

stigmata of ascidian tunicates²³, arranged in paired dorso-ventral columns like the stigmata of ascidian and doliolid tunicates²³, while the presumed atria extended far forwards right and left of the stigmata and therefore right and left of the pharynx, as in ascidian tunicates²³. Furthermore, the atria opened antero-dorsally as in ascidian tunicates²³, and these anterior openings were paired as in post-larval ascidian tunicates²⁴.

As a tunicate, *Jaekelocarpus* probably belonged to the stem group of the Tunicata because it retained the primitive features of a calcite skeleton and a downward-flexing tail which, as parsimony suggests, would not have existed in the latest common ancestor of extant tunicates. If a tunicate, *Jaekelocarpus* would necessarily belong to the crown group of the chordates, as the chordate interpretation of mitrates and cornutes has long proposed for mitrates in general^{22,25}. □

Methods

The technique we used is high-resolution X-ray computed tomography (μ CT). It is non-destructive and permits the study of non-transparent objects such as fossils, producing images that correspond to serial sections with resolution as good as 8 μ m. The sections were used to create three-dimensional computer models of the objects by reconstructing the surfaces that connected corresponding outlines on adjacent sections^{26,27}.

The specimen of *Jaekelocarpus oklahomensis* chosen for complete scanning (Burke Museum, University of Washington, UWBM74305) was selected after preliminary tests on a total of three specimens. The scanning was carried out, under the direction of T. Rowe, at the University of Texas High-Resolution X-Ray CT Facility, Department of Geological Sciences, USA. The parameters of the scan were: 150 kV; 0.053 mA; slice thickness 0.016 mm; interslice spacing 0.016 mm; diameter of field of view 4.53 mm. 276 sections were saved as 16-bit TIFF files. The matrix data size was 512 \times 512 \times 376 voxels and the voxel size was 8.84 \times 8.84 \times 16 μ m (see Supplementary Information).

The individual plates were recognized, and distinguished from each other as separate entities (segmented), using Mimics 6.3 software (Materialise N. V.). In Mimics, the data can be explored in three views: the original images in x - y planes and resliced images in x - z or y - z planes. Because of lateral changes in the X-ray attenuation values within individual skeletal plates, it was necessary to use local thresholds.

The CTM software module of Mimics interpolates the slice data to generate three-dimensional STL files, one for each plate or anatomical region. Such STL files were exported to Rhinoceros 1 (Robert McNeel) as polygon meshes, where models of the plates were moved in virtual space and so placed in the original life positions relative to each other. To prevent artefacts after these manipulations, the size parameters of the plates (length and volume) were checked in Communicator 1.6 (Materialise N. V.) by means of which we obtained secondary serial sections of the restored specimen.

Received 26 July 2001; accepted 12 March 2002; doi:10.1038/nature00805.

- Peterson, K. J. & Eernisse, D. J. Animal phylogeny and the ancestry of bilaterians: inferences from morphology and 18S rDNA. *Evol. Dev.* **3**, 170–205 (2001).
- Cameron, C. B., Garey, J. R. & Swalla, B. J. Evolution of the chordate body plan: new insights from phylogenetic analyses of deuterostome phyla. *Proc. Natl Acad. Sci. USA* **97**, 4469–4474 (2000).
- Jefferies, R. P. S. Some fossil chordates with echinoderm affinities. *Symp. Zool. Soc. Lond.* **20**, 163–208 (1967).
- Jefferies, R. P. S. in *Major Events in Vertebrate Evolution* Ch. 4 (ed. Ahlberg, P. E.) 20–66 (Systematics Association and Taylor & Francis, London, 2000).
- Jefferies, R. P. S. & Jacobson, A. G. An episode in the ancestry of the vertebrates: from mitrate to crown-group craniate. *Integr. Biol.* **1**, 115–132 (1998).
- Sutcliffe, O. E., Südkamp, W. H. & Jefferies, R. P. S. Ichnological evidence on the behaviour of mitrates: two trails associated with the Devonian mitrate. *Rhenocystis. Lethaia* **33**, 1–12 (2000).
- Jefferies, R. P. S. Ichnological evidence on the behaviour of mitrates: comments on the reply. *Lethaia* **34**, 262 (2001).
- Cripps, A. P. A new stem-group chordate (Cornuta) from the Llandeilo of Czechoslovakia and the cornute-mitrate transition. *Zool. J. Linn. Soc.* **96**, 49–85 (1989).
- Ubaghs, G. in *Treatise on Invertebrate Paleontology Part 5. Echinodermata* (ed. Moore, R. C.) S297–S650 (Kansas Univ. Press and Geological Society of America, New York, 1968).
- Parsley, R. L. in *Echinoderm Phylogeny and Evolutionary Biology* (eds Paul, C. R. C. & Smith, A. B.) 347–361 (Oxford Scientific Publications/Liverpool Geological Society, Oxford/Liverpool, 1988).
- Ruta, M. Brief review of the stylophoran debate. *Evol. Dev.* **1**, 123–135 (1999).
- David, B., Lefebvre, B., Mooi, R. & Parsley, R. L. Are homalozoans echinoderms? An answer from the extraxial-axial theory. *Paleobiology* **26**, 529–555 (2000).
- Lefebvre, B. & David, B. Ichnological evidence on the behaviour of mitrates: reply. *Lethaia* **34**, 260–261 (2001).
- Phillip, G. M. Carpoids: echinoderms or chordates? *Biol. Rev.* **54**, 439–471 (1979).
- Kolata, D. R., Frest, T. J. & Mapes, R. H. The youngest carpoid: occurrence, affinities and life mode of a Pennsylvanian (Morrowan) mitrate from Oklahoma. *J. Paleontol.* **65**, 844–855 (1991).
- Jørgensen, C. B. Water processing in ciliary feeders, with special reference to the bivalve filter pump. *Comp. Biochem. Physiol.* **94a**, 383–394 (1989).
- Martinucci, G. B., Burighele, P. & Dallai, R. in *Form and Function in Zoology* (eds Lanzavecchia, G. & Valvassori, R.) Vol. 5, 123–140 (Selected Symposia and Monographs, Unione Zoologica Italiana, Mucchi, Modena, 1991).
- Kott, P. The Australian Ascidiacea. Part 1. Phlebobranchia and Stolidobranchia. *Memoirs Queensland Mus.* **20**, 1–47 (1985).
- Kott, P. The Australian Ascidiacea. Part 2. Aplousobranchia. *Memoirs Queensland Mus.* **29**, 1–298 (1990).

- Kott, P. The Australian Ascidiacea. *Memoirs Queensland Mus.* **32**, 375–620 (1992).
- Jefferies, R. P. S. A defence of the calcichordates. *Lethaia* **30**, 1–10 (1997).
- Jefferies, R. P. S. *The Ancestry of the Vertebrates* (Cambridge Univ. Press and British Natural History Museum, London, 1986).
- Berrill, N. J. *The Tunicata with an Account of the British Species* (Ray Society, London, 1950).
- Huus, J. Genitalorgane und Ganglio-Genital-Strang bei *Corella parallelogramma* O. F. M. *Skrifter. Videnskabselskabet Christiania.* **19**, 1–50 (1924).
- Jefferies, R. P. S. In defence of the calcichordates. *Zool. J. Linn. Soc.* **73**, 351–396 (1981).
- Ketcham, R. A. & Carlson, W. D. Acquisition, optimization and interpretation of X-ray computed tomographic imagery; applications to the geosciences, three-dimensional reconstruction, modeling and visualization of geological materials. *Comp. Geosci.* **27**, 381–400 (2001).
- van Geet, Swennen, R. & Wevers, M. Quantitative analysis of reservoir rocks by microfocus X-ray computerised tomography. *Sedim. Geol.* **132**, 1–2 (2000).

Supplementary Information accompanies the paper on Nature's website (<http://www.nature.com/nature>). The original TIFF files showing the serial X-ray sections of *Jaekelocarpus* are also stored in the Digital Morphology site of the University of Texas and can be accessed on <http://www.digimorph.org>.

Acknowledgements

We are grateful to E. Nesbitt and R. Eng for making the specimens of *Jaekelocarpus* available and to T. Rowe and his co-workers for their collaboration. P.D. was supported on a post-doctoral fellowship in London by the Spanish Government (Ministerio de Educación, Cultura y Deportes).

Competing interests statement

The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to R.P.S.J. (e-mail: r.jefferies@nhm.ac.uk).

Positive interactions among alpine plants increase with stress

Ragan M. Callaway*, R. W. Brooker†, Philippe Choler‡, Zaal Kikvidze§, Christopher J. Lortie||, Richard Michalet¶, Leonardo Paolini#, Francisco I. Pugnaire☆☆, Beth Newingham*, Erik T. Aschehoug***, Cristina Armas☆☆, David Kikodze§ & Bradley J. Cook*

* Division of Biological Sciences, University of Montana, Missoula, Montana 59812, USA

† Centre for Ecology and Hydrology, CEH Banchory Research Station, Hill of Brathens, Banchory, AB31 4BY, UK

‡ Station Alpine du Lautaret et Laboratoire de Biologie des Populations d'Altitude UMR CNRS-UJF 5553, University Joseph Fourier, Grenoble, BP 53, 38041 Grenoble cedex, France

§ Institute of Botany of the Georgian Academy of Sciences, Kojori Road 1, Tbilisi 380007, Georgia

|| Department of Botany, University of British Columbia, Vancouver, British Columbia, V6T 1Z4, Canada

¶ Ecosystèmes et Changements Environnementaux, University Joseph Fourier, Grenoble, BP 53, 38041 Grenoble cedex, France

Laboratorio de Investigaciones Ecológicas de las Yungas, UNT, CC34, Yerba Buena, Tucuman, Argentina

☆☆ Estacion Experimental de Zonas Aridas, Consejo Superior de Investigaciones Cientificas, General Segura 1, 04001 Almeria, Spain

Plants can have positive effects on each other¹. For example, the accumulation of nutrients, provision of shade, amelioration of disturbance, or protection from herbivores by some species can enhance the performance of neighbouring species. Thus the notion that the distributions and abundances of plant species are independent of other species may be inadequate as a theoretical underpinning for understanding species coexistence and

** Present address: The Nature Conservancy, 201 Mission Street, San Francisco, California 94105, USA.

Table 1 Descriptions of experimental sites

Site	Latitude, longitude	Low-high elevations (m)	Low-high microtopography	Set-up-harvest dates	Low-high species number	Measurements
Central Brooks Range, Alaska	68.1, 211.0	800–1,400	Flat-weak concave	1998–99	5, 5	Leaf number & biomass
Abisko, Sweden	68.2, 18.5	580–1,000	Concave-concave	1998–99	3, 4	Leaf number & biomass
Kluane Range, Yukon	60.4, 221.9	900–1,750	Weak concave-Concave	1998–99	5, 5	Leaf number & biomass
Cairngorms, Scotland	57.1, 3.5	400–740	Concave-flat	2000	5, 5	Leaf number & biomass
Rocky Mountains, Banff	51.3, 244.0	1,400–2,300	Concave-convex	2000	4, 4	Leaf number & biomass
Rocky Mountains, Absaroka Mountains	45.1, 250.8	2,350–3,000	Flat-flat	1998–99	5, 5	Leaf number & biomass
French Alps	44.5, 6.4	2,100–2,900	Concave-convex	1997–98	10, 10	Leaf number & biomass
Central Caucasus, Kazbegi	42.5, 44.4	2,100–3,000	Flat-flat	1996–97	7, 5	Leaf number
Rocky Mountains, Colorado	40.2, 254.6	2,930–3,500	Flat-flat	1998–99	5, 5	Leaf number & biomass
Sierra Nevada, Spain	37.1, 3.4	2,400–3,100	Flat-weak concave	1998–99	4, 4	Leaf number & biomass
Central Andes, Tucuman	26.5, 294.9	2,000–3,600	Flat-flat	1997–98	5, 5	Leaf number

Species are presented in the Supplementary Information.

diversity². But there have been no large-scale experiments designed to examine the generality of positive interactions in plant communities and their importance relative to competition. Here we show that the biomass, growth and reproduction of alpine plant species are higher when other plants are nearby. In an experiment conducted in subalpine and alpine plant communities with 115 species in 11 different mountain ranges, we find that competition generally, but not exclusively, dominates interactions at lower elevations where conditions are less physically stressful. In contrast, at high elevations where abiotic stress is high the interactions among plants are predominantly positive. Furthermore, across all high and low sites positive interactions are more important at sites with low temperatures in the early summer, but competition prevails at warmer sites.

The performance of plants in communities is very different from

their performance as individuals^{3,4}, a discrepancy that is generally attributed to negative, competitive interactions^{5,6}. However, recent research has demonstrated that the overall effects of species on each other may vary as competition and facilitative mechanisms shift in relative importance^{1,2,7,8}. In an attempt to integrate biotic interactions and abiotic factors into a single conceptual model, ecologists have hypothesized that the relative importance of competition and facilitation may vary inversely along gradients of abiotic stress^{8,9}. The importance of facilitation as an organizing process in communities is predicted to increase along gradients of increasing abiotic stress and decreasing productivity, whereas the importance of competition is predicted to decrease. We tested the hypothesis that the importance of facilitation, relative to competition, increases in importance in response to increasing abiotic stress in a global experiment in subalpine and alpine plant communities.

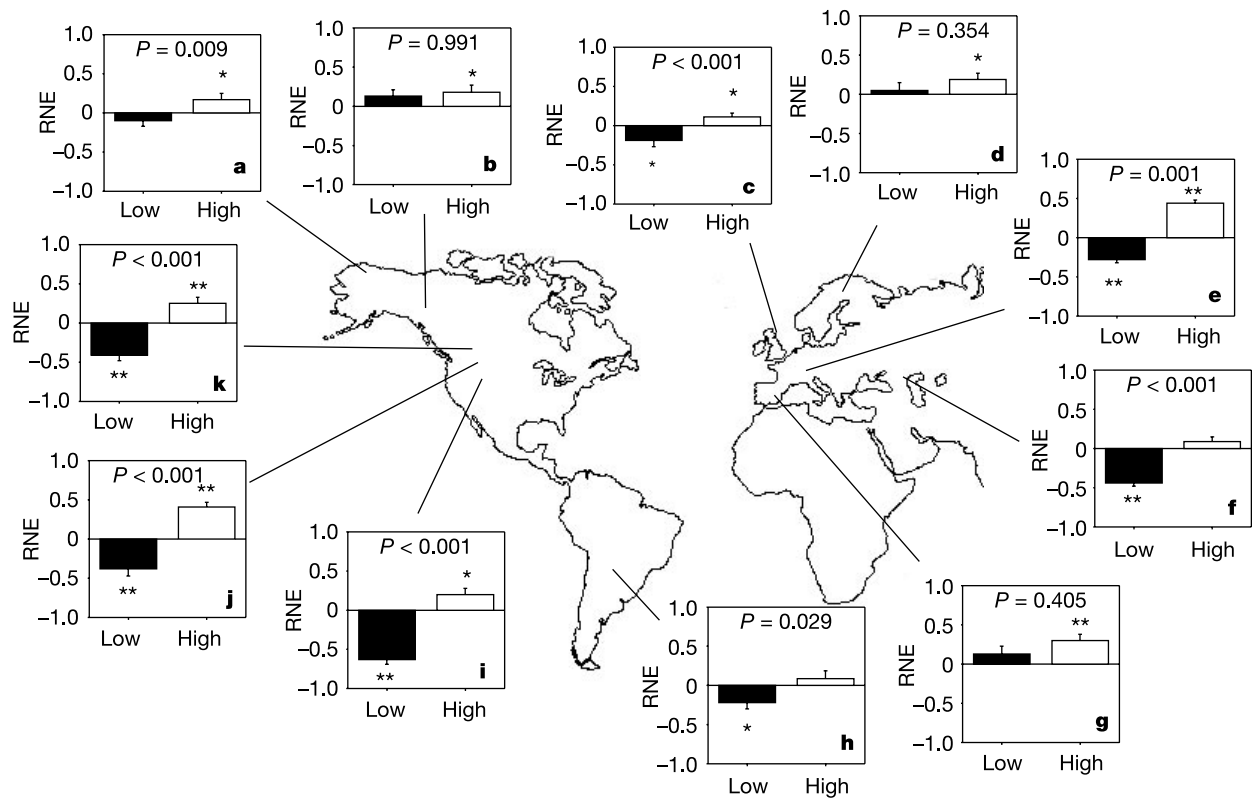


Figure 1 Relative neighbour effect (RNE) at the 11 experimental sites. Error bars represent one standard error, *P* values denote significance of differences between the two sites (ANOVA with site and species as main effects), and asterisks denote a site effect that was significantly different from zero (*P* > 0.01). RNE was calculated for biomass of target plants at all sites except for the Caucasus and the Andes sites, where RNE was calculated

using the difference in leaf number between control and removal target pairs. **a**, Brooks Range; **b**, Kluane Range; **c**, Cairngorms; **d**, Abisko; **e**, French Alps; **f**, Caucasus Mountains; **g**, Sierra Nevada; **h**, Andes; **i**, Rocky Mountains, Colorado; **j**, Absaroka Mountains, Montana; **k**, Rocky Mountains, Banff.

We compared the effects of removing neighbouring vegetation on 8–12 replicates of 115 different target plant species at low versus high elevations in 11 different mountain ranges around the world (Table 1). Over all locations combined, plant–plant interactions shifted from competition in relatively benign abiotic environments at low elevations to facilitation in more stressful environments at high elevations: Fig. 1; analysis of variance (ANOVA) for relative neighbour effect (RNE)¹⁰ for biomass (RNE_{biomass}), $F_{\text{global location}} = 1.22$, degrees of freedom, d.f. = 8, 98, $P = 0.293$; $F_{\text{site altitude}} = 51.06$, d.f. = 1, 98, $P < 0.001$; ANOVA for $RNE_{\text{leaf growth}}$, $F_{\text{global location}} = 1.34$, d.f. = 9, 93, $P = 0.262$; $F_{\text{site altitude}} = 59.97$, d.f. = 1, 93, $P < 0.001$. For the nine locations where plants were harvested, RNE_{biomass} was -0.22 ± 0.02 (1 s.e.) at the low sites and $+0.25 \pm 0.02$ at the high sites. For the nine locations where leaf growth rates were measured $RNE_{\text{leaf growth}}$ was 0.33 ± 0.02 (1 s.e.) at the low sites and $+0.16 \pm 0.02$ at the high sites. At eight of the 11 locations, removal of neighbours had effects on aboveground target plant biomass that were significantly different, and more facilitative, at high elevations than at low elevations, indicating that general interactions shifted from competition to facilitation with increasing elevation and abiotic stress. At the other three sites RNE was significantly greater than zero, indicating facilitation, but because RNE was also positive at the low sites there was no difference between sites. Two of these three sites were in highly stressful arctic environments (the Kluane Mountains in western Canada and Abisko, Sweden), and the third was in the Sierra Nevada of Spain where both high and low sites were unusually dry. No significant effect of competition on plant biomass (for all species combined) was found at any of the high-elevation experimental sites. For all species combined across all 11 locations, neighbours had weakly competitive effects on mortality of target plants at low elevations, but highly facilitative effects on mortality at high elevations (Fig. 2). Similarly, sexual reproduction was reduced by neighbours at low elevations and enhanced by neighbours at high elevations (Fig. 3). Considered together, the results of this short-term experiment demonstrate strong shifts from competitive processes in relatively benign environments to facilitation in more stressful environments as biological determinants of plant reproduction, community composition and community diversity.

We hypothesize that the shift from competition at low elevations to facilitation at high elevations is based on fundamental physiological limitations. As conceptualized by Grime¹¹ for shifts in competitive intensity on stress gradients, we believe that non-resource factors such as temperature, wind, and soil disturbances are less limiting to plant growth at low elevations, permitting plants to grow to the point where further growth or reproduction is limited

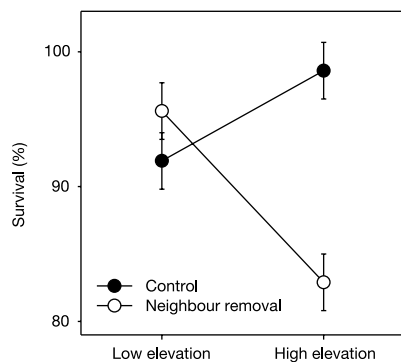


Figure 2 Proportion of surviving target species in controls and neighbour removal treatments at high and low elevation experimental sites for all 11 locations combined. Error bars show one standard error. (ANOVA, $F_{\text{treatment}} = 8.47$, d.f. = 1, 206, $P = 0.004$; $F_{\text{site}} = 2.10$, d.f. = 1, 206, $P = 0.149$; $F_{\text{treatment} \times \text{site}} = 22.13$, d.f. = 1, 206, $P < 0.001$.)

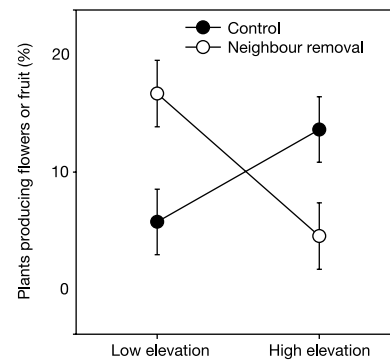


Figure 3 Proportion of flowering or fruiting target species in controls and neighbour removal treatments at high and low elevation experimental sites for all 11 locations combined. Error bars show one standard error. (ANOVA, $F_{\text{treatment}} = 0.62$, d.f. = 1, 180, $P = 0.432$; $F_{\text{site}} = 0.14$, d.f. = 1, 180, $P = 0.709$; $F_{\text{treatment} \times \text{site}} = 16.17$, d.f. = 1, 180, $P < 0.001$.) The degrees of freedom are lower than for survival because reproduction was not recorded at all sites.

by resources. At high elevations, temperature, wind scouring or soil instability may limit plant growth more than resource availability. Amelioration of these severe stresses by neighbours may favour growth more than competition for resources with the same neighbours impairs growth.

Experimental studies of facilitation and competition seldom provide unbiased, neutral estimates of the relative occurrence or importance of these interactions in communities because focal species are chosen on the basis of their spatial association with other species. We made no effort to choose species that showed particular spatial relationships with any other species or that occupied any particular position on elevational or topographic gradients. Our selection of a large proportion of the species occurring in these alpine communities provides more support for generality of the importance of facilitation than studies that have focused on few species at one or two locations. Despite the problem of scaling our experiments to the longer time frame of alpine plant community development, our demonstration of common, strong facilitation supports the general neutral model constructed by Dodds¹² for community organization, and the empirical model developed by Miller to incorporate both direct and indirect effects among plants⁴. They found that positive interactions among species were as likely as negative ones in communities as long as relatively large numbers of species and connections were considered.

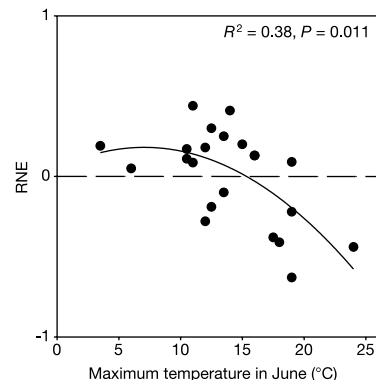


Figure 4 The relationship between relative neighbour effect (RNE) and the estimated maximum temperature in early summer (June in the Northern Hemisphere and December in the Southern Hemisphere) at each of the 22 experimental sites. Points above zero on the RNE axis indicate facilitation, whereas points below zero indicate competition.

Although the global pattern of our experiment provides compelling evidence for generality in the shift from competition to facilitation with increasing abiotic stress, the overall effect of neighbours on target species varied substantially among the geographical locations where we conducted experiments. Regression analyses of different combinations of temperature and precipitation variables with RNE values yielded only one significant relationship, a negative correlation between RNE and maximum June (December in the Andes) temperatures estimated for each of the 22 sites (Fig. 4). This correlation has important implications for predicting the response of alpine plant communities to climate change. Increased temperatures may alter the current balance of facilitation and competition in alpine plant communities and drive more rapid changes in composition and diversity than predicted by physiology-based models. Although we can only speculate about the relationship we found between the strength and direction of plant interactions and climate, understanding the effects of community-scale processes is crucial for predicting the responses of natural systems to global climate change. Studies of the effects of global warming on communities generally consider only the responses of individual plants or changes in community composition to simple environmental manipulations, and not experiments on the interactions between individuals^{13–15}.

As indicated by many other smaller-scale experiments, our large-scale experiment suggests that facilitation has been underestimated as a determinant factor in the organization and diversity of plant communities. This underestimation has consequences for fundamental community theory. The ‘individualistic’ paradigm of plant community organization is a fundamental tenet in ecology that emphasizes “the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment”¹⁶. With the exception of competitive interactions, the individualistic theory asserts that the distributions and abundances of plant species are independent of other species^{16–18}. Individualistic theory has ramifications beyond academic boundaries. For example, the view that plant species are fully individualistic and ‘interchangeable’ in communities has been used to advocate active management towards “shaping and synthesizing new ecosystems, even in the ‘natural’ environment”¹⁹. The rationale for individualistic communities is based largely on correlative gradient analyses, in which species are almost always distributed independently of one another along environmental gradients^{20–22}. In other words, the fact that the distributions of species rarely overlap completely in nature has been interpreted as a lack of interdependence among species. In our experiment, plants demonstrated species-specific responses to the removal of the surrounding community, but the design of our experiment did not examine species-specific effects of neighbours. Therefore, our results cannot address interdependence as a species-specific phenomenon²³. However, our experimental results support a growing body of experimental evidence for frequent, strong positive interactions and interdependence within plant communities^{1,2,10–12}, and provide broad-based support for a predominant role of facilitation in plant communities in physically harsh environments. □

Methods

We chose two experimental sites at each of 11 different locations around the world (Table 1, Fig. 1). At each location one site was placed in subalpine herbaceous vegetation and the other was placed from 300 m (Cairngorms) to 1,200 m (Andes) higher in alpine vegetation. This allowed us to explore interaction strengths and directions along one of the complex abiotic gradients, elevation, thought to be the most important for alpine communities²⁴. We adopted Grime’s perspective that productivity and biomass are correlated with stress⁵. The gradient from subalpine meadow to alpine tundra is correlated with large decreases in productivity and biomass because of lower temperatures and shorter growing seasons^{24,25}, and at all 11 locations in our study vegetation cover, biomass, and height were noticeably lower at the high sites than at the low sites.

Interactions among plants were assessed by the removal of all neighbouring species within 10 cm of a target individual, and comparison of the performance of target plants with neighbours removed to that of control target plants around which neighbours were

left intact. At each site 3–10 target species were chosen. We chose target individuals that were small relative to nearby conspecifics, and for which relatively distinct individuals or ramets could be found. Some of the target species were clonal, and to reduce the effect of clonality individuals within 10 cm of a conspecific were not used as targets. An analysis of non-clonal species at the experimental sites in the Alps yielded virtually the same results as the analysis for all species combined. Over all 11 of the locations a total of three species were not included in the experiments because discrete individuals were too difficult to find. For each species 8–12 pairs were chosen and one of each was randomly selected for neighbour removal.

We established removal experiments at the beginning of growing seasons from 1996 through 1999. Plants were harvested at the end of the following (second) growing season with the exception of the Cairngorms and the Banff locations where the experiment lasted only one growing season. At the time we established the experiments we counted the number of leaves for each target and control individual. At the end of the experimental periods we re-counted the number of leaves, counted flowers and fruits, recorded survival, harvested all aboveground parts of targets and controls, and measured their mass after oven drying for 3 days at 70 °C. Only the change in leaf number is presented for the Caucasus and Andes locations because of problems encountered collecting biomass; however, the results for change in leaf number were very similar to those for biomass at all locations. All statistical analyses were carried out using JMPin 4.0.2 software²⁶. We used modification of the relative competitive intensity (RCI) index where $RCI = (X_t - X_c)/X_t$. X is an estimation of plant performance in the presence (c) or in the absence (t) of neighbours. Because RCI is not symmetrical around zero we used a modified version of RCI, the ‘relative neighbour effect (RNE)’¹⁰. $RNE = (X_t - X_c)/x$ where x is the highest value of (X_t ; X_c). RNE ranges from -1 to +1 with negative values indicating facilitation and positive values competition. We present our results in the reverse, with positive values indicating facilitation and negative values competition for intuitive interpretation (that is, a positive bar equals a positive effect). In our experiments, $RNE_{biomass}$ was calculated as: (biomass of treated - biomass of control)/biomass of treated. For 20 of the replicates (about 2% of the total replicates) we used the biomass of the control (rather than the treatment) as the denominator in order to keep all RNE values between 1 and -1. RNE_{leaf} was calculated as: (final leaf number/initial leaf number of treated - final leaf number/initial leaf number of control)/(final leaf number/initial leaf number of treated). In 16 cases we used the final leaf number/initial leaf number of control as the denominator in order to keep all RNE values between 1 and -1. Differences between treated and control performance were computed for each pair of targets at a site. When any plant in a pair died the complete pair was excluded from the calculations. This approach provided a conservative estimate of plant-plant interactions, standardized across species, but retained the magnitude of variation within a species.

Using $RNE_{biomass}$ and RNE_{leaf} as dependent variables, we performed multiple ANOVAs with site altitude (low versus high) and geographical location, using the mean for all individuals within species to avoid pseudoreplication. Data were normally distributed. Survival of targets and occurrence of reproductive parts (flowers or fruits) at time of harvest were analysed by a log-linear analysis (JMPin 4.0.2).

Methodology for temperature analysis is presented in the Supplementary Information.

Received 20 February; accepted 25 March 2002; doi:10.1038/nature00812.

1. Callaway, R. M. Positive interactions among plants. *Bot. Rev.* **61**, 306–349 (1995).
2. Callaway, R. M. Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia* **112**, 143–149 (1997).
3. Berlow, E. L. Strong effects of weak interactions in ecological communities. *Nature* **398**, 330–334 (1999).
4. Miller, T. E. Direct and indirect species interactions in an early old-field plant community. *Am. Nat.* **143**, 1007–1025 (1994).
5. Grime, J. P. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* **111**, 1169–1194 (1977).
6. Connell, J. H. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* **122**, 661–696 (1983).
7. Pugnaire, F. I. & Luque, M. T. Changes in plant interactions along a gradient of environmental stress. *Oikos* **93**, 42–49 (2000).
8. Brooker, R. W. & Callaghan, T. V. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* **81**, 196–207 (1998).
9. Bertness, M. D. & Callaway, R. M. Positive interactions in communities. *Trends Ecol. Evol.* **9**, 191–193 (1995).
10. Markham, J. H. & Chanway, C. P. Measuring plant neighbor effects. *Funct. Ecol.* **10**, 548–549 (1996).
11. Grime, J. P. *Plant Strategies and Vegetation Processes* (Wiley, Chichester, 1979).
12. Dodds, W. K. Interspecific interactions: constructing a general neutral model for interaction type. *Oikos* **78**, 377–383 (1997).
13. Woodward, F. I., Smith, T. M. & Emanuel, W. R. A global primary productivity and phytogeography model. *Glob. Biogeochem. Cycles* **9**, 471–490 (1995).
14. Shaver, G. R. & Jonasson, S. Response of arctic ecosystems to climate change: result of long-term field experiments in Sweden and Alaska. *Polar Res.* **18**, 245–256 (1999).
15. Prentice, C. I. et al. A global biome model based on plant physiology and dominance, soil properties, and climate. *J. Biogeogr.* **19**, 117–134 (1992).
16. Gleason, H. A. The individualist concept of the plant association. *Bull. Torrey Bot. Club* **53**, 7–27 (1926).
17. Whittaker, R. H. *Communities and Ecosystems* (Macmillan, New York, 1975).
18. Begon, M., Harper, J. L. & Townsend, C. R. *Ecology* 2nd edn 626–628 (Blackwell, London, 1990).
19. Johnson, H. B. & Mayeux, H. S. Viewpoint: a view on species additions and deletions and the balance of nature. *J. Range Manag.* **45**, 322–333 (1992).
20. Curtis, J. T. *The Vegetation of Wisconsin* (Univ. Wisconsin Press, Madison, 1959).
21. Whittaker, R. H. A consideration of climax theory: the climax as population and pattern. *Ecol. Monogr.* **23**, 41–78 (1953).
22. Austin, M. P. Continuum concept, ordination methods, and niche theory. *Annu. Rev. Ecol. Syst.* **16**, 39–61 (1985).

23. Callaway, R. M. Are positive interactions species-specific? *Oikos* **82**, 202–209 (1998).
 24. Choler, P., Michalet, R. & Callaway, R. M. Facilitation and competition on gradients in alpine plant communities. *Ecology* **82**, 3295–3308 (2001).
 25. Archibald, O. W. *Ecology of World Vegetation* 280–318 (Chapman and Hall, London, 1995).
 26. JMPin 4.0.2 (SAS Institute Inc., Duxbury Press, Cary, North Carolina, 2000).

Supplementary Information accompanies the paper on *Nature's* website (<http://www.nature.com/nature>).

Acknowledgements

We thank the National Center for Ecological Synthesis and Analysis, The National Geographic Society, the Civilian Research and Development Foundation, and the Andrew W. Mellon Foundation for financial support.

Competing interests statement

The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to R.M.C. (e-mail: callaway@selway.umt.edu).

Consumer versus resource control of species diversity and ecosystem functioning

Boris Worm^{*†}, Heike K. Lotze^{*†}, Helmut Hillebrand[‡] & Ulrich Sommer[†]

^{*} Biology Department, Dalhousie University, Halifax, Nova Scotia, B3H 4J1, Canada

[†] Section of Marine Ecology, Institute for Marine Science, Kiel University, Diesternbrooker Weg 20, 24105 Kiel, Germany

[‡] Erken Laboratory, Department of Limnology, Uppsala University, Norr Malma 4200, 76173 Norrtälje, Sweden

A key question in ecology is which factors control species diversity in a community^{1–3}. Two largely separate groups of ecologists have emphasized the importance of productivity or resource supply, and consumers or physical disturbance, respectively. These variables show unimodal relationships with diversity when manipulated in isolation^{4–8}. Recent multivariate models^{9–10}, however, predict that these factors interact, such that the disturbance–diversity relationship depends on productivity, and vice versa. We tested these models in marine food webs, using field manipulations of nutrient resources and consumer pressure on rocky shores of contrasting productivity. Here we show that the effects of consumers and nutrients on diversity consistently depend on each other, and that the direction of their effects and peak diversity shift between sites of low and high productivity. Factorial meta-analysis of published experiments confirms these results across widely varying aquatic communities. Furthermore, our experiments demonstrate that these patterns extend to important ecosystem functions such as carbon storage and nitrogen retention. This suggests that human impacts on nutrient supply¹¹ and food-web structure^{12,13} have strong and interdependent effects on species diversity and ecosystem functioning, and must therefore be managed together.

The most striking feature of life on Earth is its diversity. Consequently, the most fundamental question in ecology is which factors maintain diversity in ecological communities². Here, we analyse the combined impacts of consumers and nutrient resources on plant diversity. The supply of limiting resources, such as nutrients, controls primary productivity; that is, the rate of production of

organic matter. On local scales, productivity and diversity are often unimodally related (Fig. 1a), such that peak diversity is observed at intermediate productivity⁸. Declining diversity at higher levels of productivity is thought to be due to competitive exclusion. Exclusion can be prevented by periodic mortality events, caused by consumers or physical disturbance^{4,6,7}. These factors also show unimodal relationships with diversity (Fig. 1b). Because the effects of productivity, disturbance and consumption on diversity have been analysed separately, their interactions in nature have remained elusive. In an attempt to unify these patterns theoretically, one study explored how traditional Lotka–Volterra competition models respond to increases in productivity and disturbance frequency⁹. The study predicted that the effects of disturbance on diversity depend strongly on productivity, and vice versa (for details see Fig. 1c). Physical disturbance and consumer pressure were predicted to give similar patterns⁹. These ideas have been mathematically elaborated¹⁰, using a spatial competition model¹⁴, in which the environment consists of a large number of discrete patches, each of which can be empty or occupied by one out of n species. The model assumes a linear competitive hierarchy where species i ($1 \leq i \leq n$) would always exclude species j if $i < j$. Multi-species coexistence in this model depends on a trade-off between competitive ability and patch colonization rate c_i or extinction rate m_i (ref. 14). Productivity is assumed to enhance colonization rates of all species by a constant R and disturbance increases extinction rates of all species by a constant D (ref. 10). The dynamics of the proportion p_i of patches occupied by species i is represented as

$$\frac{dp_i}{dt} = c_i R p_i \left(1 - \sum_{k=1}^i p_k \right) - (m_i + D) p_i - \sum_{k=1}^{i-1} c_k R p_k p_i \quad (1)$$

$(i = 1, 2, \dots, n)$

where the first term represents colonization, the second local extinction and the third competitive exclusion¹⁰. Notably, predictions from this model are almost identical to those of earlier simulations^{9,10}. Thus, general patterns emerged (Fig. 1c), despite the differences in model structure (spatial compared with non-spatial), assumptions (equilibrium versus non-equilibrium) and complexity.

We tested these models in a food-web context by experimentally manipulating consumer pressure (absent, present) and nutrient supply (no, low, medium, high nutrient enrichment; see Methods)

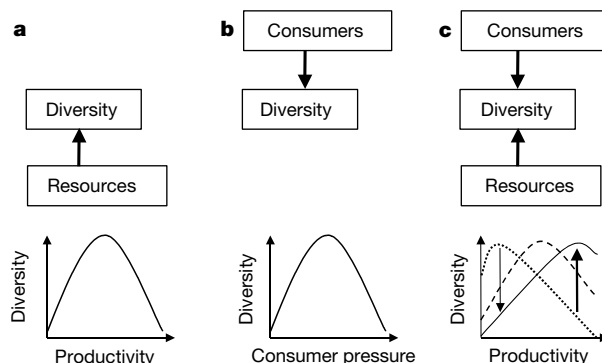


Figure 1 Consumer versus resource control of species diversity. **a, b**, Univariate models predict two independent relationships, where diversity peaks at intermediate resource supply or productivity (**a**), and at intermediate consumer pressure or physical disturbance (**b**), respectively^{4,5,7,8}. **c**, Multivariate models^{9,10} predict that the effects of consumers on diversity depend on resource supply and productivity; peak diversity shifts from low to intermediate to high productivity depending on whether consumer pressure is low (dotted line), intermediate (dashed line) or high (solid line). Consumers decrease diversity at low productivity (thin arrow) but increase diversity at high productivity (thick arrow).