higher visual centres in night vision; thus any two light stimuli causing equal rates of rhodopsin isomerization produce indistinguishable neural signals[10]. An explanation for the monogeusia analogous to that accounting for scotopic monochromacy is that the three sugars bind reversibly to a single class of membrane receptor in taste cells. On the assumptions that such binding is first-order, and that the psychophysical indiscriminability relation is transitive, our data imply that at the tongue surface the apparent relative affinities for sucrose, fructose and glucose are 1, 2/3 and 1/3, respectively.

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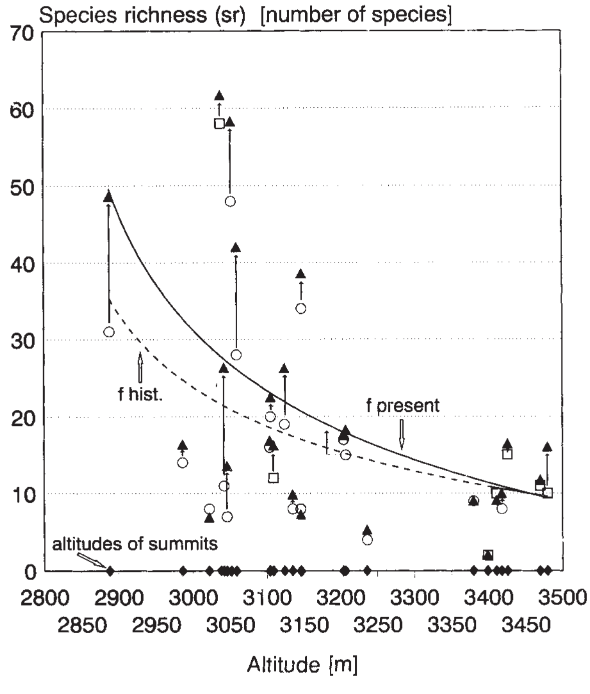
Climate effects on mountain plants

SIR — Temperature-limited environments such as boreal regions, arctic regions and high mountains are thought to be very sensitive to greenhouse warming[1]. As a result of such warming, for example, plant species and communities in high mountains will be pushed upwards in elevation and may be eliminated if already at mountain summits[2,3]. If evidence were to be found of a continuing change of summit floras, this would indicate that global warming is already having a significant ecological impact. Although preliminary observations have recently been presented[4], no conclusive evidence has yet been reported.

During the summer of 1992, we collected data on the state of the flora at 26 summits exceeding 3,000 m in the middle part of the Alps (western Austria, eastern Switzerland) and compared the actual records on cover and abundance of vascular plant species with historical records[5–10]. Species richness has increased during the past few decades (see figure), and is more pronounced at lower altitudes. However, upward movement of the alpine-nival flora is an overall trend, as indicated by the comparison of the fitted regression lines for species-richness with altitude. Although the presented data are not corrected for age of the historical record or for the expansion of the considered belt, the difference between the two regression lines is obvious. The exponential decrease of species richness with altitude is a general feature of the nival vegetation above the closed alpine grasslands.



Species richness of historical and our present-day records at nival summits in the Alps plotted against altitude. Rare species are downweighted (0.25), species of moderate abundance were given the weight 0.5, frequent species the weight 1.0. Rare species were downweighted due to the comparatively high probability that these were overlooked by the original authors. Displayed are 24 summits with siliceous bedrock. Age of the historical records is 40 to 90 years (circles, 1895–1918; squares, 1947–53; triangles, present-day). Arrows, increase in species richness, which is pronounced at lower altitudes and low to moderate at higher altitudes. Most summits considered are climbed only occasionally, so the effect of humans is negligible.

On the basis of 12 very precise historical records[8–10], we calculated moving rates for nine typical nival plant species. The maximum values approached 4 m per decade, although most of the values were below 1 m per decade. The old records used for this calculation were collected about 70–90 years ago. According to the records from meteorological stations in Austria, the mean annual temperature has increased since that time by 0.7 °C (ref. 11). Taking into account an average decrease of 0.5 °C per 100 m of increasing altitude, this warming should theoretically lead to a shift in the altitudinal vegetation belts at a rate of 8–10 m per decade. The empirical values are clearly far lower than this.

In conclusion, there is no doubt that even moderate warming induces migration processes, and that this process is under way. The example from the limits of plant life at high alpine summits is of general importance and suggests that global warming is already having a significant effect on alpine plant ecology. Even in situations where plants must move upwards, the warming is sufficient to stimulate migration, and may cause disastrous extinctions in these environments.

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Scaling and brain connectivity

SIR — From published information describing the connections between areas of macaque monkey visual cortex, Young has applied non-metric multidimensional scaling (NMDS)[1–4] to construct a two-dimensional map of 30 areas[5]. Areas are represented as points and were found to be arranged on a circle, which Young took as evidence for the 'two-streams' hypothesis of visual processing.

NMDS is designed for ordinal data. From a matrix of similarities between a given set of objects, a representation of the objects in a geometric space is sought such that the rank order of the distances between objects in the space corresponds to the reverse rank order of the similarities. In Young's case, similarity encodes the degree of connectivity for each pair of areas, with the connectivity specified as either reciprocal, unidirectional, or absent. We first explored the fit of his configuration to the original data. One goodness-of-fit measure, RSQ, is the proportion of variance in the similarities (after a monotonic transformation) accounted for by the distances. Young quotes an RSQ of 40% (see ref. 5), whereas only values close to 100% are usually regarded as acceptable. It could be that the small number of similarity levels prevents the RSQ from reaching 100%. We found by analysis (to be reported elsewhere) that the maximum value of RSQ attainable is indeed data-dependent. For the map found by Young[5] using the secondary approach to tied similarities[3], the maximum RSQ value is 76% in the case of binary similarity data — ternary data will have an even higher RSQ ceiling. This makes Young's value of 40% more respectable, but still the fit is not good.

We next looked at how low fit could compromise the form of a computed map when using the secondary approach to ties. To generate very low fit configurations, we produced two-dimensional NMDS representations of ternary similarity matrices in which the entries were assigned at random. This yields circular configurations, with low RSQ, a finding consistent with theoretical considerations[6]. (As those RSQ values lie below 0.4, the hypothesis that the visual system data is totally due to a random process can be rejected. However, such arguments do not guarantee that a derived structure is free of artefacts[7].) We also ran NMDS on dissimilarity matrices generated from a set of distances between points in the plane which had been corrupted by noise to weaken the fit. With zero noise, the structure is recovered and the RSQ is high. As more noise is added to the distances, the RSQ gets lower and the derived structure becomes more circular. Finally we applied NMDS to adjacency data from rectangular grids. Again, the fit is poor and circular configurations result.

If the circularity of Young's configuration genuinely reflects underlying structure, then the connectivity data possesses serial order (with wraparound). We therefore tested explicitly for this by taking a standard non-NMDS method[8] designed for finding serial order and tailoring it to the wraparound case[9]. If the rows and columns of the connectivity matrix can be arranged so that the non-zero entries cluster on the diagonal and corners of the matrix, then wrapped serial order is present and is specified by the row assignment. Using Young's convention that an uninvestigated connection be treated as absent, we examined the binarized connectivity matrix arranged in the order implied by his map. There is some serial order, though many connections are displaced from the appropriate regions. The degree of departure from perfect ordering can be quantified by regarding each row vector as a point in a high dimensional space and finding the shortest circuit between the points so generated[8]. Using a standard heuristic the shortest length we found was 206, whereas the circuit implied by Young's configuration has length 240. In contrast, the theoretical minimum is 60 for perfect serial ordering with wraparound, and an average random circuit has length 437.

Application of NMDS to the visual system, with similarity encoding the nature of the direct connections, produces a poor fit configuration. In cases of poor fit there is a bias towards circular structures, whether or not there is genuine serial order. It is essential to be aware of this in interpreting the structures derived. Our results suggest that Young's configuration reflects a mixture of both genuine and artefactual structure. Most of the other connectivity datasets to which he has applied his method have also yielded circular or near-circular configurations[10,11]. This striking similarity across systems points to either a deep principle of brain organization, or an artefactual component in the method.

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YOUNG *ET AL.* REPLY — Simmen *et al.* suggest that NMDS introduced artefactual structure because the fit of the solution for the primate visual system[5] was not close to 100%. We have tested this idea quantitatively[12], by examining various arbitrary multidimensional structures. When given the metric distances between the vertices of these structures, NMDS recovers their parameters with very high RSQ. When we degraded the data to the same level of measurement as connectivity data, by setting thresholds for proximity between vertices, NMDS produces solutions with RSQ typically between 0.2 and 0.5. We then tested whether the degraded-data solutions recovered the known structure of the input data. Using Procrustes rotation[5,13], we found that the fit between the structures derived from degraded data and the metric structures is excellent, typically yielding correlations around 0.95. Therefore, contrary to the suggestion of Simmen *et al.* above, serious artefact is not introduced by NMDS into solutions with RSQ comparable to that of the reported one, and the RSQ of the reported solution therefore cannot itself be interpreted as evidence for the presence of artefactual structure[12].

The traditional means of deciding whether a solution should not be trusted to be a systematic reflection of data structure is to compare the RSQ of a solution with analysis of comparable random data, thereby determining whether the solution is one in which low fit could have produced an artefact[14]. We examined the distribution of RSQ statistics from scaling 200 randomly re-ordered matrices. The probability of the RSQ of the reported solution falling within this low fit distribution is less than 10^{-30}. We found that the recovery of known structure from low level test data is badly compromised only when solutions fall in the low fit distribution of RSQ for those data. We note that Simmen *et al.* do not indicate either the RSQs or the relation of these statistics to the low-fit distributions for their artefactually circular test data and that their artefactual results are consistent with their solutions falling within the low-fit distributions, unlike the visual system solution.

A circular configuration can arise artefactually in a two-dimensional NMDS solution when fit is very poor. Data structure, however, can itself be circular, as in Shepard's famous analysis of colour judgement data[2]. These two interpretations can be further distinguished by deriving higher dimensional solutions, in which artefactual structure takes a spheroidal or hyperspheroidal form, and systematic strucure should still take a planar circular form. Accordingly, we examined solutions in up to six dimensions, which have higher RSQ (0.7 in the six-dimensional case). A near-planar circular structure would be expected if the data structure reflects a system that is divided into two gross streams[15], which possess a common origin in occiptal cortex[16,17] and reconverge after somewhat segregated processing (see, for example, ref. 18). All higher dimensional solutions are statistically significantly related to the orderings of the areas derived from independent analyses by others[15,16] that embody these organizational principles[5] (every $p < 0.000001$). The forms of all the higher dimensional solutions were near-planar, and none was spheroidal. Hence, the form of the solution is a systematic reflection of underlying data structure and is not due to artefact. Indeed, these significant correspondences constitute external validation, and would be very difficult to explain if there were any serious perturbation of the NMDS solution by artefact.

Simmen *et al.* use a non-NMDS method, normally used to examine the chronological order of grave sites[8], to assess whether there is serial order in the data. But this analysis makes the assumption that there is a single dimension, time in the application for which the method is designed, underlying the data. This assumption is breached by these data: time does not possess parallel streams between which there can be cross-talk. Lateral cross-talk connections will be displaced from the appropriate regions and elevate the circuit length. Further, the visual system is a level-spanning