LETTER

Variety in evolutionary strategies favours biodiversity in habitats of moderate productivity

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The mechanism whereby biodiversity varies between habitats differing in productivity is a 'missing link' between ecological and evolutionary theory with vital implications for biodiversity conservation, management and the assessment of ecosystem services. A unimodal, 'humped-back' relationship, with biodiversity greatest at intermediate productivities, is evident when plant[1-11], animal[12-15] and microbial[16] communities are compared across productivities in nature. However, the mechanistic, evolutionary basis of this observation remains enigmatic. We show, for natural and semi-natural plant communities across a range of bioclimatic zones, that biodiversity is greatest where communities include species with widely divergent values for phenotypic traits involved in 'resource economics' and reproductive timing, coinciding with intermediate biomass production, whilst each productivity extreme is associated with small numbers of specialised species with similar trait values. Our data demonstrate that evolution can generate a greater range of phenotypes where large, fast-growing species are prevented from attaining dominance and extreme adaptation to a harsh abiotic environment is not a prerequisite for survival.

The humped-back model (HBM)[1,2] describes a relationship between biodiversity and productivity whereby no potential exists for high biodiversities in habitats with either extremely high or low biomass production, whilst biodiversity may reach the greatest values at intermediate productivities, although this potential is not always achieved. As such, the model describes an upper limit to biodiversity-productivity relationships, or a "filled"[6] or "saturated"[17] unimodal curve. Recent attempts to falsify the HBM in herbaceous plant communities have either

specifically excluded wild species assemblages from the analysis[18] or have been restricted to a limited biomass range[19] representing only around a third of the greatest annual biomass production (>4300 g m^{-2})[20] evident for grassland communities in nature, and can be discounted.

The main theoretical implication of the HBM is that in extreme environments organisms can only survive by exhibiting a high degree of adaptive specialisation, whereas moderate conditions allow a range of intermediate evolutionary strategies, and indeed greater variability in adaptive traits between species, greater niche segregation, and thus greater biodiversity. This concept of adaptive specialisation at productivity extremes should apply as much to high productivity environments as it does to abiotically harsh environments, because organisms specialised for resource acquisition are more likely to monopolise resources and exclude other species[21]. We investigate the hypothesis, for herbaceous communities from a range of terrestrial ecosystems spanning lowland continental to alpine bioclimatic zones, that a humped-back diversity/biomass curve exists whereby greater species diversity is associated with greater variability in a range of phenotypic trait values and in the overall evolutionary strategies that emerge from these suites of traits.

Fig. 1a shows that the greatest species richness (41-42 species per 16 m^{-2} plot) is apparent at intermediate biomass (480-910 g m^{-2} of peak above ground dry matter) and diminishes towards both the lowest and highest biomasses (i.e. 5 species at 101 g m^{-2}, and 1 species at 2880 g m^{-2}, respectively). This range of biomass values, and the position of the peak in biodiversity along the biomass gradient, is similar to values found by other authors[1,2,22] and allows a high degree of confidence that our data encompass a wide productivity range, providing a sound foundation for the following novel analysis of adaptive traits and strategies along the gradient. Firstly, not only do our data demonstrate a humped-back relationship between species richness and peak biomass; Simpson's reciprocal diversity index (1/D; a widely-used measure of the number of species weighted to account for relative abundance) and the number of adaptive strategies (CSR strategies[16,21]) both show unimodal relationships with biomass, coinciding with the pattern exhibited by species richness (Fig. 1b,c).

Crucially, a multivariate analysis (Fig. 2a) including different measures of biodiversity, biomass and species traits (and, notably, the variance of trait values within each community), demonstrates that the greatest biodiversities are evident for communities incorporating species with widely divergent values for traits implicated by other authors[23] in resource economics (i.e. variance in specific leaf area, SLAvar; leaf dry matter content, LDMCvar), lateral spread (LSvar) and reproductive timing (flowering start; FSvar), at intermediate levels of biomass production. Communities producing the most biomass include small numbers of large species, characterised

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by tall canopies and large leaf masses, with relatively invariable trait values (Fig. 2a). Adaptive specialisation is also exhibited within communities of small species that reproduce early (low FS) and exhibit extremely acquisitive (high SLA, low LDMC) adaptive strategies (Fig. 2a). Variance in the traits SLA, LDMC, LS and FS (i.e. trait variances shown by the PCA to be most closely associated with biodiversity) reach the greatest values at intermediate biomasses of between 500 to 1000 g m^{-2} (Fig. 2 b,c,d,e), mirroring the humped-back biodiversity/biomass curves shown in Fig. 1. The greatest biodiversities are composed mainly of subsidiary species (i.e. with relative abundances of less than 10%; Fig. 2f), suggesting that at intermediate productivities a greater range of relatively scarce niches is available. As the peak in biodiversity at intermediate productivity is also characterised by the greatest range of CSR adaptive strategies (Fig. 1c), evolutionary divergence in the manner in which resources are partitioned between life-history traits implicated in competitive ability, stress-tolerance and regeneration appears to be central to biodiversity creation. However, canopy height exhibits a significant positive linear correlation with biomass production (Fig. 2g) suggesting that maximisation of productivity is associated in a relatively straightforward manner with large size. Thus whereas the diversity of dominant species, compared between contrasting communities, is associated simply with size diversity (the degree of C-selection), biodiversity within each community depends more on resource economics and regeneration (S- and R-selection).

Our data provide the first empirical support, in wild communities, for the hypothesis that biodiversity is limited at productivity extremes by a requirement for extreme adaptive specialisation, whilst divergence in resource economics and reproductive timing at intermediate productivities creates the potential for the survival of a greater range of subsidiary species. As humped-back curves have also been demonstrated in marine[12-15] and microbial[16] ecosystems, the conclusion that variability in resource economics and reproductive timing generates biodiversity is likely to be of widespread relevance, particularly for biodiversity conservation. For instance, the majority of rare or endangered species in herbaceous plant communities are found at intermediate biomass[11]. Now it is possible to be confident why such effects occur. Evolution has free rein, and ecosystems become more complex, when the habitat is not characterised by extremely harsh abiotic selection pressures – but also when conditions are not so benign that any single species can rise to dominance.
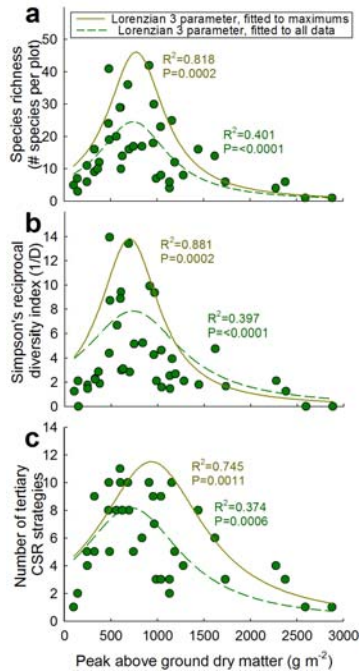
Fig. 1. Changes in biodiversity along the gradient of above ground dry weight (standing crop + litter) for 39 herbaceous plant communities: a). species richness (number of species per 16 m^2 plot), b). Simpson's reciprocal diversity index (1/D), c). adaptive strategies (tertiary CSR plant strategies).
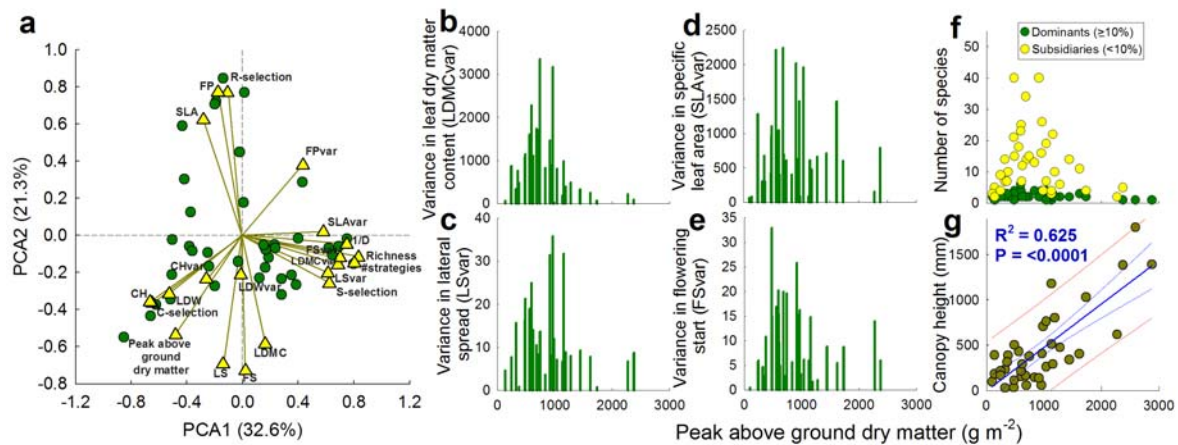

Fig. 2. Variability in the adaptive traits of herbaceous plant species in relation to biomass (peak above ground dry matter) and different measures of biodiversity. a). a principal components analysis (PCA) showing the main axes of variation in the data. Axis 1 is an axis of variation between biodiversity (trait variance and species diversity) and large plant size and biomass production, specifically: the number of species (Richness), Simpson's reciprocal index (1/D), the number of CSR strategies (# strategies), variance in the traits leaf dry matter content (LDMCvar), specific leaf area (SLAvar), lateral spread (LSvar), flowering start (FSvar), and the extent of S-selection were positively associated with PCA1, whilst peak above ground dry matter, canopy height (CH), leaf dry weight (LDW) and the extent of C-selection were negatively associated. Axis 2 is an axis of variation between ruderalism (absolute SLA, flowering period (FP), the extent of R-selection) and (negatively) biomass production (peak above ground dry matter, C-selection, LDMC, LS and FS). Panels b). – e). show variance, within communities along the biomass gradient, in values for traits positively correlated with PCA axis 1: LDMCvar, LSvar, SLAvar and FSvar, respectively. Panel f). demonstrates that the peak in biodiversity at intermediate biomass is composed mostly of subsidiary species (subordinates or transients) with relative abundances of less than 10%, and g). shows the positive linear correlation between biomass and canopy height, occurring negatively along PCA axis 2.

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Methods

We quantified species relative abundance (and identity), peak above ground dry matter (i.e. standing crop plus litter harvested at the phenological peak of production at each site[1,2]), adaptive trait values (listed below) for 39 natural and semi-natural herbaceous communities selected to represent a diverse range of seasonal, elevational and ecological conditions typical of continental Europe. We worked with plant communities for the simple logistical reason that "*plants stand still and wait to be counted*"[24], allowing us to sample all species comprising each community and over a wide range of communities, with geographic locations spanning the Po Plain of Lombardy to the high Alpine zone of Northern Italy (listed in Supplementary Table 1, including geographic locations and elevations recorded using a Garmin eTrex Summit GPS receiver (with an electronic barometer), alongside details of the particular plant communities investigated at each site).

For each community a standard quadrat size of 16 m^2 was employed during floristic surveys and point analysis, during which counts of species in contact with a needle inserted at 75 points on a grid within the survey area provided a measure of species relative abundance[25,26]. Simpson's reciprocal diversity index was calculated, as previously described[25], using these data. Sampling and subsequent analysis of functional traits were carried out for species touched by the needle during point analysis four or more times. Traits were measured from six replicate individuals, avoiding damaged or diseased plants. Canopy height (CH) and lateral spread (LS) were measured directly in the field, and leaves were collected from these plants and taken to the laboratory for the measurement of leaf fresh weight (LFW), leaf dry weight (LDW) and leaf area (LA), using standard methods as described previously[25,26]. Leaf dry matter content (LDMC) and specific leaf area (SLA) were then calculated[24]. Phenological traits, measured as the month of flowering onset for each species (flowering start, FS) and the duration of flowering, in months, (flowering period, FP). These were used alongside leaf and whole-plant traits to calculate adaptive strategies, using CSR classification[27] as detailed and justified previously[25,26,28], and as applied to over a thousand plant species *in situ* in a range of habitats throughout Europe[16].

Biomass was sampled at the phenological peak of production, between April and October, during 2009 to 2010. Dates as early as April were necessary for communities of therophytes on disturbed ground at low elevations that peak extremely early, but these communities were nonetheless sampled during the peak of biomass production and the fruiting phase of the majority of species within the community. Biomass was sampled according to Al-Mufti et al.[2]: i.e. standing crop plus litter was harvested using a battery-powered clipper and scissors from

three 0.25 m^{-2} sub-plots, with data combined to calculate the mean dry weight per m^2 at each site. Dry weight was measured following drying in a forced-air oven at 95°C for eight hours.

Acknowledgements

Supplementary Table 1. Locations and physiognomic descriptions of the plant communities sampled. Nomenclature follows Conti, F., Abbate, G., Alessandrini, A. & Blasi, C. (eds.) *An annotated checklist of the Italian vascular flora* (Palombi Editori, Roma, 2005).

Survey number	Survey date	North coordinate	East coordinate	Elevation (m a.s.l.)	Slope (°)	Exposure (°)	Physiognomic description
1	7/5/2009	45°32'9.1"	10°11'12"	130	0	0	Abandoned grassland dominated by *Poa pratensis* L.
2	14/5/2009	45°27'44.7"	10°7'55.2"	92	0	0	Wasteland dominated by *Ranunculus sardous* Crantz
3	25/6/2009	45°45'48.8"	10°34'20.1"	1050	5	195	Verge dominated by *Pteridium aquilinum* (L.) Kuhn subsp. *aquilinum*
4	4/7/2009	45°53'10.3"	10°22'31.6"	1770	0	0	Nitrophilous meadow dominated by *Poa annua* L.
5	12/7/2009	45°48'18.2"	10°20'48.7"	1000	5	220	Margins dominated by *Stachys sylvatica* L.
6	21/7/2009	46°31'09.8"	10°25'46.7"	2646	20	279	Discontinous grassland dominated by *Luzula alpinopilosa* (Chaix) Breistr. subsp. *alpinopilosa*
7	22/7/2009	46°31'54.7"	10°25'16.5"	2608	25	285	Dwarf shrub vegetation dominated by *Kalmia procumbens* (L.) Gift, Kron & Stevens ex Galasso, Banfi & F. Conti
8	23/7/2009	46°31'05"	10°25'47.1"	2600	12	330	Grassland dominated by *Carex curvula* All.
9	23/7/2009	46°31'26.6"	10°26'16.5"	2673	10	5	Dwarf shrub vegetation dominated by *Salix herbacea* L.
10	1/10/2009	45°51'15.5"	10°16'17.1"	1733	5	60	Peaty slopes dominated by *Eriophorum angustifolium* Honck.
11	1/10/2009	45°51'14.6"	10°16'17.5"	1742	5	70	Peatland dominated by *Trichophorum cespitosum* (L.) Hartm.
12	1/10/2009	45°51'14.5"	10°16'17.1"	1742	5	70	Peatland dominated by *Carex panicea* L.
13	10/4/2010	45°39'28.9"	10° 4'35.1"	504	5	205	Wasteland dominated by *Capsella grandiflora* (Fauché & Chaub.) Boiss.
14	26/4/2010	45°33'06.1"	10°10'18.4"	148	0	0	Understorey dominated by *Ranunculus ficaria* L. and *Anemone nemorosa* L.
15	6/5/2010	45°19'01.5"	9°58'32.6"	52	0	0	Wasteland dominated by *Stellaria media* (L.) Vill.
16	24/5/2010	45°31'11.8"	10°13'40.1"	130	0	0	Wasteland dominated by *Avena fatua* L.
17	28/5/2010	45°19'39.5"	9°56'26"	44	0	0	Wasteland dominated by *Saxifraga tridactylites* L.
18	1/6/2010	45°20'11.4"	9°54'40.8"	39	0	0	River margin dominated by *Elymus athericus* (Link) Kerguélen
19	9/6/2010	45°35'56.6"	8°43'27.2"	207	0	0	Meadow dominated by *Filago minima* (Sm.) Pers.
20	29/6/2010	45°32'45.6"	10°16'45.7"	790	20	150	Meadow dominated by *Bromus erectus* Huds.
21	5/7/2010	45°54'00.2"	10°24'12.4"	2010	15	185	Pasture grassland dominated by *Horminum pyrenaicum* L.
22	5/7/2010	45°53'46"	10°23'51.9"	2020	30	250	Pasture grassland dominated by *Carex sempervirens* Vill.
23	9/7/2010	45°44'48.8"	10°09'56.6"	1571	0	0	Seasonal livestock enclosure dominated by *Rumex alpinus* L.
24	12/7/2010	45°38'41.4"	10°09'00.3"	720	15	198	Meadow dominated by *Arrhenatherum elatius* (L.) P. Beauv. ex J. & C. Presl
25	15/7/2010	45°44'45.2"	10°10'14.7"	1492	30	235	Grassland dominated by *Festuca paniculata* (L.) Schinz & Thell. subsp. *paniculata*
26	19/7/2010	45°37'25.1"	10°04'36.1"	190	0	0	Wasteland dominated by *Sorghum halepense* (L.) Pers.
27	22/7/2010	45°44'56"	10°09'44.6"	1621	10	190	Meadow dominated by *Phleum alpinum* L.
28	4/8/2010	45°52'01.1"	10°22'39.5"	2150	5	300	Pasture dominated by *Nardus stricta* L.
29	4/8/2010	45°52'46.3"	10°23'17.1"	1890	25	266	Stream margin dominated by *Senecio alpinus* (L.) Scop.
30	6/8/2010	45°45'18.7"	10° 9'50.12"	1780	20	260	Pasture dominated by *Geum montanum* L.
31	18/8/2010	45°48'22.8"	10°24'26.1"	1726	15	74	Grassland dominated by *Sesleria caerulea* (L.) Ard.
32	31/8/2010	45°27'20"	10°10'18.1"	97	0	0	Wasteland dominated by *Setaria viridis* (L.) P. Beauv.
33	15/9/2010	46°01'52.7"	8°36'62.4"	1018	10	100	*Pteridium aquilinum* (L.) Kuhn subsp. *aquilinum* stand
34	15/9/2010	46°02'11.2"	8°35'19.4"	1380	30	165	Abandoned oldfield meadow dominated by *Molinia caerulea* (L.) Moench subsp. *arundinacea* (Schrank) K. Richt.
35	29/9/2010	45°28'03.1"	10°12'25.7"	95	0	0	Wasteland dominated by *Abutilon theophrasti* Medik.
36	11/10/2010	45°36'34.3"	10°12'25.3"	211	0	0	Wasteland dominated by *Helianthus tuberosus* L.
37	13/10/2010	45°32'57.9"	8°48'40.7"	180	0	0	Wasteland dominated by *Artemisia verlotiorum* Lamotte
38	13/10/2010	45°34'15.1"	8°42'22.2"	192	0	0	Margin dominated by *Solidago canadensis* L.
39	28/10/2010	45°45'20.8"	10°35'47.5"	602	1	272	Stream margin dominated by *Fallopia japonica* (Houtt.) Ronse Decr.