



What drives plant species diversity? A global distributed test of the unimodal relationship between herbaceous species richness and plant biomass

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Nomenclature

Hitchcock & Cronquist (1973)

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Introduction

Patterns of species diversity have long been of interest to ecologists (McIntosh 1985). This topic has only become more important and relevant due to loss of biodiversity caused by human activity, which is higher now than at any other time in human history (Vitousek et al. 1997; Millennium Ecosystem Assessment 2005). One of the potential consequences of biodiversity loss is a negative effect on ecosystem function (Chapin et al. 1998; Tilman et al. 2012). Therefore, an understanding of patterns and processes in species diversity is critical for ecosystem management and conservation measures. As theories develop and improve (Jentsch & Beierkuhnlein 2008) they can be more readily challenged through empirical investigation.

The relationship between diversity and productivity is among the most widely documented patterns, applying to both plant and animal distributions (Rosenzweig &

Abstract

Question: For over a century, ecologists have grappled with the question “what drives species diversity?” Urgent global issues such as loss of biodiversity and the relative importance of species richness for ecosystem function and services has heightened the relative importance of understanding processes that control species diversity. Here we present the plans for a global coordinated distributed experiment for herbaceous communities, the HerbDivNet, to test the hump-backed model, a unimodal relationship between species richness and above-ground plant biomass plus dead plant litter HBM, to determine whether scale may influence the HBM, and to explore drivers of plant diversity.

Location: Globally distributed experiment.

Methods: We propose a nested, standardized sampling design 8 × 8 m, with 1 m² plots, taken from multiple site locations along a range of sites varying in primary productivity.

Results and Conclusions: We welcome others with an interest in using global, standardized, coordinated distributed experiments to explore patterns and processes in herbaceous plant communities to join HerbDivNet in the search of new insights to drivers of plant species diversity.

Abramsky 1993; Tilman & Pacala 1993; Gaston 2000). One promising general model for the prediction of herbaceous plant diversity is the above-ground biomass/species richness relationship (‘hump-backed model’ – HBM) first proposed by Grime (1973a,b, 1979), which states that species richness reaches a maximum at intermediate primary productivity (or biomass production). Grime suggests that species richness is limited at low biomass production by minimal availability of mineral nutrients and, in some cases, high levels of disturbance. Examples of low biomass production environments include alvars (Catling & Brownell 1998), fens (Gorham 1961; Vitt 1990), pitcher plant bogs (Peet & Allard 1993), cliffs (Goldsmith 1973), dry acidic grasslands (Jentsch & Beyschlag 2003), gravel shorelines (Keddy 1984), desert and semi-arid shrublands (Golodets et al. 2013). The herbaceous plants found in these environments are generally small, long-lived and slow growing. At high biomass production, Grime suggests

that species richness is limited by interspecific competition (e.g. freshwater marshes; Wilson & Keddy 1986; Twolan-Strutt & Keddy 1996). Plants in these environments are generally tall and fast-growing, with extremely high productivity examples often forming monospecific stands (e.g. *Phalaris*, *Typha*). At intermediate standing crop, Grime suggests that species richness is released from these extremes and controlled by a combination of these factors (e.g. calcareous grasslands; Al-Mufti et al. 1977).

Many studies have found patterns consistent with the HBM: Al-Mufti et al. (1977; semi-natural grassland landscapes), Wheeler & Giller (1982; fens and marshes), Moore & Keddy (1989; temperate marshes), Puerto et al. (1990; Mediterranean grasslands), Muotka & Virtanen (1995; bryophytes in streams). Others have not: Vermeer & Verhoeven (1987; fens), Wisheu & Keddy (1989; infertile lakeshores), Gough et al. (1994; salt marshes). Some experiments have shown that, in grassland ecosystems, primary productivity is positively related to plant species diversity (see reviews of Schlipfer & Schmid 1999; Loreau et al. 2001; Roy 2001). And a recent multi-site experiment also did not show conclusive evidence for the HBM (Adler et al. 2011).

Following over 30 yrs of study, three meta-analyses (Mittelbach et al. 2001; Gillman & Wright 2006; Pärtel et al. 2007) plus a critical review of those same meta-analyses (Whittaker 2010), the HBM continues to be debated. Whittaker (2010) alluded to the need for a broad experimental approach, rather than a meta-analysis, to address this important question. A recent paper by Peter Adler and others does just that, where they present data from 48 globally dispersed sites (although 35 – ca. 73%, of these sites were in the USA), with 10 1-m² plots sampled at each site (Adler et al. 2011). Data collected were species richness and live above-ground biomass. They use linear and quadratic regressions at each of the 48 sites to determine a best fit. Thirty-three of the sites showed a non-significant relationship, five were linear negative, five linear positive, three were convex and only one displayed the hump-backed convex relationship. They conclude that, 'We found no clear relationship between productivity and fine-scale (meter⁻²) richness within sites, within regions, or across the globe.' Fridley et al. (2012) replied that the design and the interpretation were flawed because of low representation of high productivity sites, the fact that only live above-ground biomass, not plant litter, was included in the measure of productivity, and that sites with anthropogenic effects were excluded from the analysis.

The importance of scale

The debate is ongoing regarding the mechanism behind the unimodal distribution of species richness (Garcia et al.

1993; Oksanen 1996, 1997; Grime 1997; Rapson et al. 1997; Stevens & Carson 1999; Rajaniemi 2003; Chiarucci et al. 2004; Scheiner et al. 2011). Oksanen (1996, 1997) suggested that the observed 'hump-backed model' is an artifact arising from the use of small sample plot size. Consider, for example, a small 1-m² plot. This plot may contain many small individuals, but because space is limited it can only contain a few large individuals. Since the combined volume of the large individuals is greater than that of the small individuals the total biomass of the plot containing the large individuals is higher. Therefore, there is a negative relationship between total biomass and species density. This relationship has been quantified for single species, even-aged stands and is termed 'self-thinning' (Yoda et al. 1963; White 1980). The point that Oksanen (1996) makes is that if there is a reduction in density then the number of possible species is also necessarily reduced. Furthermore, Oksanen's (1996) 'no-interaction model' demonstrated that the humped relationship could be produced without assuming any biological interactions. Stevens & Carson (1999) experimentally tested the relative importance of stem density and competitive ability along a fertility (and thus, biomass) gradient and found that stem density exerted a larger influence in determining plant species richness. Chiarucci et al. (2004) also found evidence to suggest density can have a significant effect in controlling species richness, but that species also interact and that competitive exclusion can occur, perhaps simultaneously.

If the sample size is increased beyond the square meter plot, thereby removing the criticisms of Oksanen (1996) and Stevens & Carson (1999), is the unimodal relationship between biomass and species richness apparent? Rapson et al. (1997) sampled species richness along a productivity gradient at nine different scales from 10 × 10 cm to 2 × 2 m. At each of these scales, the unimodal relationship was evident. Scheiner & Jones (2002) investigated the productivity–diversity relationship at much larger geographic and ecological scales, from 20 × 20 km to 240 × 240 km. For the state of Wisconsin, they found a U-shaped relationship between terrestrial vascular plant species richness and net primary productivity. An understanding of how and at what scale the relationship between species richness and productivity may change is still missing. Does the relationship change between the scale of 2 × 2 m and 20 × 20 km? If the HBM is supported at the 1-m² scale, keeping in mind that individual plants within a 1-m² area are likely to interact, will the HBM also be supported at larger scales, e.g. 8 × 8 m, where a herbaceous plant in one corner is unlikely to interact directly with a herbaceous plant in another corner? A new comprehensive study is needed to test spatial scale and its effect on the relationship between species

richness and herbaceous plant biomass in different ecosystems.

Why should plant litter be included in a test of the HBM?

The original HBM proposed by Grime included plant litter, because plant litter is a function of annual net primary productivity in most grasslands (Grime 1979). Plant litter can have effects on the plant community, from altering nutrient cycling to impeding vegetative growth and seedling recruitment (Knapp & Seastedt 1986; Foster & Gross 1998; Patrick et al. 2008). In addition, plant litter provides clues to site history. For example, if a site has been moderately to heavily grazed over the past few years, there will be less litter (Su et al. 2005). Likewise, if there had been a recent fire, litter loads would be minimal (Noy-Meir 1995). Therefore, it cannot always be assumed that litter biomass is correlated with live biomass, which makes it an important element of the plant community to measure. Plant litter not only directly affects soil biota, nutrients and plant community dynamics, but can be an important reflection of past management/disturbance practices. The plant litter layer can originate from previous years, and it is not possible to distinguish between the litter of different years. Therefore litter will not necessarily be an accurate reflection of annual primary production, but the accumulation of litter is an indicator of primary productivity and relates to plant community processes. Plant litter was not included in the Adler et al. (2011) analysis of species richness and plant biomass.

A global test of the HBM biomass/species richness relationship

The urgency to understand what drives plant diversity in the era of global changes and observed biodiversity losses necessitates the testing of promising models and theories. Towards this end, a comprehensive experiment is needed to test the HBM. With this aim in mind, and to explore future research directions in the study of herbaceous plant diversity, we propose the following rationale for a test of the HBM.

The fact that the HBM has been supported by some studies and rejected by others begs the question of why there are apparently contradictory results. Much of the problem may lie in the use of inadequate data sets. Moore & Keddy (1989) made this observation when they compared within site and among site comparisons of the biomass/species richness relationship in wetland communities. The hump-backed relationship was only evident when tested among sites (see also Guo & Berry 1998). As an example, Fig. 1 displays a conceptual of the HBM model. The solid line is

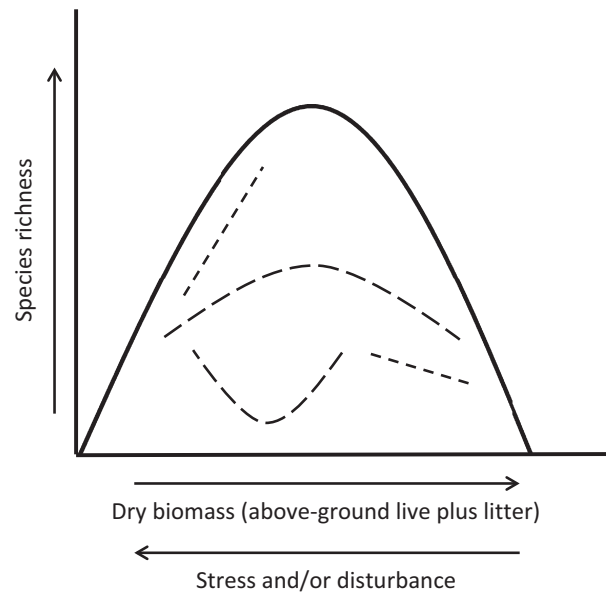


Fig. 1. The hump-backed model (HBM) relationship between species richness and dry above-ground biomass and stress/disturbance. The solid line represents the HBM maximum potential species richness. The dashed lines represent hypothetical linear and quadratic regressions found by subsampling 1-m² plots with limited range in biomass.

the HBM model, representing the maximum potential species richness along a gradient of live above-ground biomass plus plant litter. Considering that the solid line represents a boundary, any points that fall below the line are feasible. Therefore, the dashed curves represent potential linear and quadratic relationships one might find, given the range in 1-m⁻² biomass within a subsample. Plainly, all four scenarios are possible: a positive linear, a negative linear, a concave quadratic, and a convex quadratic. The relationship depends on the range of biomass sampled. For this reason, a robust test of the HBM in herbaceous plant communities must include an adequate range in biomass production (from 1 to at least 3000 dry·g·m⁻²·y⁻¹), with good representation of biomass by square meter along the range. The dry biomass measurements must also include not only live above-ground biomass, but plant litter as well. Biomass must be sampled at peak of the growing season and no <3 mo disturbance-free, or disturbance-free history to that particular plant communities peak standing crop; i.e. no mowing, haying, grazing or fire. It is important to point out that prior disturbance, even if it is sustained and/or intense, is irrelevant in terms of site selection. Disturbance is a factor in the HBM, sharing the same gradient as stress on the x-axis (increasing from right to left, the opposite direction of biomass; Fig. 1). Historical disturbance can affect community composition, but the inclusion of plant litter can provide evidence of disturbance history.

The Herbaceous Plant Diversity Network (HerbDivNet) has been established to address the need to test the HBM. So far, HerbDivNet includes more than 66 participants from six continents and 19 countries (Fig. 3).

A call for a coordinated distributed experiment

Twenty-two representatives from the HerbDivNet met on 28th June 2013 in Tartu, Estonia, during the 56th Annual Symposium of the International Association for Vegetation Sciences (IAVS; Öpik et al. 2014). We propose a Coordinated Distributed Experiment (CDE) to test the HBM. A CDE is a standardized, geographically distributed experiment conducted by multiple collaborators simultaneously (see Fraser et al. 2013 for details). The design is an 8×8 -m grid containing 64 1-m^2 plots (Fig. 2). We encourage the use of permanent markers so that there is the opportunity to revisit plots for future testing and monitoring. Bury two magnets in opposite corners of the 64-m^2 sample grid approximately 20-cm deep; in combination with GPS coordinates, this guarantees accurate position of plots without fear of human interference. Our study will focus primarily on grassland herbaceous community types (tropical and temperate). For each plot, the number of species should be identified and counted. Total above-ground biomass (including plant litter) at peak biomass will then be harvested, dried and weighed by plot. Live biomass and litter is separated prior to drying and weighing. There is no need to separate biomass by species. Restrict sampling to herbaceous plant communities; however, the occasional small woody plant may be found within a sample area. If a woody plant is encountered, identify the species, add to species list but in a clearly marked column that labels the species as a woody plant, and measure the height and canopy spread. If the woody plant covers more than a 1-m^2 plot, include the percentage cover of the shrub for each of the 1-m^2 plots the shrub covers. Harvesting woody plant

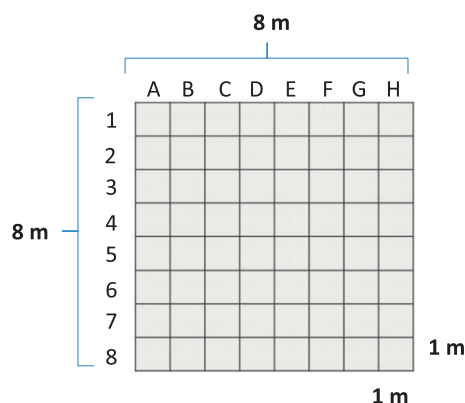


Fig. 2. The proposed sampling grid for testing the hump-backed model of species richness and biomass in relation to scale.

above-ground biomass is not necessary, as this is not included in the community live biomass. Cryptogams are not counted in the species richness nor are they included in the harvest for biomass. Including information on species pools is ideal but optional because not all sites will be in locations well studied and with known species pools. There is also ambiguity regarding the definition and calculation of the species pool. At the very least, the basic data will allow estimates of species pools by region simply by compiling the list of species present in the 64-m^2 grids.

The ideal level of participation for each investigator would be to sample at least six grids, two each at three relatively different levels of productivity from low ($\sim 1\text{--}300\text{ g}\cdot\text{m}^{-2}$) to medium ($\sim 300\text{--}800\text{ g}\cdot\text{m}^{-2}$) to high ($>800\text{ g}\cdot\text{m}^{-2}$). It is likely that many sites will have a history of grazing or fire and may currently be under some form of management. Therefore, sampling should be done at least 3 mo after it was last grazed or burned.

Future directions

The HerbDivNet data set will be used to comprehensively test the HBM with respect to scale. The current data set has been produced by over 60 researchers from 19 countries and includes 157 64-m^2 grids (Fig. 3). The worldwide environmental representation of the HerbDivNet data set makes it of unique value in all standards, and will secure a much broader representation of herbaceous plant communities when testing the HBM. Nevertheless, more participants, especially from under-represented geographical locations or grassland types (e.g. Russia, Kazakhstan, Australia, northern Africa, western Africa and Central America) are very welcome to join by delivering data.

The data can be parsed according to grassland type and site management. Similar to Adler et al. (2011), we will use linear and quadratic regressions to test the relationship between biomass and species richness. We will also use quantile regression to test the boundary limits of the relationship between biomass and species richness.

In addition to the basic data collected by all groups (biomass and species richness), we encourage sampling and collaboration on other data collections, including e.g. soil nutrient concentrations, leaf nutrient concentrations and mycorrhizal fungi community analysis. With the basic data, and other coordinated sampling, the following research topics can be addressed: whether beta diversity indices vary with productivity; whether phylogenetic diversity varies with productivity and follows the same patterns as species richness; the relationship between productivity, plant functional groups and species richness; whether species pools and 'dark diversity' (sensu Pärtel et al. 2011) is related to local site productivity and species richness patterns; back-casting with satellite imagery to



Fig. 3. World map identifying current HerbDivNet site locations, with the expectation that the participant list will expand, especially in under-represented locations.

explore other estimates of primary productivity by site; determining whether climatic variability by site can explain variance in species richness and biomass production patterns; determining whether mycorrhizal diversity is related to productivity and plant species richness; and, exploring spatial relationships between soil nutrient concentrations, plant species richness and biomass production.

The limitation to the current HerbDivNet data set is that it is purely descriptive, and not based on experimental manipulation. There was unanimous interest at the 28 June 2013 meeting at the IAVS Conference in Estonia in expanding the goal of HerbDivNet to explore experimental research projects. We welcome others with an interest in using global, standardized, coordinated distributed experiments to explore patterns and processes in herbaceous plant diversity to join HerbDivNet. We are convinced that through joint large-scale collaboration initiatives, it will be easier to discover ‘what drives species diversity?’

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