

Species richness and evenness as a function of biomass in arable plant communities

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Summary

We evaluated the hypothesis that competitive dominants change the species richness and evenness of arable plant communities. Three field experiments including cool-season crops and unsown short fallows were carried out in Buenos Aires, Argentina. Ground cover, biomass and species richness of crops and weeds were assessed. Evenness was calculated by using species biomass data. Richness and evenness were correlated with total community biomass, and with the biomass of either weeds or the dominant species in the community. Crops, through growth and shading effects, affected the species richness and evenness of arable plant communities. Conversely, the dominant weed in fallows was not as suppressive as crops. Species richness and evenness were constrained by

community biomass. Species richness of understory weeds decreased as crops suppressed weed growth. Evenness also decreased as the dominant species became increasingly productive, regardless of their identity (weeds or crops). Our findings provide valuable models to characterise the trajectories that species richness and evenness may follow in different farming scenarios. Community biomass is a major constraint on the maximum diversity of local communities and, consequently, of substantial ecological importance for both biodiversity conservation and weed management purposes.

Keywords: agro-ecosystems, biodiversity, dominance, ecological succession, fallows, sustainable agriculture, weed suppression.

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Introduction

Conserving farmland biodiversity has become a paramount issue for maintaining ecological functions in temperate, intensively managed agro-ecosystems. Despite the dramatic reductions in the arable flora owing to agriculture intensification, weeds within fields still support part of the biodiversity in agro-ecosystems, for instance, by providing food for insects and birds (Marshall *et al.*, 2003). The loss of farmland biodiversity can be counteracted by adopting appropriate farming management and on-farm conservation schemes to

preserve species-rich plant communities within fields and the nearby uncultivated areas (Marshall, 2009; Ulber *et al.*, 2009). This can be accomplished by agronomic practices aimed to diminish herbicide use, such as sowing crop mixtures and smother crops, increasing seed rates and narrowing row spacing of crops (Liebman & Dyck, 1993; Holt, 1995; Liebman & Davis, 2000). On the other hand, fields left fallow between two successive crops may also retain arable plant diversity. Although weeds can be intensively controlled during fallows (Derksen *et al.*, 2002), they also supply food for insects and birds (Marshall *et al.*,

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2003; Holland *et al.*, 2008). Furthermore, many schemes for managing field margin flora have been developed in Europe to conserve the farmland biota and supply ecosystem services to agriculture, including uncultivated wildlife strips and set-aside margins, which do not need any sowing (Marshall & Moonen, 2002). Designing and implementing these initiatives therefore need the understanding of the ecological processes determining species diversity in arable plant communities.

The relationship between plant species richness and standing biomass is a curve, which has its maximum at intermediate levels of above-ground biomass, widely known as the humped-back model (Grime, 1973). The humped-back shape of the relationship has been obtained across a gradient of habitats differing on stress intensity, disturbance or habitat fertility (Grime, 1973), and for herbaceous communities across different vegetation types (Grace, 1999; Keddy, 2005). The right-hand side of the curve, where richness decreases as standing biomass increases, can be explained by increasingly fewer species that are optimally suited to exploit habitat fertility or tolerate high-stress environments (Fig. 1). When soil fertility is low, restrictions in soil resources result in low plant productivity. When fertility is high, plant communities are more productive, resulting in increased shading, size inequality and thinning, owing to asymmetry in light competition (Newman, 1973; Weiner, 1990). The richness–biomass relationship has been used to study the local factors that determine plant richness changes across different vegetation types. The humped-back shaped curve has been used to predict species richness in response to management practices (Keddy, 2005), but has not been used yet to study the diversity patterns of weed communities.

Concerns over economic, environmental and public health issues associated with agricultural intensification have encouraged interest in designing weed management strategies relying more on ecological principles than exclusively on chemical weed control (Liebman & Davis, 2000). When densely sown and appropriately fertilised, crops can effectively suppress weed growth and reduce both richness and evenness of understory weeds (Mohler & Liebman, 1987; Poggio, 2005). Manipulating crop canopies can, thus, be used to maximise the sunlight that is intercepted, resulting in increased shading effects on weeds (Holt, 1995). Weeds occurring during fallow periods have been much less studied than weeds accompanying crops, particularly in association with weed management strategies (Derksen *et al.*, 2002). Weeds in fallows have been recently recognised as a valuable source of food for seed-eaters (Marshall *et al.*, 2003; Holland *et al.*, 2008).

Here, we evaluated the hypothesis that competitive dominants modulate the species richness and evenness

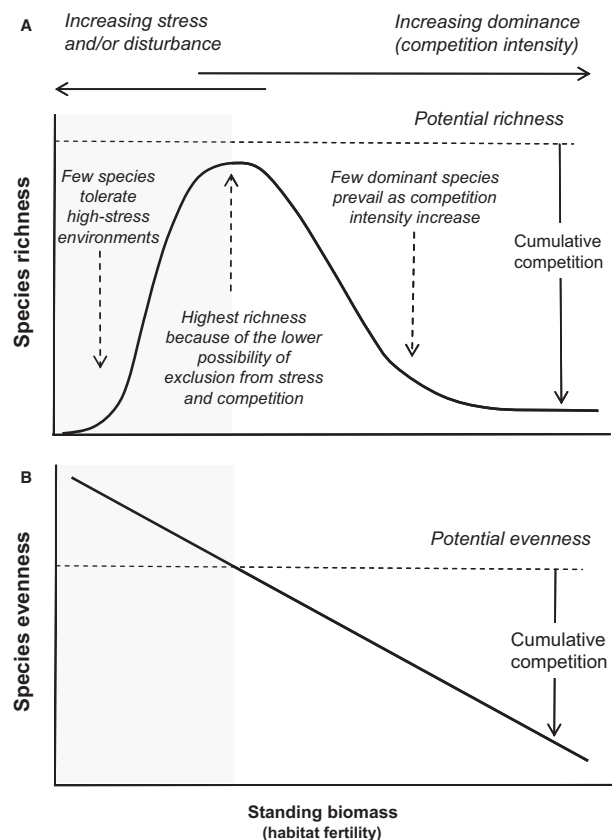


Fig. 1 Hypothetical relations between (A) species richness and standing biomass, as predicted by the Grime (1973), and (B) evenness and standing biomass, as predicted in Drobner *et al.* (1998). Grey areas on the left indicate the environmental conditions not evaluated in the present paper.

of arable plant communities. Under regular cropping conditions, competition between crops and weeds is usually asymmetric, meaning that crop plants dominate. This is mostly due to the growth potential of crops, the provision of resources through fertilisation, which is tailored to the crop, and the high sowing density of crops. Hence, the competitive advantage of crops is cumulative over time and competitive exclusion of weeds increases with increasing crop growth. We predict that richness and evenness will decrease as the standing biomass of arable plant communities increases, either because of the growth of highly productive crop plants or because of the growth of a dominant weed in the community when crops are absent. To test these predictions, richness and evenness were correlated with total community biomass, which also included crop species, when present (Fig. 1). In addition, richness and evenness were associated with the biomass of either all understory weeds or the dominant species in the community, namely the one with the highest biomass in the community, irrespective of being a crop or weed. The predictions tested here are only valid under condi-

tions of low-stress/high-fertility used to grow crops, represented in the right-hand side of the humped-back relationship where competitive exclusion is the main driver of species diversity (Fig. 1).

Methods

Field experiments

Three field experiments were carried out at the School of Agronomy, University of Buenos Aires, Argentina (34° 35' lat. S, 58° 35' long. W), on 1 July 1999, 9 August 1999, and 6 August 2000, using a complete randomised blocks design with three replicates. Treatments were monocultures of pea (*Pisum sativum* L., Radley, Sharpes International Seed Ltd., UK) and barley (*Hordeum vulgare* L., Busch-1614, Anheuser-Busch, USA), additive mixtures of both peas and barley and unsown treatments (hereafter referred as fallows, which lasted the same length of time as the crops). Weeds were allowed to grow in all plots, which measured 3 m by 4 m (12 m²). All plots were managed identically. Soil was ploughed and fertilised before sowing. Crop density was the same for monocultures and mixtures (80 plants m⁻²). Pea and barley seeds were treated with fungicides compatible with nitrogen-fixing bacteria (Carbendazim + Thiram, 0.1 L + 0.1 L a.i. L⁻¹, dose: 0.625 L per 100 kg of seeds). Pea seeds were inoculated with *Rhizobium leguminosarum* var. *pisi* (IMYSA, EEA INTA Castelar, Buenos Aires, Argentina). Experiments were periodically watered. Neither pest nor leaf disease controls were necessary.

Measurements

Ground cover of crops and weeds was measured at emergence of barley spikes, henceforth referred to as flowering, using a point-quadrat optical device that estimates the relative leaf area (RLA) of each species in mixtures (Beaumer & De Wit, 1968). A 45° inclination was used so as to not overestimate the frequency of planophile or erectophile plants. The RLA was calculated as the frequency of leaf point interceptions of crop and weed plants and is a measure of maximum crop leaf area and shading over underlying weeds. At flowering crop and weed plants were sampled in one quadrat of 0.5 m by 0.5 m per plot, and at crop harvest maturity crop and weed plants were sampled in one quadrat of 1 m by 1 m per plot. Crop and weed species per sample were sorted and the number of weed species counted. Weed species richness (S) was expressed as the number of weed species per sampled area (Magurran, 2004). Plants were dried at 60°C for 72 h and weighed.

Analysis

Species evenness was calculated using the index E' proposed by Camargo (1993):

$$E' = 1 - \left(\sum_h^K |p_{ih} - p_{jh}| \right) / S^*$$

where S^* is the species richness including crops (i.e. the number of all competing species in the plant community h), p_{ih} and p_{jh} are the relative abundances of the species i and j , and K is the maximum number of possible binary differences between competing species, being $K = S(S - 1)/2$ (Camargo, 1993). The maximum possible value of E' is 1 ($p_i = 1/S$), whereas the minimum value tends towards $1/S$. This index was chosen because it is independent of species richness, the foremost requirement of adequate evenness measurement, and because it fulfils other desirable properties of evenness indices (Smith & Wilson, 1996). Calculations were based on specific biomass data for each sampling quadrat, considering biomass as the most appropriate estimate of species abundance to make ecological inferences and interpretations about species evenness in plant communities (Guo & Rundel, 1997).

Relationships between species diversity and biomass were tested using regression analysis. Above-ground dry matter (DM) was used as an explanatory variable because it integrates the use of resources among competing individuals in plant communities in response to habitat fertility during the growing period (Grime, 1973; Guo & Rundel, 1997). Associations between variables were analysed by using Pearson's product-moment correlations, when necessary.

Species richness and evenness were correlated with the total DM of plant communities, including crops and weeds ($DM_{\text{community}}$), the DM of weeds in crop understories and fallows (DM_{weed}), which included all weed species in fallows, and the DM of the dominant species in the community (DM_{dominant}), which is the one with highest DM in the community whether it was a crop or a weed, to test whether the decline in richness on the right-hand side of the humped-back curve could be explained by biomass (Fig. 1A). A single value of E' index was used, whereas different values of S were used:

- The total number of species in plant communities, including crops and weeds (S^*), was correlated with $DM_{\text{community}}$; thus, $S^* = S + 1$ in crop monocultures, $S^* = S + 2$ in crop mixtures, and $S^* = S$ in fallows.
- Weed richness (S) was correlated to DM_{weed} in the crop understories and fallows.
- Species richness of understory weeds (S_u) was correlated to DM_{dominant} , with $S_u = S^* - 1$ when the dominant was a crop, and $S_u = S - 1$ in fallows.

Regression lines were fitted using generalised linear models. Poisson (log link) and normal (identity link) errors were used for richness–biomass and evenness–biomass relationships, respectively. Plant biomass (DM) was \log_e -transformed (Drobner *et al.*, 1998). Overdispersion was accounted for by calculating the sum of squared Pearson's residuals (ΣR_p^2), which was then compared to the degrees of freedom (d.f.) (i.e. overdispersion is apparent when $\Sigma R_p^2 > \text{d.f.}$). The error family was changed from Poisson to negative binomial when overdispersion was detected. After fitting the models, deviance residuals were plotted against the predicted values to evaluate the presence of systematic trends in the goodness of fit (data not shown). Occasionally, overdispersion remained or heteroscedasticity was evident, indicating that ordinary least squares regression to estimate the mean was not robust enough. Therefore, an alternative and more appropriate model, namely quantile regression model, was fitted at the 90th percentile, as commonly used to characterise upper boundaries in ecological data (Cade *et al.*, 1999). This upper limit characterises the direct influence of community biomass on species richness, whereas the vertical distances from points to that boundary represent the effects of the non-considered variables. Previously, similar patterns of variability in richness have been better modelled by using upper boundaries or enveloping curves than by fitting central trend lines (Grace, 1999). Cook's distances were used to detect influential points. When present, these were excluded and the model then refitted. In addition, the best models for each richness–biomass and evenness–biomass relationship were selected, using Akaike information criterion with a second-order correction for small sample sizes (AICc), and Akaike weights (w_i) to choose the best-fitting

models (Burnham & Anderson, 1998). The use of AICc is suggested when $n/K < 40$, where n is the sample size and K the number of estimated parameters. The best model is that with the lowest AIC value (Burnham & Anderson, 1998). When differences between the AIC values are small (< 2 AIC units), w_i are used as indicators of the strength of evidence supporting each model and are interpreted as the approximate probability that model i is the best among the set of models being evaluated (Burnham & Anderson, 1998). The w_i values were normalised to sum 1. Analyses were performed using R 2.9.2 (R Development Core Team, 2008).

Results

Crops dominated in all sown treatments and weed biomass decreased with increasing crop biomass ($\log_e \text{DM}_{\text{crop}}$) at both flowering ($r = -0.494$, $t_{25} = -2.84$, $P < 0.01$) and crop harvest ($r = -0.695$, $t_{25} = -4.84$, $P < 0.0001$). Weed biomass was negatively related to the RLA of crops at flowering ($r = -0.589$, $t_{25} = -3.64$, $P < 0.01$) and harvest ($r = -0.619$, $t_{25} = -3.94$, $P < 0.001$). Fallow plots, on average, were dominated at flowering by *Coronopus didymus* (L.) Smith [$55 \pm 6.9 \text{ g m}^{-2}$ (mean \pm SEM)] or *Stellaria media* (L.) Vill. ($41 \pm 6.7 \text{ g m}^{-2}$), whereas *Anthemis cotula* L. ($167 \pm 63.0 \text{ g m}^{-2}$) or *C. didymus* ($89 \pm 20.9 \text{ g m}^{-2}$) dominated at crop harvest.

Richness–biomass relationship

At flowering, the relationship between total richness (S^*) and community biomass ($\log_e \text{DM}_{\text{community}}$) was not significant ($P = 0.189$, Table 1a, Fig. 2A), in contrast to what was expected (Fig. 1A). At crop harvest, the

Table 1 Summary of regressions fitted, after removing influential data and adapting the error distribution, to the relations between species richness of the community (S^*), weeds in crop understories and fallows (S), and subordinated weeds (S_U), and biomass of the community ($\text{DM}_{\text{community}}$), all weeds (DM_{weed}) and the dominant species ($\text{DM}_{\text{dominant}}$), respectively, at flowering (a) and crop harvest (b)

		Estimate	SE	z value	Pr(> z)	ΣR_p^2	AICc	w_i
(a)								
S^*	(Intercept)	3.18	0.505	6.30	<0.0001	19.5	180.5	0.00
	$\log_e (\text{DM}_{\text{community}})$	-0.145	0.1089	-1.33	0.1840			
S	(Intercept)	2.17	0.102	21.2	<0.0001	11.7	162.1	1.00
	$\log_e (\text{DM}_{\text{weed}})$	0.12	0.036	3.31	0.0009			
S_U	(Intercept)	3.01	0.301	10.1	<0.0001	19.5	177.5	0.00
	$\log_e (\text{DM}_{\text{dominant}})$	-0.136	0.0702	-2.15	0.0523			
(b)								
S^*	(Intercept)	5.6	0.61	9.24	<0.0001	44.0	215.2	0.00
	$\log_e (\text{DM}_{\text{community}})$	-0.45	0.093	-4.81	<0.0001			
S	(Intercept)	2.0	0.11	18.5	<0.0001	16.7	171.9	1.00
	$\log_e (\text{DM}_{\text{weed}})$	0.17	0.019	7.41	<0.0001			
S_U	(Intercept)	4.8	0.38	12.5	<0.0001	43.7	210.9	0.00
	$\log_e (\text{DM}_{\text{dominant}})$	-0.34	0.061	-5.57	<0.0001			

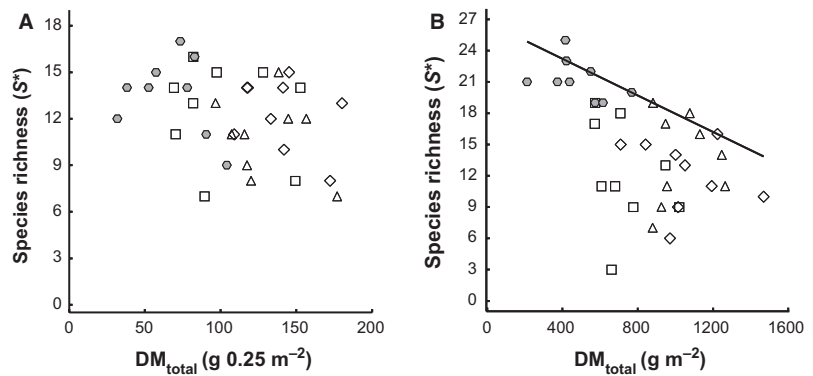


Fig. 2 Relationships between species richness (S^*) and total community biomass ($DM_{community}$) at flowering (A) and crop harvest (B). The line in (B) is the fitted upper boundary. See text for statistical information. Symbols: no crop (○), pea (□), barley (△), mixture (◇).

relationship was significant; however, overdispersion was apparent (Table 1b), even when the model was fitted using negative binomial errors ($\Sigma R_p^2 = 40.6$, d.f. = 34). Moreover, variance was inconstant (i.e. heteroscedasticity, Fig. 2B). Using quantile regression, species richness declined by about one species with every $c. 100 \text{ g m}^{-2}$ increase in community biomass ($S^* = 27 \pm 1.9 - 0.009 \pm 0.0021 \times \log_e DM_{community}$, $t_{34} = 4.09$, $P < 0.001$). Deviations from the upper boundary were greater at intermediate levels of community biomass; they were lower in fallows (low $DM_{community}$) and at high crop biomass (Fig. 2B). Higher deviations suggest that some unmeasured explanatory variables are defining species richness at intermediate levels of community biomass.

Weed species richness (S) increased with increasing weed biomass ($\log_e DM_{weed}$) at both flowering and crop harvest (Table 1, Fig. 3). After examination of Cook's distances, two influential points were detected in both models, which were excluded and the models refitted (Fig. 3). Overdispersion was not suspected for the associations between S and $\log_e DM_{weed}$, as $\Sigma R_p^2 < \text{d.f.}$ (Table 1). The best-fitting models at flowering and crop harvest were those that described the relationship between S and $\log_e DM_{weed}$ ($AIC_c = 11.7$ and 16.7 , respectively, $w_i = 1$ for both flowering

and crop harvest; Table 1). However, when species richness of understory weeds (S_u) was related to the biomass of the dominant species in the community ($\log_e DM_{dominant}$), the trend was marginal ($P = 0.052$; Table 1a). Although the relationship between S_u and $\log_e DM_{dominant}$ at crop harvest seemed highly significant, overdispersion was suspected (Table 1b). The model was thus refitted, using negative binomial errors, but overdispersion persisted ($\Sigma R_p^2 = 42.5$, d.f. = 34). Hence, the model describing weed species richness, S , based on weed biomass, DM_{weed} , emerged as the best at both flowering and crop harvest (Fig. 3).

Evenness–biomass relationship

As expected, the E' was unrelated to species richness (flowering: $r = 0.139$, $t_{34} = 0.116$, $P = 0.9085$; crop harvest: $r = -0.020$, $t_{34} = 0.829$, $P = 0.419$), thus fulfilling the requirement of independence. At both flowering and crop harvest, evenness decreased with increasing biomass of the dominant species in the community ($\log_e DM_{dominant}$) (Table 2, Fig. 4). Two points at flowering and three points at crop harvest, detected as influential using Cook's distances, were excluded after which the models were refitted (Fig. 4). At both flowering and crop harvest, the models using the

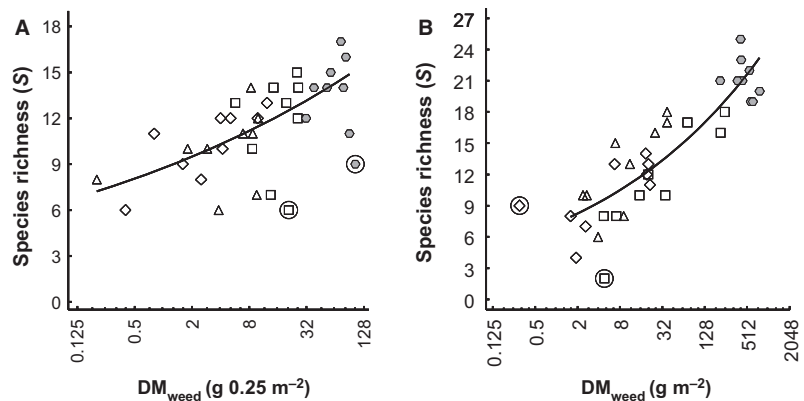


Fig. 3 Relationships between species richness (S) and biomass of weeds (DM_{weed}) at flowering (A) and crop harvest (B). Circled points were excluded from the analyses. See Table 1 for statistical information. Symbols: no crop (○), pea (□), barley (△), mixture (◇).

Table 2 Summary of regressions fitted, after removing influential data and adapting the error distribution, to the relations between evenness (E') and biomass of either the community ($DM_{\text{community}}$), weeds (DM_{weed}) or the dominant species (DM_{dominant}) at flowering (a) and crop harvest (b)

	Estimate	SE	z value	Pr(> z)	ΣR_p^2	AICc	w_i
(a)							
(Intercept)	0.65	0.121	5.36	<0.0001	0.148	-91.3	0.00
$\log_e(DM_{\text{community}})$	-0.11	0.026	-4.09	0.0003			
(Intercept)	0.09	0.021	4.37	0.0001	0.161	-88.3	0.00
$\log_e(DM_{\text{weed}})$	0.03	0.008	3.56	0.0011			
(Intercept)	0.54	0.059	9.1	<0.0001	0.062	-113.4	1.00
$\log_e(DM_{\text{dominant}})$	-0.09	0.013	-6.68	<0.0001			
(b)							
(Intercept)	0.69	0.163	4.38	0.0001	0.121	-98.6	0.00
$\log_e(DM_{\text{community}})$	-0.08	0.024	-3.51	0.0013			
(Intercept)	0.12	0.021	5.45	<0.0001	0.152	-90.2	0.00
$\log_e(DM_{\text{weed}})$	0.01	0.005	1.65	0.1080			
(Intercept)	0.50	0.050	10.10	<0.0001	0.026	-137.8	1.00
$\log_e(DM_{\text{dominant}})$	-0.06	0.080	-7.51	<0.0001			

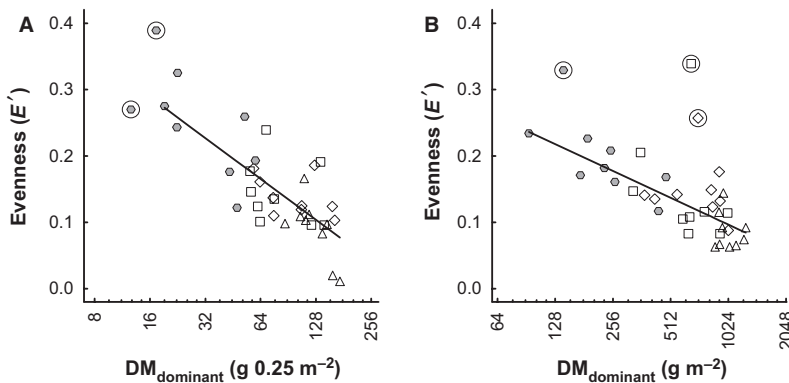


Fig. 4 Relationships between evenness (E') and biomass of dominant species (DM_{dominant}) at flowering (A) and crop harvest (B). Circled points were excluded from the analyses. See Table 2 for statistical information. Symbols: no crop (\circ), pea (\square), barley (\triangle), mixture (\diamond).

dominant species biomass, DM_{dominant} , as a predictor gave the best description of evenness (AICc = -113.4 and -137.8, respectively, $w_i = 1$ for both flowering and crop harvest; Table 2). Evenness thus decreased as the dominant species in the community became more productive, regardless of whether the dominant species was a crop or weed. Indeed, evenness tended to be higher in fallows than in crop treatments (Fig. 4).

Discussion

The dominant species, that is the one with the highest biomass, modulated the species richness and evenness of arable plant communities, whether the dominant species was a crop or a weed. An upper boundary appeared more appropriate than a central trend model to describe the relationship between species richness and total community biomass as it was initially predicted (Figs 1A and 2B). Species richness of understory weeds decreased with their decreasing biomass, which in turn was caused by competition by either the crop or the dominant weed in fallows (Fig. 3). Similarly, evenness decreased as the

dominant species in the community became increasingly productive, regardless of whether the dominant species were weeds or crops (Fig. 4).

Dominant weeds in fallows were not as suppressive as crops

Weed-dominant species in fallows were not as suppressive as crops. Crops are selected to grow fast and produce high yields and sown in relatively constant densities. In addition, despite specific differences in biomass production, crops may have some competitive advantage over weeds due to the more uniform planting and synchronic emergence patterns that enables rapid and efficient space pre-emption (Mohler & Liebman, 1987; Holt, 1995; Poggio, 2005). In fallows, however, limitations of both species and seeds may constrain changes in richness (Figs 2 and 3). Limited species availability is suggested by the low number, or total absence, of competitive species, highly responsive to fertility, such as annual grasses like *Lolium multiflorum* Lam. If dominant grasses at high densities had domi-

nated in fallows, suppressive effects on species diversity would have been similar to those from barley plants in either monocultures or mixtures (Figs 3 and 4). Because of the absence of weeds with traits conferring abilities to dominate (competitive dominants *sensu* Grime, 1979), few short-lived forbs dominated in fallows, such as *A. cotula*, *C. didymus*, and *S. media*. The higher success of establishment of short-lived species, probably due to recent soil disturbance and field abandonment and less asymmetric competition of weed species dominating in fallows, suggests the occurrence of seed limitation (Turnbull *et al.*, 2000). Thus, manipulating the densities and proportions of dominant and subordinate species is crucial for restoring plant communities in abandoned fields (Brown & Fridley, 2003).

Richness–biomass relationship

The decline of species richness as community biomass increased was better explained by an upper boundary than by a central trend linear model, as originally predicted. Biomass would control the maximum number of species that may occur in the community, regardless of the availability of species and propagules. Variation of richness below the upper boundary would be caused by the influence of additional explanatory variables that were not considered here, such as unmeasured ecological factors, temporal fluctuations, or within-plot heterogeneity (Grace, 1999). Differential expansion and decay of leaf area in pea and barley crops could have caused some of the variability in species richness observed in our experiments. Canopy gaps, usually more frequent in pea than in cereal crops, may lead to lower crop competition, promoting greater weed richness in pea (Poggio *et al.*, 2004). In addition, while barley plants usually remain upright at maturity, pea plants frequently lodge when bearing seeds and canopy is decaying. Thus, lodging in pea could help to explain the decrease in weed richness without changing total biomass (Fig. 2B). Conversely, the lower variability in richness in fallows suggests that dominant weeds in fallows were not as suppressive of the understory weeds as crops. Thus, the asymmetric competition of crops may explain the decreasing pattern of species richness in arable plant communities. As crop productivity increases, crop shading regulates the growth conditions of the understory weeds, which are increasingly restricted owing to early canopy closure. The difference in direct sunlight reaching the leaves of crops and weeds is accounted by RLA, which drives the negative correlation between RLA of crops and weed biomass. Hence, an increasing number of subordinate weed species are competitively excluded and species richness consequently decreases (Fig. 3).

Our findings thus agree with that of previous research reporting a decrease in species richness in semi-natural vegetation as less solar radiation reaches the ground (Goldberg & Miller, 1990). Results thus support the shading hypothesis, which states that standing biomass affects the diversity of plant communities, mainly by restricting the sunlight reaching understory plants (Newman, 1973). Besides modulating weed growth, crop shading reduced weed diversity by modifying the light quality and thermal environments of the crop understory. Both variables are key signal factors determining germination and secondary dormancy of seeds, seedling recruitment and self-thinning in crop/weed canopies (Ballaré & Casal, 2000; Benech-Arnold *et al.*, 2000).

Evenness–biomass relationship

Crops dominated over understory weeds and hence reduced evenness by imposing a strongly asymmetric competition for light (Weiner, 1990). The decrease in evenness indicates that the dominance hierarchy becomes progressively stronger as the dominant crop species becomes more productive (Fig. 4). The negative correlations between evenness and biomass agree not only with what is predicted by theory, but also with the very few studies on plant communities (Drobner *et al.*, 1998; Weiher & Keddy, 1999). These two investigations, however, could not be conclusive about the ecological factors explaining the observed pattern, because the negative tendency of the evenness–biomass relationship was not different from that obtained after permutation procedures. In both studies, the decreasing correlation was thus considered an artefact arising from the nearly geometric distribution of biomass among species in most plant communities, although each study gave different support to this explanation (Drobner *et al.*, 1998; Weiher & Keddy, 1999).

Evenness was negatively associated with biomass of the dominant species in arable plant communities, but not with total community biomass as originally predicted (Figs 1B and 4). Moreover, our analytical procedure attempted to overcome the eventual sources of artefactual associations between evenness and biomass (Drobner *et al.*, 1998; Weiher & Keddy, 1999). First of all, as the evenness measure used here was independent of species richness, evenness calculations were not affected by how species-rich plant communities were (Smith & Wilson, 1996). Second, standing biomass and species richness have been consistently sampled by using standard quadrat sizes across sampling dates and experiments. The sample sizes used here allowed accurate ecological measurements (Grime, 1997) and agreed with previous studies on species diversity

determination in herbaceous plant communities (see Table 2 in Grace, 1999). Finally, we also assumed that the distribution of total standing biomass among species in herbaceous plant communities is usually geometric (i.e. highly uneven with low species richness as dominance increase (Wilson, 1991)). Biomass distribution is thus expected to be steeper as the dominant species in the community becomes increasingly productive, because it has pre-empted a greater share of available resources and evenness is consequently lower. Dominance usually results from traits conferring greater competitive ability, which allow the dominant population to prevail in the community while others are competitively suppressed (Grime, 1979). Hence, species identity emerges as a key aspect that needs to be considered to understand how dominance/evenness patterns in herbaceous plant communities are determined. This is indicated by the different effects on evenness between crops and dominant weeds in fallows (Fig. 4).

Conclusions

Our findings provide models of widespread application in different farming scenarios to characterise the trajectories that species richness and evenness may follow, as the growth of both dominant and subordinate species varies. Species richness and evenness are constrained by community biomass. Maximum species richness can be established by estimating community biomass. However, biomass of the dominant species, which determines a large proportion of the community biomass, may also be used as a predictor for variation in both species richness and evenness. This supports the design of cropping systems based on ecological and agronomical knowledge to suppress weed growth, such as the management of crop density by using mixed and smother crops, and even breeding of highly competitive crop varieties. Our results also suggest that restoration of species-rich arable plant communities after cropping abandonment needs the manipulation of species composition and density by reintroducing desirable species. This practice would be essential to maintain ecological functions associated with biodiversity in temperate, intensively managed agro-ecosystems.

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