Ecology or mythology? Are Whittaker's "gradient analysis" curves reliable evidence of continuity in vegetation?

Ekologie nebo mytologie? Je Whittakerova „gradientová analýza" důkazem kontinuity vegetace?

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Dedicated to the memory of Emil Hadač

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Whittaker was one of the leading ecologists of his generation, introducing several ideas to plant community ecology. One approach involved deriving environmental-correlation curves in attempts to determine how the abundance of individual species changed along environmental gradients. These curves have been used extensively in the ecological literature of the last 50 years. However, there has been no examination of whether the methods used were sufficiently rigorous to justify Whittaker's conclusions, let alone the very widespread use of them by others to draw general conclusions. Whittaker's curves were based on large amounts of fieldwork. However, the sampling methods used were subjective, and the analyses of the data were often circular. When the curves are compared to the data on which they were based, it can be seen that many of the features that Whittaker claimed to see in his graphs are not supported. Whittaker's main conclusions may have been correct but his studies do not stand up as pieces of scientific work.

Keywords: community ecology, environmental gradients, gradient analysis, species abundance, Whittaker's curves

Introduction

Clear results are not common in community ecology because, although there are topics of great interest to ecologists, they are not easy to investigate (Southwood 1987). When a clear result is obtained, it is a cause for rejoicing. The "Gradient Analysis" curves of Whittaker (1956), which were based on an impressive amount of fieldwork, and claimed to shew that the abundances of species change gradually but individualistically along environmental gradients, were therefore received with enthusiasm. Not only did Whittaker himself cite and reproduce them whenever possible in reviews and his textbook, but they were reproduced as received fact in textbooks for the next 40 years. They still appear in textbooks as essentially facsimilie curves (Huston 1994, Barbour et al. 1999) and as redrawn/schematic curves (Begon et al. 1996, Molles 2002, Attiwill & Wilson 2003). The gradients used have been described as obtained "directly from environmental data" (Dodson et al. 1998) and "with data on various abiotic variables, such as soil moisture" (Stiling 2002). In fact, Whittaker (1956) made it quite clear that this was not so: "The complex-gradient from valley bottoms to dry slopes will be called the 'moisture gradient', but with no assumption that the moisture factors directly control the distribution of any plant population along it". Whittaker makes clear that the "gradients" he uses are ones derived from indicator species, not direct environmental ones. We shall shew that the methods by which the gradients and curves were obtained comprised a combination of subjectivity, circularity and over-simplification. Clearly, none of those citing the curves investigated how they were derived.

Whittaker's (e.g. 1975, Fig 4.1) aim was to express the types of distribution he expected from various models of community structure, and he tried to look at these distributions along environmental gradients. He called this a "gradient analysis". He was tireless in his wide-ranging botanical field work, but admitted that he could not obtain site specific environmental parameters other than altitude, aspect and slope to characterise each sampled stand. He argued that in any case the species responded to complex interrelationships between environmental parameters, which would be impossible to analyse in the regional context. Therefore, to order his samples along a gradient of conditions, he used locally derived indicator species, by carefully choosing samples along topographical gradients. He presented data from the Great Smoky Mts, Siskiyou Mts and Santa Catalina Mts that seem to test between models of community structure.

Whittaker was a pioneer of plant ecology and we pay homage to his innovative spirit. It may be that many of his conclusions are correct. However, the subject is so fundamental to plant synecology that it is important that his methods were valid, and thus his results reliable. Our aim in this paper is to assess whether this was so. We conclude that his data and analyses are not of sufficient quality to support his conclusions.

Whittaker's methods

Great Smoky Mts

Whittaker (1956) laid six transects from a valley bottom to the ridge above. At each site, there was apparently no fixed quadrat size; trees were chosen in some unspecified way ("about 100 stems were the usual sample"). For trees, density was "preferred" over the available basal area information (we wonder how it was derived since no sample area is cited), while cover was "estimated" (by eye we presume) for undergrowth. The major conclusions concern tree species distributions, and we discuss these here.

On each valley-to-ridge transect, the species were subjectively divided according to their distribution along the transect into four classes, from 'mesics' (score 0) to 'xerics' (score 3). How this information was collated between the five transects is not stated. Each quadrat was then placed along a 'moisture gradient' by calculating the mean score of the species in it, weighted by the number of stems of the species.

It is not clear whether the actual data points are present on the Great Smoky Mts graphs (Whittaker 1956). For example, in Fig. 2, top subgraph, there are clear points astride the lines, in the x-axis positions of real points, which might be taken as the data points. Fig. 2, middle subgraph, has similar points, but here they do not coincide with the x-axis positions being plotted; they all fall almost exactly on the line, whereas a plotting of the real data from Whittaker (1951) shews that there is considerably more scatter than this (Fig. 1, this paper).

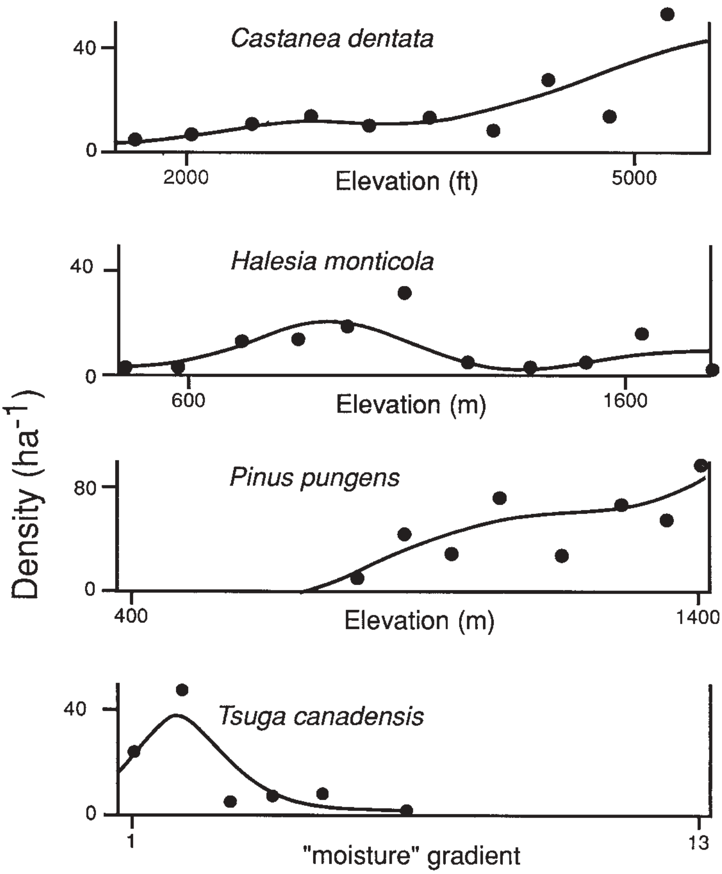


Fig. 1. – Whittaker's "fitted" "gradient analysis" curves, and his data, from the Great Smoky Mts. *Castanea dentata* curve from Whittaker (1956: Fig. 9); *Halesia monticola* from Whittaker (1967: Fig. 7); *Pinus pungens* from Whittaker (1967: Fig. 1); *Tsuga canadensis* from Whittaker (1967: Fig. 3).

The graphs from the 1956 Great Smoky Mts data that are given in Whittaker (1967) are said to include "stems over 1 cm d.b.h.", which is odd because in the original sampling stems were counted "from 1 in. up".

Siskiyou Mts

Whittaker (1960) took 60 quadrats on each rock type. The areas were selected subjectively, at least as being "homogenous and relatively undisturbed". The transect lines within the areas were traversed subjectively. Along these lines, quadrats were selected subjectively at positions "which seemed favorable for sampling". The last twenty of the 60 samples were placed subjectively "to obtain a reasonably even representation of the types of topographic sites". The quadrat size for counting tree stems at a position was subjectively chosen from two standard sizes. Herbs, shrubs and tree seedlings were counted in a smaller subsample, of a size subjectively chosen from two alternatives. With such methodology there is a danger that subconscious bias is reflected in the data.

In the analysis, "moisture" scores were subjectively assigned to quadrats. Species were then grouped into four "moisture" classes using the modes of these scores. A subjective selection of species was then used to provide a weighted average of "moisture" score for each quadrat. After this circular argument it was still necessary to use "judgement" to discard ten of each set of 60 quadrats as being "deviant".

Santa Catalina Mts

For this dataset, Whittaker & Niering (1965) did not specify how the quadrats were positioned. Subsample size was subjectively chosen from two alternatives.

Whittaker (1967) gave gradient analysis curves drawn from the Santa Catalina Mts data of Whittaker & Niering (1965). However, their data, in the paper and in the material deposited in the Library of Congress, were in terms of the six original "moisture" categories; it is unclear whether the graphs are such direct data, but more probably, in spite of the descriptive names for categories, they are a "composite moisture gradient".

Analysis seems to have been similar to the Siskiyou data, except that the score modes were not used rigorously ("based primarily on modes"), and apparently a variable number of quadrats (5–10) were discarded as being "deviant".

Evaluation of Whittaker's curve fitting

Great Smoky Mts

Comparison of the published curves with the data shews that reasonable smoothing has been applied for some species. However, for others, e.g. *Castanea dentata* (Fig. 1), the smoothing is misleading in that it hides the considerable scatter, and proposes trends for which the evidence is weak.

Whittaker (1967) later produced further curves from the data, leaving ambiguous whether they were smoothed or not. Amongst these, *Halesia monticola* is drawn with a bimodal curve, which in view of the discrepancy between the data and the fitted curve must remain very doubtful. The secondary peak is based on one deviant point, yet a larger deviation at mid elevations is ignored. The curve for *Pinus pungens* is complex, with a distinct shoulder, unsupportable in view of the scatter of the points. *Tsuga canadensis* is drawn with a 'textbook' bell-shaped curve, for which the data offer minimal support.

Siskiyou Mts

Most of the curves for this dataset cannot be checked with the tables, because the former are plotted by density and the latter give frequency. For the trees, comparison is possible. This comparison assumes that "low elevation" in Table 3 is the same as "low elevation" in his Figs 20 & 21.

Some of the curves (Fig. 2) fit the points well, with only minor, and acceptable, smoothing (e.g. *Quercus chrysolepis* on diorite, though even here the slight bimodality in the curve is doubtful). Others show such a degree of smoothing that it is difficult to see a real relation between the fitted curve and the data (e.g. *Pinus lambertiana* on both diorite and serpentine, and *Pinus monticola*).

Of particular interest in such distributions is bimodality. Whittaker (1960) describes the curve for *Pseudotsuga menziesii* on all three substrates (diorite, gabbro and serpentine) as "apparently bimodal". Yet, for example, the "peak" on diorite in Moisture class 9 is based on the rise between classes 8 and 10, whereas an equal-sized anomaly in class 2 is treated as noise, and fitted by a curve bending in the opposite direction. Similarly, for the "bimodal" distributions of *Castanopsis chrysophylla* (on diorite) and *Lithocarpus densiflora* (on diorite and on gabbro), the bimodality is based on deviation of one point. The "bimodal" distributions of *Arbutus menziesii* (on diorite) and *Quercus chrysolepis* (on diorite and on gabbro) are subtle even in the fitted graph, and not supported by the data.

Santa Catalina Mts

Comparison of data and curves for the Santa Catalina Mts data is complicated by the tables using a 6-point scale and the graphs a 10-point one. However, it is difficult to see a justification for the dip at the right-hand end of the curve for *Pinus cembroides* (Fig. 3).

Reproduction of Whittaker's curves

Collier et al. (1973) reproduced Whittaker's curves, accepting Whittaker's conclusion that the curves were bell-shaped, and tended to be more scattered along the gradient than would be expected at random. They also accepted Whittaker's conclusion of bimodality for some species and his assumption that this was due to the presence of two ecotypes.

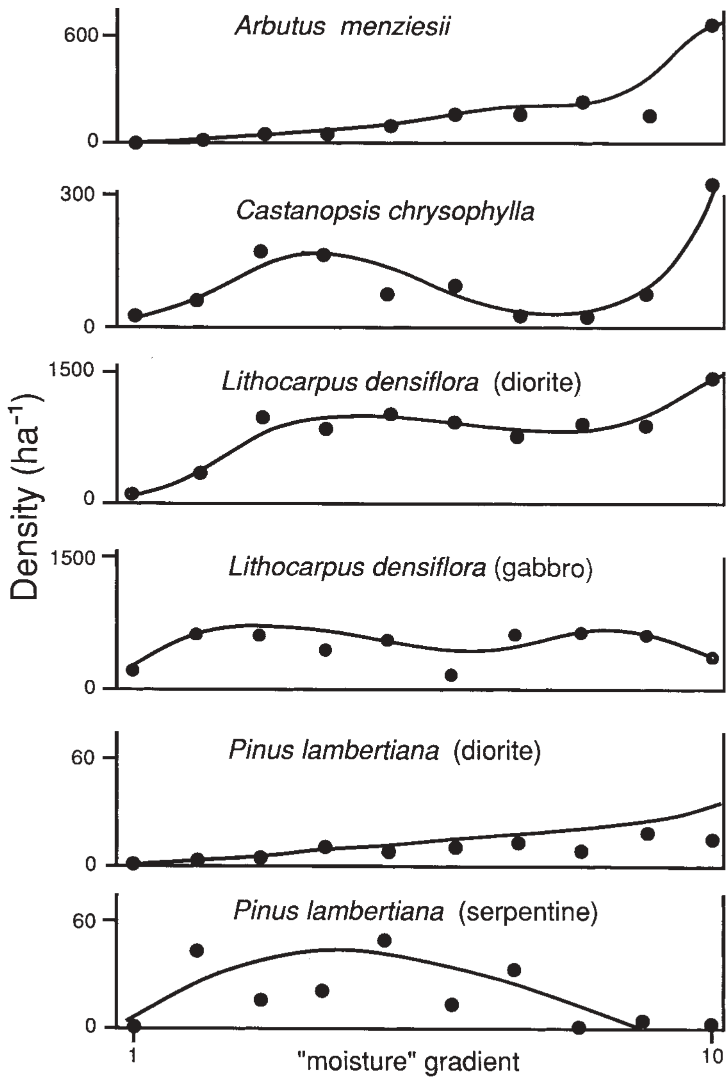
Colinvaux (1973), Whittaker (1975), Smith (1977), McNaughton & Wolf (1979), Ricklefs (1979), Pianka (1983), Barbour et al. (1999), Begon et al. (1996) and Stiling (2002) all reproduced Whittaker's curves, with no warning that they were smoothed, let alone of the degree of smoothing involved. Whittaker (1975), Pianka (1983) and Barbour et al. (1999) even described them as "actual distributions".

Kormondy (1984) interpreted these dots as the data points, and presented graphs in which the curve appears to be a fitted one, but to fit closely. As has been demonstrated, the real scatter is considerable, and the marks on Whittaker's graphs are spurious.

Conclusions

Whittaker brought several ideas to plant community ecology. One could almost say that he began the idea of modelling the structure of plant communities and testing them with real data.

One of the particular ways he attempted to compare ideas with data, however, was to draw conclusions on plant community structure from the modes of the derived curves of species presence along his constructed gradients (Whittaker 1956, 1967). For example: "species populations form a complex, flowing population continuum along the environmental gradient" (Whittaker 1967: 220); "the population peaks [are] scattered along the gradient" (Whittaker 1967: 219); "population densities of the species change gradually along the gradient" (Whittaker 1965: 259). "species evolve toward scattering of their pop-



ulation centers in habitat hyperspace" (Whittaker et al. 1973: 330); "the curves show a range of variation of forms ... to bimodal curves having two peaks along the gradient" (Whittaker 1967: 219); "some species have more than one local population optimum, for different ecotypes" (Whittaker et al. 1973: 329). Others have seen great significance in these results. Wiens (1989) credited Whittaker's gradient analysis with the "crumbling of the edifice of Clementsian communities" and its replacement with the "Gleasonian alternative". Whilst it is largely true that this has happened, it is unfortunate if any part of the cause was the flawed data and analysis discussed here.

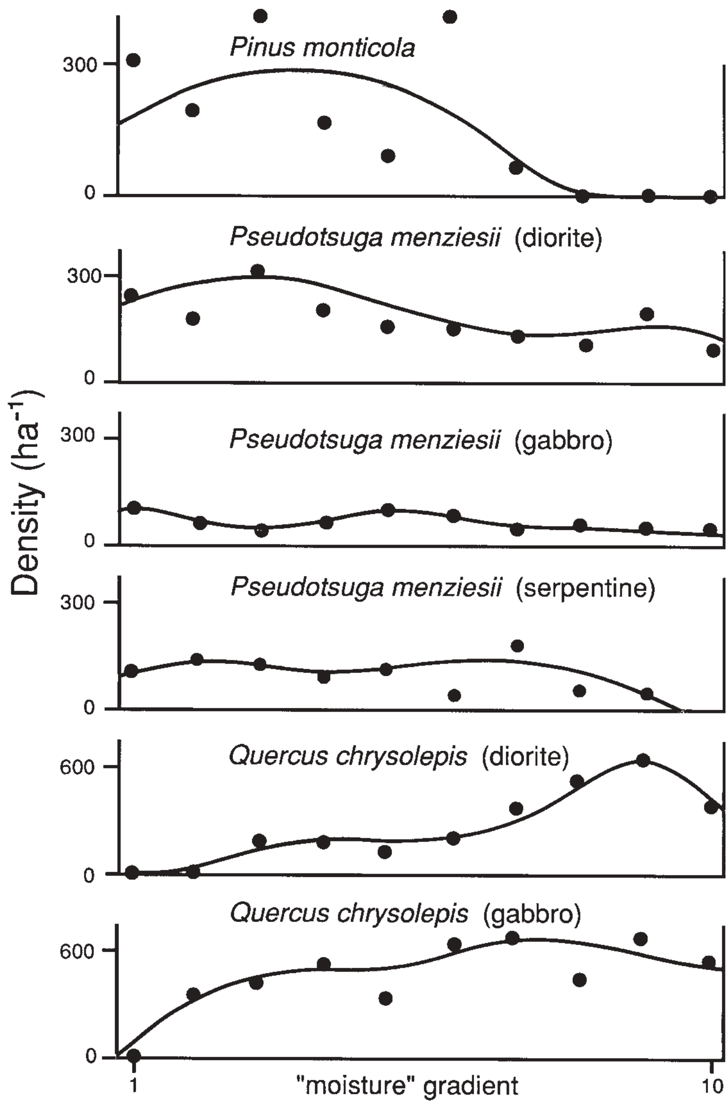


Fig. 2. – Whittaker's "fitted" "gradient analysis" curves, and his data, from the Siskiyou Mts. Curves from Whittaker (1960: Figs. 20 & 21).

One other point should be made about Whittaker's conclusions: the lack of recognizable noda and coincident modes of distribution convinced him that the physical environment is the overwhelming influence on tree and shrub species' distribution (Whittaker 1956: 32). He does not consider any possible interspecific effects, either through competition or facilitation. Yet, since trees modify most features of their own physical environment, such effects must be present. Emil Hadač, to whose memory this paper is dedicated, was a protagonist of the importance of interspecific and intraspecific facilitation (E. Hadač 2002, in lit.). We hope that we have shewn that Whittaker's analyses do not deny the potential for such effects.

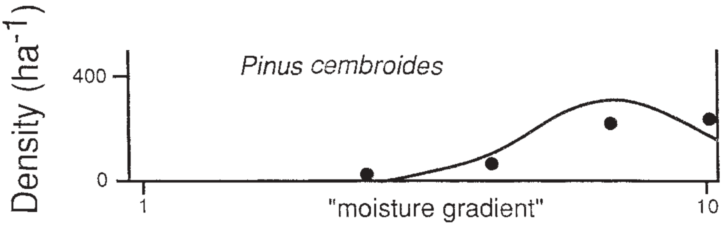


Fig. 3. – Whittaker's "fitted" "gradient analysis" curve, and his data, from the Santa Catalina Mts. Curve from Whittaker (1967: Fig. 8).

Gradient analysis may be capable of leading to worthwhile ecological conclusions. Genuine bimodality is especially interesting. However, it is clear from careful examination of Whittaker's methods, and by comparison of his curves with the data on which they are based, that the conclusions Whitaker drew cannot be made from the quality of data that he had gathered. The problem of gradient definition applies almost entirely to the 'moisture' gradient, for altitude could hardly be misrepresented. The problems of curve fitting are certainly worse with the 'moisture' gradient, perhaps because it bore less relation to reality. However, the sampling problems apply to both the altitude and the 'moisture' gradient. Whittaker himself drew attention (Whittaker 1956) to the circularity of his analytical methods, but thereafter ignored the problem because his results appeared to be internally consistent.

Perhaps Gradient Analysis can make a contribution to our understanding of plant community structure. More careful analysis of species' distribution along gradients has been made before or concurrently with Whittaker's work (Curtis & McIntosh 1951, Bray & Curtis 1957), and more recently using modern numerical techniques (Austin et al. 1990). However, definition of the environmental scale is a continuing problem.

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Souhrn

Whittaker byl jedním z nejvýznamnějších ekologů svojí generace a zavedl do studia rostlinných společenstev několik přístupů. Jeden z nich byl založen na odvozování křivek, jež měly dokladovat, jak se na gradientech prostředí mění abundance rostlinných druhů. Tyto křivky byly v ekologické literatuře posledních 50 let hojně užívány. Nikdo však nezkoumal, zda Whittaker k prokládání křivek používal rigorózní metody a zda jsou tedy skutečným podkladem pro závěry, které na jejich základě činil (ponechme stranou, že křivky k vyvozování obecných závěrů používala řada ostatních badatelů). Whittakerovy křivky jsou založeny na rozsáhlých terénních datech. Výběr ploch, ze kterých jeho data pocházejí, byl však velmi subjektivní a analýzy jsou často postaveny na důkazu kruhem. Srovnání křivek s daty, na kterých jsou založeny, ukazuje, že mnohé z toho, co podle Whittakera z grafů vyplývalo, z nich ve skutečnosti vyvozovat nelze. Whittakerovy hlavní závěry mohou být správné, ale jako solidní vědecká práce jeho studie neobstojí.

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