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A TEST OF THE HUMPED-BACK THEORY OF SPECIES RICHNESS IN NEW ZEALAND NATIVE FOREST

Summary: The Humped-back theory of plant species richness, a theory related to Grime's *C-S-R* 'triangular' model, has been widely discussed, and some evidence has been claimed in support of it. The theory suggests that species richness is maximal at intermediate levels of productivity, i.e., at intermediate positions on a stress/favourability gradient.

We sought evidence for the theory from 90 stands of native podocarp/broadleaved and beech forest in the Coastal Otago region, with an adjustment made for the effect of stand area on species richness. There was no relation between adjusted species richness and an index of site stress/favourability, i.e., no support for the Humped-back theory. The theory may be inapplicable to woody vegetation, or it may be applicable only when the 'favourable' end of the spectrum comprises agricultural communities, or support for the theory might be inflated in the literature by a wish to find ecological generalisations.

Keywords: *C-S-R* theory; forest; Grime's 'triangular' theory; humped-back curve; productivity; species-area relations; species richness; stress.

Introduction

The Humped-back theory of species richness, first proposed by Al-Mufti *et al.* (1977), is well established in the ecological literature. It suggests that species richness is maximal at intermediate levels of community productivity, and is lower both in sites of low productivity and in sites of high productivity. The Humped-back theory is related to Grime's (1979) triangular '*C-S-R*' model of plant communities (Grime, 1985), which suggests that in high-stress / low-productivity sites few species will be able to tolerate the severe physical environment, and that in low-stress / high-productivity sites most species will suffer 'competitive exclusion'. Taylor *et al.* (1990) suggested an alternative explanation of low species richness in productive sites: that those sites were agricultural communities, which were too new in evolutionary terms for species to have evolved for them.

Many workers (e.g., Klinkhamer and de Jong, 1985; Shipley *et al.*, 1991) have claimed that their data shew some conformity with the Humped-back theory, though in many cases the fit seems forced, and rarely has there been a statistically-demonstrated and close fit to the theory. Moreover, many of the demonstrations have been in communities that are agriculturally disturbed, and almost all have been in herbaceous communities.

We investigated whether there was support for the Humped-back theory in one vegetation type in

one area - native forest in the Coastal Otago region, New Zealand - selected as a community type with several examples covering a wide environmental range. The sampling unit was a whole stand. We made a statistical correction for the inevitable effect of area on species richness. We attempted a direct (albeit imprecise) estimate of site stress/favourability, rather than use standing crop as surrogate for the environment. Since the basis of *C-S-R* theory is that soil factors underlie all habitat stresses (Grime and Campbell, 1991), we emphasised soil factors in our site stress/favourability estimates. Although it was not practicable to perform replicated soil tests for each site, we calibrated the two ends of the fertility spectrum by a simple bioassay.

Thus, our aim was to test the Humped-back model in a vegetation-type quite different from those used in most previous tests.

Methods

The data comprised full floristic enumerations of native vascular plant species in 90 remnant stands of native forest in Coastal Otago, southeast New Zealand (incorporating and extending the database of Allen and Wilson, 1991). The climate of the area is cool temperate, with rainfall 800-1500 mm. Sampling was restricted to podocarp/broadleaved or *Nothofagus* forest with a native tree canopy.

*Nothofagus menziesii*¹ was present in six stands, and dominant in two of those. The podocarps present at various sites were *Dacrydium cupressinum*, *Prumnopitys ferruginea*, *Prumnopitys taxifolia*, *Podocarpus cunninghamii*, and occasional *P. totara* and *Dacrycarpus dacrydioides*. The most abundant broadleaved trees were *Pittosporum tenuifolium*, *P. eugenioides*, *Griselinia littoralis*, *Carpodetus serratus* and *Pseudopanax* spp. All stands were subjected to selective logging at some time in the period 1850-1920. All are liable to herbivory from introduced ungulates, rodents and possums.

Since the stands surveyed differed in size, and since area is a strong determinant of species richness (Connor and McCoy, 1979; Gitay, Roxburgh and Wilson, 1991), we adjusted for area effects before examining the effect of stress/favourability.

The environmental factors used as predictors included three used by Allen and Wilson (1991) to predict forest species composition of forest in the region:

1. Distance from the coast (km), square-root transformed. Proximity to the sea was coded as favourable on the grounds of the ameliorating effect of the sea on the temperature regime, distance was coded as stressful (but see the next factor).
2. Exposure to coastal winds, coded subjectively on a 0-3 scale (*cf.* 0-2 in Allen and Wilson, 1991), square transformed. Low exposure was coded as favourable, high exposure as stressful.
3. Altitude (m, the minimum altitude in the stand). Low altitude was coded as favourable, higher altitude as stressful. Altitude was used instead of rainfall because it was easier to relate to a stress/favourability gradient.

Allen and Wilson (1991) found a coarse classification by geology to be an effective predictor of species composition. Because the previous characterisation of the substratum was broad, and difficult to relate to a stress gradient, we determined the soil type of each stand from soil maps, and used the characteristics of that soil type to determine four soil factors relevant to plant growth. Where more than one soil type was present in the stand, the most common type was used, but this was not a serious problem. The soil factors were:

4. Potential rooting depth (to a layer or horizon that would inhibit root extension) on a 1-6 scale (category 6 representing > 1.2 m depth). Soil depth was selected as "obviously of great import

to plants" (Warming, 1909). Following Warming, deep was coded as favourable, and shallow as stressful.

5. Relative water deficit, in three categories, i.e., relative length of water deficit period, as judged by soil order and profile available water capacity. Low water deficit was coded as favourable, and high deficit as stressful.
6. Drainage, on a 1-5 scale, expressing the relative period of, and depth to, water saturation, based on profile gley morphology and expressed in the New Zealand Soil Classification (Hewitt, 1992). Well-drained was coded as favourable, and poorly drained as stressful.
7. Base saturation, on a 1-5 scale, expressing the percentage of cation exchange sites occupied by basic cations. High base saturation, 80-100%, was counted as favourable, and low, <20%, as stressful.

In order to avoid using a range of indices of stress/favourability, with consequential problems of the effect of multiple tests on significance levels, the seven factors above were combined into one composite index of stress/favourability: each factor was standardised to zero mean and unit variance to eliminate differences in scale. The seven values for each site were then summed to form the stress/favourability index for that site. The index arbitrarily gave the same weight to each factor, but also avoided arbitrary differential weightings. The index also assumes a linear effect of each factor, which we intend only as an approximation. This environmental gradient was intended to apply to the type and range of sites being used; we make no claim that it is a general realisation of Grime's (1977) stress/favourability gradient.

The region includes two forest types: podocarp forest and *Nothofagus menziesii* forest, though below the canopy there is rather little difference in species composition (Wilson and Allen, 1990). Even so, we included the difference between these types as a binary predictor variate, in case they might have an overall difference in species richness, as has often been claimed (Wardle, 1984).

To check on our assumption of a stress gradient for soil favourability (including fertility), we performed a soil bioassay for two extreme sites: Mt Cargill with a low stress/favourability index, and Woodhaugh with the highest index. In addition, a third site with a fertile agricultural soil was used as a standard (Wingatui deep silt loam, with a high base saturation: 84% in the A horizon: Beecroft, Hewitt and Smith, 1991). In all three sites, ten soil samples were collected by restricted randomisation. A pot of each sample was sown with 1.25 g of *Lolium perenne* seed (equivalent to 5 seeds cm⁻²). After two

¹ Nomenclature follows Connor and Edgar (1984) and references therein.

months of growth in a unheated greenhouse, the above-ground plant material was harvested, dried at 70 °C, and weighed.

Results

A species-area curve, of the Gleason type (i.e., species richness on log of area: Gitay *et al.*, 1991), explained 50.7% of variation in species richness between stands (Fig. 1; $P < 0.001$). The relation was very close to linear (a second-order polynomial explained 51.1% of the variation, only trivially more). This demonstrates that we could efficiently factor out differences in area between stands by performing subsequent analysis on the residuals from the regression of richness on log area, with the overall mean richness added to give an adjusted species richness.

The bioassay supported the interpretation of the stress/favourability index as including a soil favourability gradient (Table 1). The Mt Cargill soil, from an upland forest on highly-leached soil, gave a bioassay index value somewhat less than the agricultural soil, and Woodhaugh, a lowland recent alluvial soil, a value considerably greater.

Linear regression of the adjusted species richness on the composite index of site stress/favourability (Fig. 2) explained only 0.007% of the variation in species richness (not significant). A quadratic regression, allowing for a Humped-back curve, explained only 1.514% (not a significant

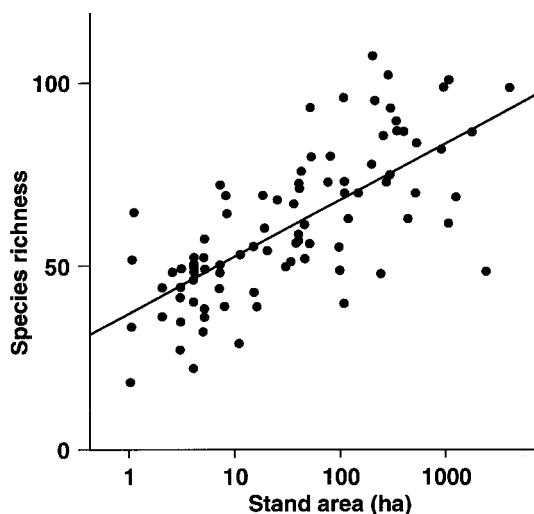


Figure 1: The relation between plant species richness and the area of native forest stands in Coastal Otago. The line is a linear regression of richness on log of area.

Table 1: Bioassay results. The differences in growth between the three soils are significant by analysis of variance ($P < 0.001$), and all soils are different from all others by Duncan's test (at $P = 0.01$).

| Site | Stress/favourability index | Growth in bioassay (g per pot) |
|-------------------|----------------------------|--------------------------------|
| Mt Cargill | -2.3 | 1.11 |
| Woodhaugh | +7.5 | 1.75 |
| agricultural soil | n/a | 1.30 |

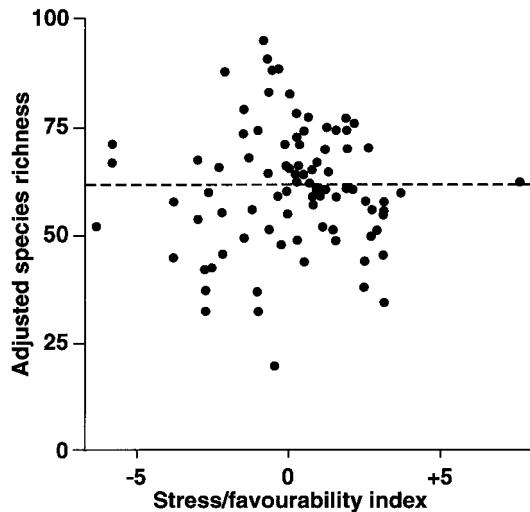


Figure 2: The relation between plant species richness (adjusted for the effect of stand area) and a composite index of site stress/favourability (sensu Grime, 1979). Negative values indicate the stressful end of the gradient, positive ones the favourable end. The non-significant quadratic regression is shown.

increase, nor a significant total amount). Adding the presence of *Nothofagus* improved on the fit only slightly (from 0.007% to 0.115% with the linear regression, 1.514% to 1.666% with the quadratic fit). In both cases the effect of *Nothofagus* was not significant.

All analyses were duplicated using the square root of richness or adjusted richness (after adding 0.5); the results were very similar, and indicated no different conclusions.

Discussion

Our analyses failed to produce any support for the Al-Mufti *et al.* (1977) and Grime (1979) Humped-back theory of the control of plant species richness.

We used one composite index of stress/favourability to avoid the problems with significance levels that are explicit in multiple significance tests, and implicit in multiple regression (Flack and Chang, 1987). The direction of the soil favourability gradient was supported by bioassay. Probably the most debatable decision was that nearness to the sea would be the favourable state, but even reversing this in the index made no difference to the results (e.g., the quadratic regression on the index explained 1.9% of the variance in adjusted species richness, instead of 1.5%). This demonstrates that our conclusion is robust against details of coding in the stress/favourability index.

Tilman and Pacala (1993) displayed eight graphs that they claimed shewed Humped-back curves of species richness on site favourability, apparently selected from the literature as the best examples. After examination of the data and of the curve fitting one could at best say that half of them were convincing.

Some workers have found a Humped-back curve of species richness on biomass (Klinkhamer and de Jong, 1985; Moore and Keddy, 1989; Shipley *et al.*, 1991; Oomes, 1992) or on site favourability (Burns, 1995), usually with considerable scatter. Other workers have claimed evidence for curvature, but either gave no significance for the quadratic effect, or failed to shew that it represented a Humped-back, rather than a flattening off (Kutiel and Danin, 1987; Day *et al.*, 1988; Wilson and Keddy, 1988; Garcia *et al.*, 1993). Yet others have found maximum richness at low biomass (e.g., ter Heerd *et al.*, 1991; Wheeler and Shaw, 1991; Smith and Rushton, 1994), or at high biomass (e.g., Wisheu and Keddy, 1989), or essentially no relation (e.g., Gough, Grace and Taylor, 1994).

There is a natural bias in the literature, that those who find evidence for a 'Humped-back' curve in their data are more likely to publish the test (Keddy, 1989). The wish to find support for the theory can be seen in those papers which claim a Humped-back relation with only weak evidence. It is therefore possible that the Humped-back theory applies much less often than the literature superficially suggests.

The original Humped-back hypothesis of Al-Mufti *et al.* (1977) was based on data from herbaceous communities, as have been most of the convincing subsequent demonstrations of Humped-back curves (Klinkhamer and de Jong, 1985; Moore and Keddy, 1989; Shipley *et al.*, 1991; Oomes, 1992). Indeed, Grime's whole C-S-R theory was originally developed for herbaceous communities (Grime, 1988). Our results suggest that it is possible the Humped-back theory does not apply to woody

communities, such as forest, though more evidence would be needed before we could be sure of this. In some investigations, there may be an effect of the type that Taylor *et al.* (1990) suggest, of a deficit of species adapted to very productive agricultural sites.

It is possible that one might fail to find a Humped-back curve by sampling only part of the stress/favourability gradient. This would tend to give an upward or downward regression (depending on which part of the gradient had been omitted). There is no curvature here to suggest that. It is possible that our estimate of 'stress/favourability' was inappropriate, though extremes were intuitively reasonable. Our 90 stands covered a wide environmental range, from the leached hill forest sites of montane forest to *Dacrycarpus dacrydioides* forest on the most fertile site in the region. If the Humped-back theory does not apply over such a range, we have to ask when it does apply, outside agricultural lands.

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References

- Al-Mufti, M.M.; Sydes, C.L.; Furness, S.B.; Grime, J.P.; Band, S.R. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *Journal of Ecology* 65: 759-791.
- Allen, R.B.; Wilson, J.B. 1991. A method for determining indigenous vegetation from simple environmental factors, and its use for vegetation restoration. *Biological Conservation* 56: 265-280.
- Beecroft, F.G.; Hewitt, A.E.; Smith, S.M. 1991. *Soils of the Taieri Plain, northeast of the Taieri River, Otago, New Zealand*. DSIR Land Resources Scientific Report No. 17. Department of Scientific and Industrial Research, Lower Hutt.
- Burns, B.R. 1995. Environmental correlates of species richness at Waipoua Forest Sanctuary, New Zealand. *New Zealand Journal of Ecology* 19: 153-162.
- Connor, E.F.; McCoy, E.D. 1979. The statistics and biology of the species-area relationship. *American Naturalist* 113: 791-833.
- Connor, H.E.; Edgar, E. 1987. Name changes in the indigenous New Zealand flora, 1960-1986 and

- Nomina Nova IV, 1983-1986. *New Zealand Journal of Botany* 25: 115-170.
- Day, R.T.; Keddy, P.A.; McNeill, J.; Carleton, T. 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. *Ecology* 69: 1044-1054.
- Flack, V.F.; Chang, P.C. 1987. Frequency of selection of noise variables in subset regression analysis. *American Statistician* 41: 84-86.
- Garcia, L.V.; Maranon, T.; Moreno, A.; Clemente, L. 1993. Above-ground biomass and species richness in a Mediterranean salt marsh. *Journal of Vegetation Science* 4: 417-424.
- Gitay, H.; Roxburgh, S.H.; Wilson, J.B. 1991. Species-area relations in a New Zealand tussock grassland. *Journal of Vegetation Science* 2: 113-118.
- Gough, L.; Grace, J.B.; Taylor, K.L. 1994. The relationship between species richness and community biomass: the importance of environmental variables. *Oikos* 70: 271-279.
- Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169-1194.
- Grime, J.P. 1979. *Plant strategies and vegetation processes*. Wiley, Chichester, U.K. 222 pp.
- Grime, J.P. 1985. Towards a functional description of vegetation. In: White, J. (Editor), *The Population Structure of Vegetation*, pp. 503-514. Junk, Dordrecht, The Netherlands. 669 pp.
- Grime, J.P. 1988. A comment on Loehle's critique of the triangular model of primary plant strategies. *Ecology* 69: 1618-1620.
- Grime, J.P.; Campbell, B.D. 1991. Growth rate, habitat productivity, and plant strategy as predictors of stress response. In: Mooney, H.A.; Winner, W.E.; Pell, E.J. (Editors), *Response of Plants to Multiple Stresses*, pp. 143-159. Academic Press, San Diego, U.S.A. 422 pp.
- Hewitt, A.E. 1992. *New Zealand soil classification*. DSIR Land Resources Scientific Report no. 19, DSIR Land Resources, Lower Hutt, NZ. 133 pp.
- Keddy, P.A. 1989. *Competition*. Chapman and Hall, London. 202 pp.
- Klinkhamer, P.G.L.; de Jong, T.J. 1985. Shoot biomass and species richness in relation to some environmental factors in a coastal dune area in The Netherlands. *Vegetatio* 63: 129-132.
- Kutiel, P.; Danin, A. 1987. Annual-species diversity and aboveground phytomass in relation to some soil properties in the sand dunes of the northern Sharon Plains, Israel. *Vegetatio* 70: 45-49.
- Moore, D.R.J.; Keddy, P.A. 1989. The relationship between species richness and standing crop in wetlands: the importance of scale. *Vegetatio* 79: 99-106.
- Oomes, M.J.M. 1992. Yield and species density of grasslands during restoration management. *Journal of Vegetation Science* 3: 271-274.
- Shipley, B.; Keddy, P.A.; Gaudet, C.; Moore, D.R.J. 1991. A model of species density in shoreline vegetation. *Ecology* 72: 1658-1667.
- Smith, R.S.; Rushton, S.P. 1994. The effects of grazing management on the vegetation of mesotrophic (meadow) grassland in Northern England. *Journal of Applied Ecology* 31: 13-24.
- Taylor, D.R.; Aarssen, L.W.; Loehle, C. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos* 58: 239-250.
- ter Heerd, G.N.J.; Bakker, J.P.; De Leeuw, J. 1991. Seasonal and spatial variation in living and dead plant material in a grazed grassland as related to plant species diversity. *Journal of Applied Ecology* 28: 120-127.
- Tilman, D.; Pacala, S. 1993. The maintenance of species richness in plant communities. In: Ricklefs, R.E.; Schluter, D. (Editors), *Species diversity in ecological communities*, pp. 13-25. University of Chicago Press, Chicago, U.S.A. 414 pp.
- Wardle, J.A. 1984. *The New Zealand beeches: ecology, utilisation and management*. New Zealand Forest Service, Wellington, N.Z. 447 pp.
- Warming, E. 1909. *Oecology of plants: an introduction to the study of plant-communities*. Oxford University Press, Oxford. 422 pp.
- Wheeler, B.D.; Shaw, S.C. 1991. Above-ground crop mass and species richness of the principal types of herbaceous rich-fen vegetation of lowland England and Wales. *Journal of Ecology* 79: 285-301.
- Wilson, J.B.; Allen, R.B. 1990. Deterministic v. Individualistic community structure: a test from invasion by *Nothofagus menziesii* in southern New Zealand. *Journal of Vegetation Science* 1: 467-474.
- Wilson, S.D.; Keddy, P.A. 1988. Species richness, survivorship and biomass accumulation along an environmental gradient. *Oikos*, 53: 375-380.
- Wisheu, I.C.; Keddy, P.A. 1989. Species richness - standing crop relationships along four lakeshore gradients: constraints on the general model. *Canadian Journal of Botany* 67: 1609-1617.