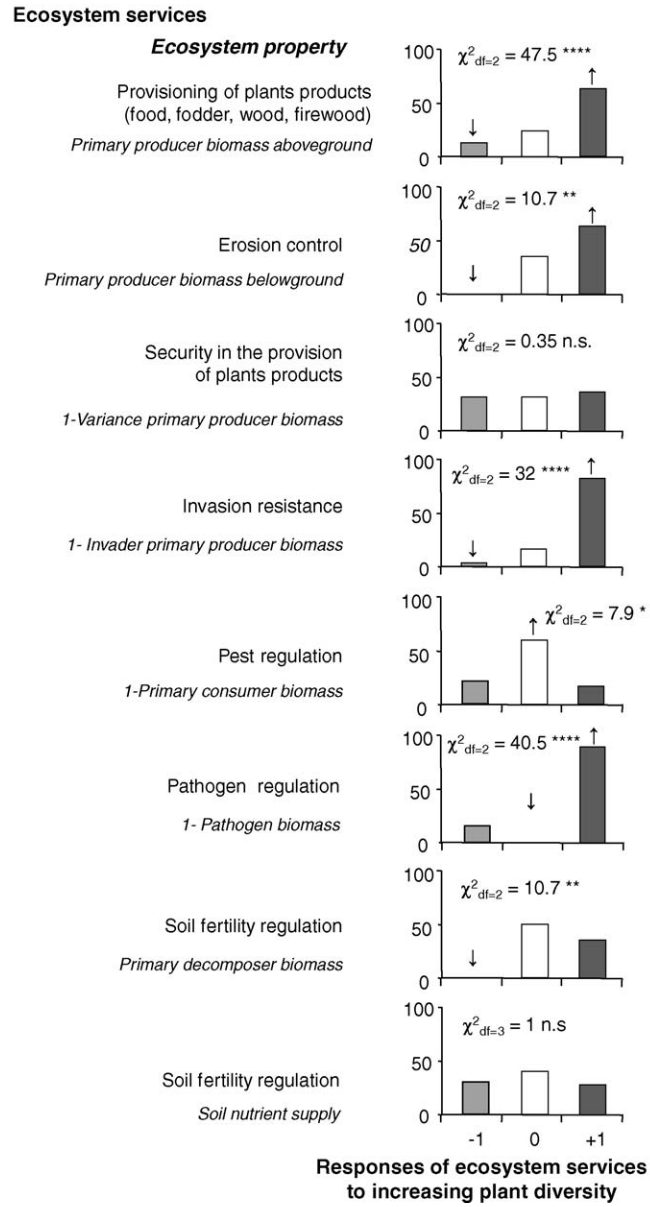

Fig. 2. Frequency of measurements showing negative (−1 = the more diversity the less service), neutral (0 = no effect) or positive (+1) effects of terrestrial plant diversity on the provision of ecosystem services. Ecosystem properties in italics are listed below the corresponding ecosystem services; 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, 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, 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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