



## Plant species richness: the world records

J. Bastow Wilson, Robert K. Peet, Jürgen Dengler & Meelis Pärtel

### Keywords

Biodiversity; Canonical hypothesis; Macroecology; Oligo- to mesotrophic grassland; Paradox of the Plankton; Power function; Rooted presence; Scale dependence; Shoot presence; Spatial grain; Spatial scale; Species–area relation; Tropical rain forest; World flora

Received 19 September 2011

Accepted 31 January 2012

Co-ordinating Editor: Michael Palmer

**Wilson, J.B.** (corresponding author, bastow@bastow.ac.nz): Botany Department, University of Otago, PO Box 56, Dunedin, New Zealand

**Peet, R.K.** (peet@unc.edu): Department of Biology, University of North Carolina, Chapel Hill, NC, 27599-3280, USA

**Dengler, J.** (dengler@botanik.uni-hamburg.de): Biodiversity, Evolution and Ecology of Plants, Biocentre Klein Flottbek and Botanical Garden, University of Hamburg, Ohnhorststr. 18, 22609, Hamburg, Germany

**Pärtel, M.** (meelis.partel@ut.ee): Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, Tartu, 51005, Estonia

### Abstract

**Questions:** The co-existence of high numbers of species has always fascinated ecologists, but what and where are the communities with the world records for plant species richness? The species–area relationship is among the best-known patterns in community ecology, but does it give a consistent global pattern for the most saturated communities, the global maxima?

**Location:** The world.

**Methods:** We assembled the maximum values recorded for vascular plant species richness for contiguous areas from 1 mm<sup>2</sup> up to 1 ha. We applied the power function to relate maximal richness to area and to make extrapolations to the whole Earth.

**Results:** Only two community types contain global plant species maxima. The maxima at smaller spatial grain were from oligo- to meso-trophic, managed, semi-natural, temperate grasslands (e.g. 89 species on 1 m<sup>2</sup>), those at larger grains were from tropical rain forests (e.g. 942 species on 1 ha). The maximum richness values closely followed a power function with  $z = 0.250$ : close to Preston's 'canonical' value of 0.262. There was no discernable difference between maxima using rooted presence (i.e. including only plants rooted in the plot) vs shoot presence (i.e. including any plant with physical cover over the plot). However, shoot presence values must logically be greater, with the curves flattening out at very small grain, and there is evidence of this from point quadrats. Extrapolating the curve to the terrestrial surface of the Earth gave a prediction of 219 204 vascular plant species, surprisingly close to a recent estimate of 275 000 actual species.

**Conclusions:** Very high richness at any spatial grain is found only in two particular habitat/community types. Nevertheless, these high richness values form a very strong, consistent pattern, not greatly affected by the method of sampling, and this pattern extrapolates amazingly well. The records challenge ecologists to consider mechanisms of species co-existence, answers to the 'Paradox of the Plankton'.

### Introduction

Very species-rich communities fascinate biologists and challenge them to find world records. For example, Whitmore et al. (1985) claimed that their tropical rain forest plot was much richer than any previously reported, Proctor (1988) dismissed a previous value to assert his value as the record for forest trees and Kull & Zobel (1991, p. 717) reported: 'Species richness in the Laelatu wooded meadow is higher than reported in other calcicolous grasslands in Europe'. Moreover, areas with very high richness are often

valued as biological conservation hotspots (Myers et al. 2000).

The co-existence of large numbers of species is also of theoretical importance as a challenge to the 'Paradox of the Plankton' (Hutchinson 1961; Wilson 1990, 2011; Palmer 1994). The principle of Gause states that two species occupying the same niche cannot co-exist long term, so how do 942 plant species co-exist in 1 ha of tropical rain forest (Balslev et al. 1998)? Can there be 942 niches? These very rich communities are also those where the controversy on limitations to richness – sometimes saturated

vs never saturated – can be tested (Cornell & Lawton 1992; Stohlgren et al. 2008).

Studies of richness in tropical rain forests are typically made on spatial grains (i.e. scale of sampling) of up to 1 ha, but questions of richness can be asked at any spatial grain. Especially, since plants are sedentary, it is possible and meaningful to ask about plant species richness at very fine grain, even at a point (Rosenzweig 1995). However, it is still unknown where and in what types of community the maximum values occur. Nor is it known whether the values are idiosyncratic, or whether they form a consistent relationship comparable to a species–area curve.

Here we present record richnesses at the complete range of spatial grains for which quadrats are used.

## Methods

We assembled the values of vascular plant species richness on plots of any size that we could find in the literature and in unpublished sources known to us, including extensive reviewing of the literature by all four authors over more than a decade. This covered, so far as the literature was available, all regions of the world. We did not include any richness value that was lower than one we had for a smaller plot size. As richness counts are usually much higher for composite areas of non-contiguous subplots than for contiguous plots of the same area (Dengler & Oldeland 2010), we excluded such samplings, e.g. ‘a 0.1-ha area’ which comprised ten 2 m × 50 m transects separated by 20 m or more (Gentry & Dodson 1987). Most of our records are for squares or circles, only rarely for rectangles with a length–width ratio of 2.5–4.2 (Duivenvoorden 1994). While elongated plots usually have more species than compact plots of the same size, the differences are usually small so long as the plots do not have an extreme length–width ratio (Dengler 2008). However, we excluded one otherwise valuable record of 489 species in 4000 m<sup>2</sup> of tropical lowland rain forest in Columbia because of its length–width ratio of 40 (Galeano et al. 1998). In the studies with maximum richness, any epiphytes present were included. Finally, some protocols call for recording a species as present only if a plant of the species is rooted in the sample area (‘rooted presence’; Greig-Smith 1983), whereas others record also species that root outside the sample area but lean into it (‘shoot presence’). This strongly affects species richness values at small grains (Williamson 2003; Dengler 2008). The rain forests were probably sampled by rooted presence, but many of the herbaceous communities were sampled with shoot presence, which must be equal to or (probably) higher than rooted presence for a given sample.

We plotted all richness–area pairs in log–log space and observed close to a power function (Preston 1962; Fridley

et al. 2005; Dengler 2009). We therefore fitted an ordinary least squares linear regression to this space, i.e. using the transformed values. Such a regression minimizes the residuals of the log of the number of species. This was our intention, since minimizing residuals in the raw number of species would be unrealistic over a range from three to 942 species. We extrapolated this regression to the terrestrial ice-free surface of the Earth (130 million km<sup>2</sup>; Williamson et al. 2001).

## Results and discussion

The maximum richnesses found at smaller grains ( $\leq 50$  m<sup>2</sup>) proved to be in semi-natural, oligo- to mesotrophic, temperate grasslands, managed by chronic mowing, grazing or fire (Table 1, Fig. 1a). Those at the larger grains ( $\geq 100$  m<sup>2</sup>) were in unmanaged (natural) tropical lowland rain forest (Fig. 1b). Only those two broad vegetation types – managed temperate grassland and tropical rain forest – occur among the global maxima. The grasslands were only from Eastern Central Europe, the Southern Baltic and Argentina (Fig. 2), even though grasslands in other regions such as the USA, Western Europe and South Africa have been thoroughly surveyed. Tropical rain forest representation is restricted to Mesoamerica and NW South America, even though there has been interest in species-rich tropical rain forest worldwide.

We had scanned richness records from many other vegetation types worldwide, including types reputedly species-rich, and they proved not to yield worldwide richness maxima. For example, Mediterranean climate heathland in southwestern Australia is said to be species-rich, but Naveh & Whittaker (1979) recorded only 82 species in 1000 m<sup>2</sup>, lower than the 179 species that Naveh & Whittaker (1979) record from Mediterranean shrubland in Israel, and far below the 313 species in Colombian tropical rain forest recorded by Duivenvoorden (1994). Gioia & Pigott (2000) reported only 68 species in 400 m<sup>2</sup> and 69 in 900 m<sup>2</sup> in southwestern Australian forests, both less than the worldwide maximum for 1 m<sup>2</sup> (Table 1). Southern African fynbos is said to be species-rich, but the highest values found by Schmiedel et al. (2010) in 50 plots were hardly half of the world maxima: 128 at 100 m<sup>2</sup> and 169 at 1000 m<sup>2</sup>. The Carolina Vegetation Survey (Peet et al. in press a) includes species-rich pine savanna and riparian shrubland, but the species richnesses across spatial grains were only 55–81% of our maxima, e.g. 35 at 0.1 m<sup>2</sup>, 129 at 100 m<sup>2</sup> (Fridley et al. 2005, Supplement; Peet et al. in press b).

The change with spatial grain between grasslands and forests is not simply because grassland plots are typically much smaller than forest plots (Chytrý & Otýpková 2003), for the same pattern is also found in regional studies where

**Table 1.** The communities used as the richest in vascular plant species at a range of spatial grains.

Area (m <sup>2</sup> )	Richness	Method	Community	Region	References
0.000001	3	Shoot	Dry, sandy grassland	Germany	J. Dengler et al. (unpubl.; see Dengler et al. 2004)
0.000009	3	Shoot	Dry, sandy grassland	Germany	J. Dengler et al. (unpubl.; see Dengler et al. 2004)
0.0001	5	Shoot	Dry, sandy grassland	Germany	J. Dengler et al. (unpubl.; see Dengler et al. 2004)
0.0009	8	Rooted	Mountain grassland	Argentina	J.J. Cantero (unpubl.)
0.001	12	Shoot	Limestone grassland	Sweden	van der Maarel & Sykes (1993) <sup>1</sup>
0.004	13	Rooted	Semi-dry basiphilous grassland	Czech Republic	Klimeš et al. (2001)
0.01	25	Rooted	Wooded meadow	Estonia	Kull & Zobel (1991)
0.04	42	Rooted	Wooded meadow	Estonia	Kull & Zobel (1991)
0.1	43	Shoot	Semi-dry basiphilous grassland	Romania	Dengler et al. (2009)
0.25	44	Rooted	Semi-dry basiphilous grassland	Czech Republic	Klimeš et al. (2001)
1	89	Rooted	Mountain grassland	Argentina	Cantero et al. (1999)
10	98	Shoot	Semi-dry basiphilous grassland	Romania	Dengler et al. (unpubl.; see Dengler et al. 2009)
16	105	Shoot	Semi-dry basiphilous grassland	Czech Republic	Z. Otýpková (unpubl.)
25	116	Shoot	Semi-dry basiphilous grassland	Czech Republic	Z. Otýpková (unpubl.)
49	131	Shoot	Semi-dry basiphilous grassland	Czech Republic	Z. Otýpková (unpubl.)
100	233	Rooted	Tropical lowland rain forest	Costa Rica	Whitmore et al. (1985)
1000	313	Rooted	Tropical lowland rain forest	Colombia	Duivenvoorden (1994)
10 000	942	Rooted	Tropical rain forest	Ecuador	Balslev et al. (1998)

<sup>1</sup>Correction of a higher, incorrect value in the original publication.

the same set of plot sizes has been used for all vegetation types. For example, Dolnik (2003) studied all major vegetation types of the Curonian Spit (on the eastern coast of the Baltic Sea), using plot sizes of 0.0001–900 m<sup>2</sup> and including also bryophytes and lichens. He found, as in our global results, that below 100 m<sup>2</sup> a grassland community was richest, while from 100 m<sup>2</sup> upwards one shrub and several forest communities were richest (Dolnik's Fig. 62 and Table 11).

In a few cases, high richness approaching our maximum at a particular grain can be found in a quite different area. For example, at 1 m<sup>2</sup> the record of 89 species from mountain grassland in Argentina (Table 1) is closely matched by the 87 species at that grain from Russian steppe (Lysenko 2007), and 79 species in a semi-dry basiphilous grassland from Romania (Dengler et al. unpubl.; see Dengler et al. 2009). However, in some cases the maximum values stand out from any others that we know of. For example, at the 10 000 m<sup>2</sup> scale, the record of 942 species from Ecuador stands out amongst the admittedly few available values (Table 1).

From the plot size of 1 mm<sup>2</sup> (0.000001 m<sup>2</sup>) up to 1 ha (10 000 m<sup>2</sup>), the species–area relationship closely followed a power law (Fig. 3), with  $R^2 = 0.976$  and a relation of

$$\text{Richness} = 64.6 \text{ Area}^{0.250} \text{ (Area in m}^2\text{)}$$

Despite covering ten of orders of magnitude, there was no noticeable deviation from log-log linearity, contrary to some other studies (e.g. Crawley & Harral 2001; Fridley

et al. 2006). Even though shoot richness in a sample will always equal or exceed rooted richness, there is no sign of that in the range of record values we have assembled (Fig. 1). The slopes of a regression using just the shoot presence values and of one using just the rooted presence values are not significantly different (but  $P = 0.087$ ), and assuming parallel slopes the intercepts are not significantly different either ( $P = 0.222$ ), with that for shoot presence actually being slightly lower. This indicates that the difference between the two types of record has little influence on our compilation.

The value of 0.250 is close to the 0.262 value predicted by Preston's (1962) 'canonical' theory, even though the assumptions of that theory were not met. Perhaps this is coincidence, but perhaps it is because if any plant communities are 'saturated', surely these are.

### Smaller and larger grain

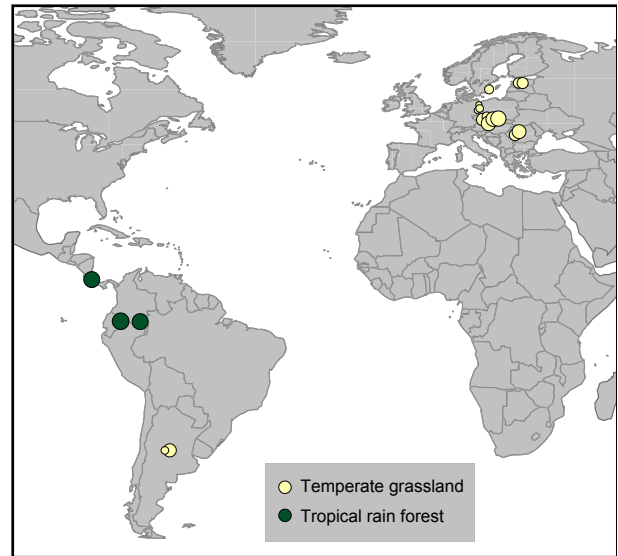
The reported maximum values for the three smallest grains (100 mm<sup>2</sup> down to 1 mm<sup>2</sup>) were recorded with square targets mounted on a pin (Dengler et al. 2004). The smallest size of 1 mm × 1 mm is close to that of many true point quadrats (unfortunately, many 'point quadrats' are far from a point, giving spurious values). Reliable data for areas below 1 cm<sup>2</sup> for Table 1 were available only from one study of grassland types in one location (Dengler et al. 2004), so our value of three species is certainly below the global maximum.

Although Fig. 3 appears relatively linear right down to three species in 1 mm<sup>2</sup> (the extent of the fitted line),

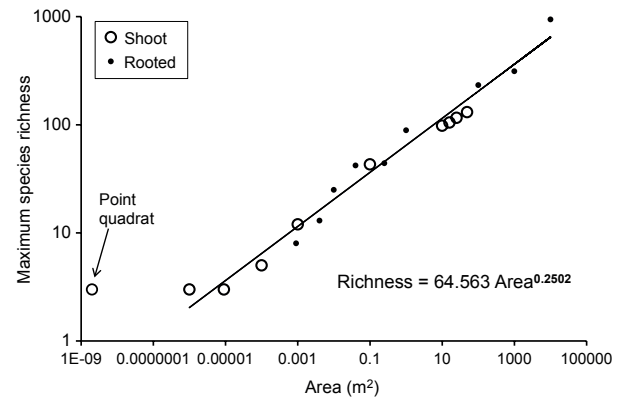


**Fig. 1.** High-richness community types: **(a)** Semi-dry basiphilous grassland near Cluj-Napoca, Romania, the site that holds the global richness record at the 0.1- and 10-m<sup>2</sup> scales (photo J. Dengler 2009), and **(b)** Tropical rain forest in French Guiana, the vegetation type that holds the global richness record at the 100–10 000-m<sup>2</sup> scales (Photo: M. Pärtel, 2006).

species–area relations recorded with the shoot presence inevitably have a lower limit. For example, in the study of Dengler et al. (2004) the 9-mm<sup>2</sup> quadrat completely covered the three species hit. The nested 1-mm<sup>2</sup> quadrat therefore also contained three species (Table 1), and a point would also have hit these three. Point quadrat richness is difficult to obtain from the literature because results



**Fig. 2.** The location of sites with world maxima for species richness, at a range of spatial grains, with the diameter of the symbol proportional to the log of grain size. Some locations have been moved slightly to make them visible.



**Fig. 3.** Maximum richness values for vascular plants at a range of spatial grains, with a power function fitted in log-log space. A point-quadrat value from Wilson & Roxburgh (1994) is indicated, but not included in the regression.

are rarely reported for individual points, just overall cover, but Wilson & Roxburgh (1994) reported three vascular plant species with ‘point quadrats’ of < 0.000000002 m<sup>2</sup> (Fig. 3). Therefore, the curve will flatten out at very small grain, i.e. to z of 0 in a power function (Williamson 2003; Dengler 2008). Point sampling would be very difficult in stratified rain forests, but there could easily be six species at a point there (David W. Goodall, pers. comm. 2010). We suggest that the true curve of maximum richness values for shoot presence will flatten below ca. 0.0001 m<sup>2</sup> to a value of about six species.

The relation of Fig. 3 cannot rise above the number of vascular plant species worldwide in 130 million km<sup>2</sup>, most recently estimated as 275 000 (Chapman 2009; Mora et al. 2011). A test of a scientific concept is extrapolation to other situations, and in spite of our values being maxima the curve of Fig. 3 extrapolates to 219 204 species for the area of the world. Considering that the extrapolation is from 942 species in 1 ha to the world, this is surprisingly close, especially since there are almost certainly richer communities in the world than the literature records. Crawley & Harral (2001) attempted similar extrapolation, but backwards from the flora of the Earth to 1 m<sup>2</sup>. They concluded, unlike us, that extrapolation failed. However, their data were confined to one English county, which is not a good basis for worldwide extrapolation. Moreover, their extrapolation to 72.7 species in 1 m<sup>2</sup>, which they considered poor, is not far from our world maximum of 89 species, and using the latest estimate for the Earth's flora their formula gives 79.9 species, even closer. Why the maximum values give such good extrapolations is not clear.

### Community and species types

The difference in vegetation type at which record richnesses are known parallels the size of the plants – grass tillers vs rain forest trees – but may also reflect intrinsic differences in the community. The high-richness short grasslands are all subject to repeated disturbance – mowing, grazing or fire – and this leads to more symmetric competition, and hence slower competitive exclusion (Peet & Christensen 1988). The most common management of these grasslands has been by mowing, practiced regularly for many years. For one of these extraordinarily rich, semi-dry grasslands, that in the Czech part of the White Carpathians, which holds the record at five spatial scales (Table 1), continuity as a managed grassland since Neolithic times has been suggested (Hájková et al. 2011), giving thousands of years for the immigration and sorting of species and for evolution to occur. Tropical rain forests have a more stable environment, the disturbances being mainly occasional windthrow. Their richness has been explained in many ways, including continuous speciation in a 'stable' ecosystem and high energy input. Wright (2002) highlighted niche differentiation, pest pressure and life-history differences (Wilson 2011).

While our data are for vascular plants only, other taxonomic guilds can also reach high plot-level richness, e.g. an average of 18.3 bryophyte species in 0.01 m<sup>2</sup> (Steel et al. 2004). Plot richness values are rare for bryophytes and lichens, in particular in combination with vascular plants, and are almost unknown for freshwater algae (Dengler et al. 2011).

### Conclusions

The plant richness values in Table 1 and Fig. 3 are almost certainly not the maximum values that exist, at any grain. We hope, therefore, that they might spur others to beat these records. However, the close relation in Fig. 3 suggests that the true maxima are not much greater, since it is unlikely that a selection of sub-maximal values would give such a close fit. The results do not provide any answer to the 'Paradox of the Plankton' (Hutchinson 1961; Wilson 1990, 2011), but they highlight where the Paradox is strongest, and the extent of the problem ecologists have in trying to explain species co-existence.

### Acknowledgements

We thank Zdenka Otýpková (Brno, Czech Republic) and Juan José Cantero (Rio Cuarto, Argentina) for permission to use their unpublished richness values. The comments of the referees and the co-ordinating editor were constructive, and helped to improve the paper. MP was supported by the European Union through the European Regional Development Fund (Centre of Excellence FIBIR).

### References

- Balslev, H., Valencia, R., Paz y Miño, G., Christensen, H. & Nielsen, I. 1998. Species count of vascular plants in one hectare of humid lowland forest in Amazonian Ecuador. In: Dallmeier, F. & Comiskey, J.A. (eds.) *Forest biodiversity in North, Central and South America, and the Caribbean: Research and monitoring*. pp. 585–594. UNESCO, Paris, FR.
- Cantero, J.J., Pärtel, M. & Zobel, M. 1999. Is species richness dependent on the neighbouring stands? An analysis of the community patterns in mountain grasslands of central Argentina. *Oikos* 87: 346–354.
- Chapman, A.D. 2009. *Numbers of living species in Australia and the world*, 2nd edn. Australian Department of the Environment, Water, Heritage and the Arts, Canberra, AU.
- Chytrý, M. & Otýpková, Z. 2003. Plot sizes used for phytosociological sampling of European vegetation. *Journal of Vegetation Science* 14: 563–570.
- Cornell, H.V. & Lawton, J.H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities – a theoretical perspective. *Journal of Animal Ecology* 61: 1–12.
- Crawley, M.J. & Harral, J.E. 2001. Scale dependence in plant biodiversity. *Science* 291: 864–868.
- Dengler, J. 2008. Pitfalls in small-scale species–area sampling and analysis. *Folia Geobotanica* 43: 269–287.
- Dengler, J. 2009. Which function describes the species–area relationship best? – A review and empirical evaluation. *Journal of Biogeography* 36: 728–744.

- Dengler, J. & Oldeland, J. 2010. Effects of sampling protocol on the shapes of species richness curves. *Journal of Biogeography* 37: 1698–1705.
- Dengler, J., Bedall, P., Bruchmann, I., Hoeft, I. & Lang, A. 2004. Artenzahl-Areal-Beziehungen in uckermärkischen Trockenrasen unter Berücksichtigung von Kleinstflächen – eine neue Methode und erste Ergebnisse. *Kieler Notizen zur Pflanzenkunde in Schleswig-Holstein* 32: 20–25.
- Dengler, J., Ruprecht, E., Szabó, A., Turtureanu, D., Beldean, M., Uğurlu, E., Pedashenko, H., Dolnik, C. & Jones, A. 2009. EDGG cooperation on syntaxonomy and biodiversity of *Festuco-Brometea* communities in Transylvania (Romania): report and preliminary results. *Bulletin of the European Dry Grassland Group* 4: 13–19, Hamburg, DE.
- Dengler, J., Jansen, F., Glöckler, F., Peet, R.K., De Cáceres, M., Chytrý, M., Ewald, J., Oldeland, J., Finckh, M., Lopez-Gonzalez, G., Mucina, L., Rodwell, J.S., Schaminée, J.H.J. & Spencer, N. 2011. The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. *Journal of Vegetation Science* 22: 582–597.
- Dolnik, C. 2003. Artenzahl-Areal-Beziehungen von Wald- und Offenlandgesellschaften – Ein Beitrag zur Erfassung der botanischen Artenvielfalt unter besonderer Berücksichtigung der Flechten und Moose am Beispiel des Nationalparks Kuriische Nehrung (Russland). *Mitteilungen der Arbeitsgemeinschaft Geobotanik in Schleswig-Holstein und Hamburg* 62: 1–183.
- Duivenvoorden, J.F. 1994. Vascular plant species counts in the rain forests of the middle Caquetá area, Colombian Amazonia. *Biodiversity and Conservation* 3: 685–715.
- Fridley, J.D., Peet, R.K., Wentworth, T.R. & White, P.S. 2005a. Connecting fine- and broad-scale species-area relationships of southeastern U.S. flora. *Ecology* 86: 1172–1177.
- Fridley, J.D., Peet, R.K., van der Maarel, E. & Willems, J.H. 2006. Integration of local and regional species-area relationships from space-time species accumulation. *The American Naturalist* 168: 133–143.
- Galeano, G., Suárez, S. & Balslev, H. 1998. Vascular plant species count in a wet forest in the Chocó area on the Pacific coast of Colombia. *Biodiversity and Conservation* 7: 1563–1575.
- Gentry, A.H. & Dodson, C. 1987. Contribution of non-trees to species richness of a tropical rain forest. *Biotropica* 19: 149–156.
- Gioia, P. & Pigott, J.P. 2000. Biodiversity assessment: a case study in predicting richness from the potential distributions of plant species in the forests of south-western Australia. *Journal of Biogeography* 27: 1065–1078.
- Greig-Smith, P. 1983. *Quantitative plant ecology*, 3rd edn. Blackwell, Oxford, UK.
- Hájková, P., Roleček, J., Hájek, M., Horsák, M., Fajmon, K., Polák, M. & Jamrichová, E. 2011. Prehistoric origin of the extremely species-rich semi-dry grasslands in the Bílé Karpaty Mts (Czech Republic and Slovakia). *Preslia* 83: 185–204.
- Hutchinson, G.E. 1961. The paradox of the plankton. *The American Naturalist* 95: 137–145.
- Klimeš, L., Dančák, M., Hájek, M., Jongepierová, I. & Kučera, T. 2001. Scale-dependent biases in species counts in a grassland. *Journal of Vegetation Science* 12: 699–704.
- Kull, K. & Zobel, M. 1991. High species richness in an Estonian wooded meadow. *Journal of Vegetation Science* 2: 715–718.
- Lysenko, H.M. 2007. Comparative phytoindication estimate of forest and steppe ecotopes of Kazatskiy site of Central-Black-soil reserve. *Journal of V. N. Karazin Kharkov National University Series, Biology* 5: 99–105. [in Russian].
- Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. & Worm, B. 2011. How many species are there on earth and in the ocean? *PLoS Biology* 9: e1001127.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Naveh, Z. & Whittaker, R.H. 1979. Structural and floristic diversity of shrublands and woodlands in northern Israel and other Mediterranean areas. *Vegetatio* 41: 171–190.
- Palmer, M.W. 1994. Variation in species richness: towards a unification of hypotheses. *Folia Geobotanica & Phytotaxonomica* 29: 511–530.
- Peet, R.K. & Christensen, H.L. 1988. Changes in species diversity during secondary forest succession on the North Carolina Piedmont. In: During, H.J., Werger, M.J.A. & Willems, J.H. (eds.) *Diversity and pattern in plant communities*. pp. 233–245. SPB Academic Publishing, The Hague, NL.
- Peet, R.K., Lee, M.T., Boyle, F., Wentworth, T.R., Schafale, M.P. & Weakley, A.S. In press a. Vegetation plot database of the Carolina Vegetation Survey. *Biodiversity and Ecology* 4: in press.
- Peet, R.K., Palmquist, K.A. & Tessel, S.M. In press b. Herbaceous layer species richness of southeastern forests and woodlands: Patterns and causes. In: Gilliam, F.S. & Roberts, M.R. (eds.) *The herbaceous layer in forests of eastern North America*, 2nd edn. In press. Oxford University Press, New York, NY, US.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity. Part I. *Ecology* 43: 185–215.
- Proctor, J. 1988. Tropical rain forest: structure and dynamics. *Progress in Physical Geography* 12: 405–420.
- Rosenzweig, M.L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.
- Schmiedel, U., Dengler, J., Luther-Mosebach, J., Gröngroft, A., Mucina, G., Petersen, A., Strohbach, B.J. & Jürgens, N. 2010. Patterns and dynamics of vascular plant diversity along the BIOTA transects in southern Africa. In: Schmiedel, U. & Jürgens, N. (eds.) *Biodiversity in southern Africa. Volume 2: Patterns and processes at regional scale*. pp. 118–135. Klaus Hess, Göttingen, DE.
- Steel, J.B., Wilson, J.B., Anderson, B.J., Lodge, R.H.E. & Tangney, R.S. 2004. Are bryophyte communities different from higher-plant communities? Abundance relations. *Oikos* 104: 479–486.
- Stohlgren, T.J., Barnett, D.T., Jarnevich, C.S., Flather, C. & Kartesz, J. 2008. The myth of plant species saturation. *Ecology Letters* 11: 313–322.

- van der Maarel, E. & Sykes, M.T. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *Journal of Vegetation Science* 4: 179–188.
- Whitmore, T.C., Peralta, R. & Brown, K. 1985. Total species count in a Costa Rican tropical rain forest. *Journal of Tropical Ecology* 1: 375–378.
- Williamson, M. 2003. Species–area relationships at small scales in continuum vegetation. *Journal of Ecology* 91: 904–907.
- Williamson, M., Gaston, K.J. & Lonsdale, W.M. 2001. The species–area relationship does not have an asymptote. *Journal of Biogeography* 28: 827.
- Wilson, J.B. 1990. Mechanisms of species co-existence: twelve explanations for Hutchinson's 'Paradox of the Plankton': evidence from New Zealand plant communities. *New Zealand Journal of Ecology* 13: 17–42.
- Wilson, J.B. 2011. The twelve theories of co-existence in plant communities: the doubtful, the important and the unexplored. *Journal of Vegetation Science* 22: 184–195.
- Wilson, J.B. & Roxburgh, S.H. 1994. A demonstration of guild-based assembly rules for a plant community, and determination of intrinsic guilds. *Oikos* 69: 267–276.
- Wright, S.J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130: 1–14.