the bio- and chemostratigraphic breakpoints may not coincide precisely. The restricted facies distribution of distinctive early Mesoproterozoic acritarchs, however, suggests that biostratigraphic confidence will necessarily be tied to careful palaeoenvironmental characterization.

Process-bearing microfossils were once thought to be restricted to Phanerozoic strata. Two decades ago, their range was extended to the beginning of the Neoproterozoic era. Now, it is clear that process-bearing microfossils have been present for nearly half of life's recorded history. The Roper Group provides an unusually clear window on aspects of biology in the early Mesoproterozoic oceans, demonstrating that 1,500 Myr ago marine protists included cytologically sophisticated organisms that lived in ecologically differentiated communities. □

1. Woese, C. R., Kandler, O. & Wheelis, M. L. Towards a natural system of organisms: proposal for the domains Archaea, Bacteria, and Eucarya. *Proc. Natl. Acad. Sci. USA* **87,** 4576–4579 (1990).
2. Brocks, J. J., Logan, G. A., Buick, R. & Summons, R. E. Archean molecular fossils and the early rise of eukaryotes. *Science* **285,** 1033–1036 (1999).
3. Hayes, J. M. in *Early Life on Earth* (ed. Bengtson, S.) 220–236 (Columbia Univ. Press, New York, 1994).
4. Zhang, Z. Clastic facies microfossils from the Chaunlingguo Formation (1800 Ma) near Jixian, North China. *J. Micropalaeontol.* **5,** 9–16 (1986).
5. Summons, R. E., Powell, T. G. & Boreham, C. J. Petroleum geology and geochemistry of the Middle Proterozoic McArthur Basin, Northern Australia. III. Composition of extractable hydrocarbons. *Geochim. Cosmochim. Acta* **51,** 3075–3082 (1988).
6. Han, T.-M. & Runnegar, B. Megascopic eukaryotic algae from the 2.1-billion-year-old Negaunee Iron Formation, Michigan. *Science* **257,** 232–235 (1992).
7. Knoll, A. H. in *Palynology: Principles and Applications* (eds Jansonius, J. & McGregor, D. C.) Vol. I 51–80 (American Association of Stratigraphic Palynologists Foundation, Tulsa, Oklahoma, 1996).
8. Yin, L. Acanthomorphic acritarchs from Meso-Neoproterozoic shales of the Ruyang Group, Shanxi, China. *Rev. Palaeobot. Palynol.* **98,** 15–25 (1998).
9. Butterfield, N. J., Knoll, A. H. & Swett, K. Paleobiology of the Neoproterozoic Svanbergfjellet Formation, Spitsbergen. *Fossils Strata* **34,** 1–84 (1994).
10. Jansen, R.-P. RNA-cytoskeletal associations. *FASEB J.* **13,** 455–466 (1999).
11. Schmidt, A. & Hall, M. N. Signalling the actin cytoskeleton. *Annu. Rev. Cell Dev. Biol.* **14,** 305–338 (1998).
12. Xiao, S., Knoll, A. H., Kaufman, A. J., Yin, L. & Zhang, Y. Neoproterozoic fossils in Mesoproterozoic rocks? Chemostratigraphic resolution of a biostratigraphic conundrum from the North China Platform. *Precambrian Res.* **84,** 197–220 (1997).
13. Jackson, M. J., Sweet, I. P., Page, R. W. & Bradshaw, B. E. in *Integrated Basin Analysis of the Isa Superbasin Using Seismic, Well-log, and Geopotential Data: an Evaluation of the Economic Potential of the Northern Lawn Hill Platform* (eds Bradshaw, B. E. & Scott, D. L.) (Australian Geological Survey Organisation Record 1999/19, Canberra, Australia, 1999).
14. Kralik, M. Rb–Sr age determinations on Precambrian carbonate rocks of the Carpentarian McArthur Basin, Northern Territory, Australia. *Precambrian Res.* **18,** 157–170 (1982).
15. Abbott, S. T. & Sweet, L. P. Tectonic control on third-order sequences in a siliciclastic ramp-style basin: an example from the Roper Superbasin (Mesoproterozoic), northern Australia. *Aust. J. Earth Sci.* **47,** 637–657 (2000).
16. Jackson, M. J. & Raiswell, R. Sedimentology and carbon-sulfur geochemistry of the Velkerri Formation, a mid-Proterozoic potential oil source in northern Australia. *Precambrian Res.* **54,** 81–108 (1991).
17. Peat, C. R., Muir, M. D., Plumb, K. A., McKirdy, D. M. & Norvick, M. S. Proterozoic microfossils from the Roper Group, Northern Territory. *Bur. Min. Res. J. Austr. Geol. Geophys.* **3,** 1–17 (1978).
18. Jankauskas, T. V. *Precambrian microfossils from the USSR* 5–33 (Nauka, Leningrad, 1989).
19. Veis, A. F. & Vorobyeva, N. G. Riphean and Vendian microfossils of the Anabar Uplift. *Isvest. Akad. Nauk. USSR Ser. Geol.* **8,** 114–130 (1992).
20. Zhou, H. *et al. Sequence Stratigraphic Research in Meso- to Neoproterozoic Successions of the Southern North China Platform* 5–36 (Geological Publishing House, Beijing, 1999).
21. Jacobsen, S. R. Acritarchs as paleoenvironmental indicators in Middle and Upper Ordovician rocks from Kentucky, Ohio, and New York. *J. Paleontol.* **53,** 1197–1212 (1979).
22. Vidal, G. & Nysteun, J. P. Micropaleontology, depositional environment, and biostratigraphy of the Upper Proterozoic Hedmark Group, southern Norway. *Am. J. Sci. A* **290,** 170–211 (1990).
23. Butterfield, N. J. & Chandler, F. W. Palaeoenvironmental distribution of Proterozoic microfossils, with an example from the Agu Bay Formation, Baffin Island. *Palaeontology* **35,** 943–957 (1992).
24. Petrov, P. Yu. & Veis, A. F. Facial-ecological structure of the Derevnya Formation microbiota: Upper Riphean, Turukhansk Uplift, Siberia. *Stratigr. Geol. Correl.* **3,** 435–4605 (1995).
25. Canfield, D. E. A new model for Proterozoic ocean chemistry. *Nature* **396,** 450–453 (1998).
26. Anbar, A. D. & Knoll, A. H. Trace metal limitation of primary production 1.85–1.25 Ga. *1999 American Geophysical Union Fall Meeting* (http://www.agu.org/meetings/fm99top.html) (1999).
27. German, T. N. *Organic World One Billion Years Ago* 1–50 (Leningrad, Nauka, 1990).
28. Samuelsson, J., Dawes, P. R. & Vidal, G. Acid-resistant palynomorphs from the Proterozoic Thule Group, northwest Greenland. *Precambrian Res.* **96,** 1–23 (1999).

Acknowledgements

The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus *Daphnia*

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The vertical migration of zooplankton into lower and darker water strata by day is generally explained by the avoidance of visually orienting predators, mainly fish[1–4]; however, it is unclear why daily zooplankton migration has been maintained in fishless areas[5]. In addition to predation, ultraviolet radiation—a hazardous factor for zooplankton in the surface layers of marine and freshwater environments[6–8]—has been suspected as a possible cause of daytime downward migration[9]. Here we test this hypothesis by studying several *Daphnia* species, both in a controlled laboratory system and under natural sunlight in an outdoor system. We selected *Daphnia* species that differed in their pigmentation as both melanin and carotenoids have been shown to protect *Daphnia* from ultraviolet light[10,11]. All *Daphnia* species escaped into significantly deeper water layers under ultraviolet radiation. The extent to which the daphnids responded to this radiation was inversely linked to their pigmentation, which reduced ultraviolet transmission. These results suggest that ultraviolet avoidance is an additional factor in explaining daytime downward migration. Synergistic benefits might have shaped the evolution of this complex behaviour.
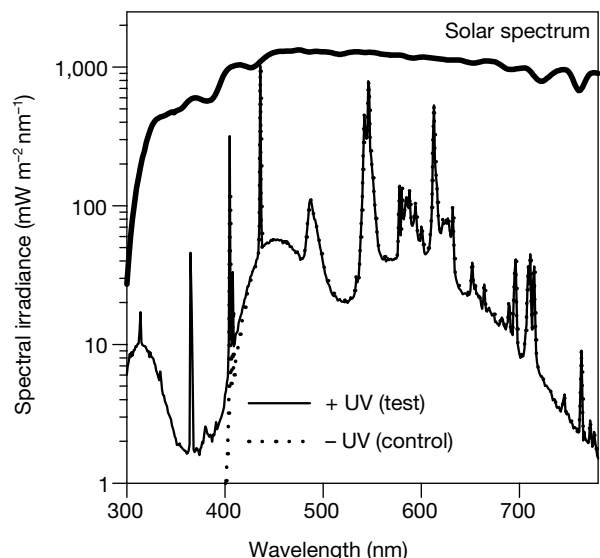
Figure 1 Spectral irradiation in mesocosms with (test) and without (control) ultraviolet radiation. Ultraviolet radiation above the water surface was lower than on a cloudless September day at noon in 1995 in Munich, when we performed the experiments under natural solar irradiation (solar spectrum).

Diel vertical migration (DVM) in zooplankton is an impressive phenomenon, involving tons of biomass changing its vertical position in a daily rhythm, both in marine and freshwater environments, with profound impact on all trophic levels. This phenomenon was noticed by the earliest scientists in this field and is reflected in the implicit knowledge of fishermen over the centuries. In cases of predator-induced DVM, zooplankton avoid 'light-dependant mortality'[1,2] from visually feeding predators by staying in deeper, darker water layers during the day[13]. Changes in light intensity trigger upward and downward DVM of zooplankton[14]; chemical or physical stimuli stemming from predators can also induce DVM behaviour[15]. However, migrating zooplankton normally have to cross temperature gradients in the natural water column, and the smaller growth rates at cooler temperatures in lower water strata is a major cost[16]. Thus, additional benefits to predator avoidance may be necessary to explain the evolution and persistence of this complex and costly behaviour. Furthermore, there are vertically migrating zooplankton communities even in the absence of fish predators in arctic lakes[5], a result that has yet to be explained.

Another harmful factor for zooplankton is ultraviolet-B radiation[6–8], which may penetrate to significant depth. In clear marine water 10% of surface ultraviolet radiation penetrated down to 25 m (ref. 17), and in low dissolved organic carbon (DOC) freshwater lakes a maximum penetration depth for 1% of the surface level of UV-B was measured at 33 m (ref. 18). For *Daphnia magna*, ultraviolet receptors[19] and the ability to see ultraviolet radiation[20] have been shown. Given that ultraviolet radiation is a selective ecological factor, a similar avoidance reaction could be expected. To test this hypothesis we performed depth-selection experiments with daphnids. Our goal was to test if the ultraviolet perception, enabling for a negative phototactic short-term response to ultraviolet radiation[21–23], would result in appropriate depth selection of differently pigmented daphnids when exposed to ultraviolet radiation. We performed experiments under both natural and artificial sunlight. We measured the stabilized vertical distribution of pigmented and unpigmented daphnids in experimental mesocosms. Under natural sunlight we found a significant deeper migration when the daphnids were exposed to ultraviolet irradiation (Mann–Whitney U-test, $P \leq 0.0001$; Table 1). We verified our results in laboratory experiments. Our experimental ultraviolet intensity of $0.505 \, mW \, m^{-2}$

Table 1 Median depth distributions of adult and juvenile *Daphnia* under simulated and natural sunlight

	Median of depth distribution (m)					
	Ultraviolet		Control		Difference	
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
Under laboratory irradiation						
D. cucullata	0.65	0.50	0.20	0.15	0.45	0.35
D. pulex (unpigmented)	0.85	0.85	0.15	0.10	0.70	0.75
D. pulex (melanized)	0.15	0.20	0.10	0.10	0.05	0.10
D. rosea	0.20	0.30	0.10	0.10	0.10	0.20
Under solar irradiation						
D. pulex (unpigmented)	0.85	–	0.45	–	0.40	–
D. pulex (melanized)	0.60	–	0.55	–	0.05	–

(285–400 nm) falls below the natural ultraviolet radiation of temperate cloudless spring, summer and autumn days at noon (Fig. 1). By applying steep temperature and irradiation gradients (Fig. 2e, f), we chose experimental conditions that allowed detection of graded responses in our small-scale set-up. All of our experiments in mesocosms showed a significant downward migration of ultraviolet-exposed daphnids into the colder part of the mesocosms (Mann–Whitney U-test, $P \leq 0.0001$; Fig. 2 and Table 1). The daphnids avoided ultraviolet radiation despite the anticipated cost.

Melanin pigmentation as well as carotenoids increase the ultraviolet tolerance of planktonic species[10,11]. To minimize the cost of colder temperatures in deeper water layers, a less pronounced downward response to ultraviolet light would be predicted for zooplankton with a higher ultraviolet tolerance. This was confirmed by the fact that the response to ultraviolet light was weaker in both of the pigmented forms (Fig. 2, Table 1). Under ultraviolet radiation pigmented *Daphnia pulex* and *Daphnia rosea* stayed closer to the surface than unpigmented *D. pulex* and *Daphnia cucullata*. This is reflected in a smaller difference in median depth between the control groups and the ultraviolet treatments for either of the pigmented clones. Under natural solar radiation in outdoor experiments our results confirmed a more pronounced downward response of adult unpigmented *D. pulex* compared with melanized *D. pulex* (Table 1). Melanin in the carapace effectively reduces
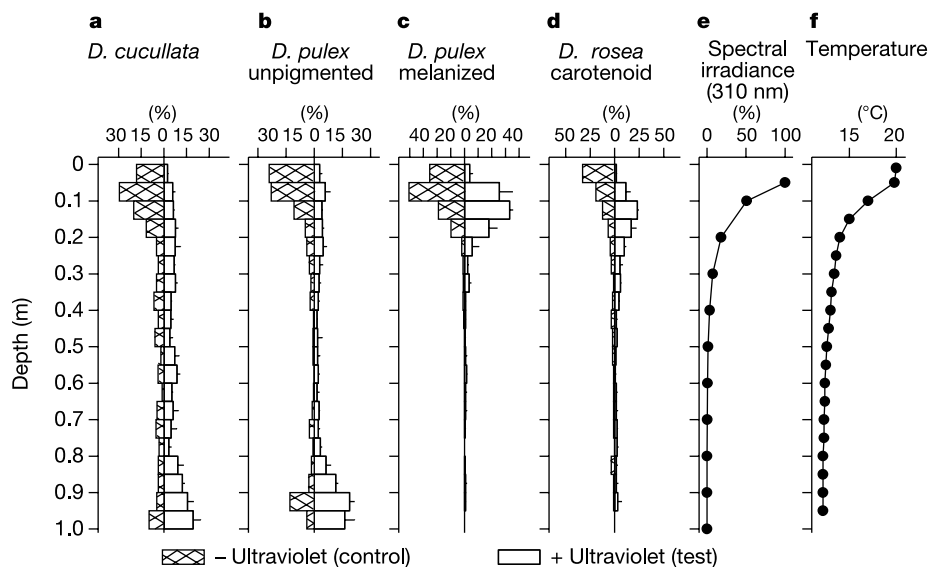

Figure 2 Results from laboratory experiments. **a–d**, Vertical distribution of unpigmented *D. cucullata* (**a**) and *D. pulex* (**b**); melanized *D. pulex* (**c**); and *D. rosea* with carotenoids (**d**), in mesocosms (height 1 m; diameter 46 mm). **e, f**, We measured the vertical gradient of radiation (**e**) and the vertical temperature gradient (**f**). Data represent means of three replicates (± 1 s.d.) taken as the mean of five repeated measurements. Measured values of depth distribution in all experiments showed a significantly deeper position of daphnids in ultraviolet treatments (Mann–Whitney U-test; $P < 0.0001$).
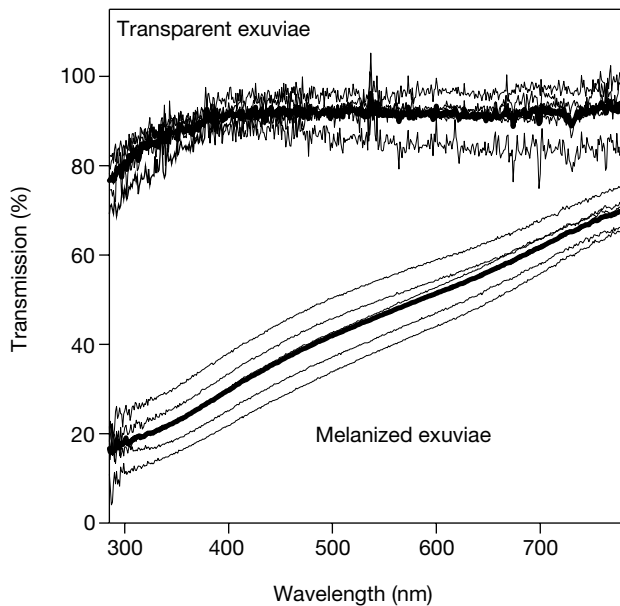
Figure 3 Spectral transmission of exuviae from transparent and melanized *D. pulex* measured in 1-nm intervals from 280 to 780 nm. Thick lines represent means. Melanin pigmentation effectively reduced transmission of ultraviolet irradiation.

ultraviolet transmission (Fig. 3). The downward migration of both pigmented and unpigmented daphnids during the day indicates that ultraviolet radiation is a proximate factor in depth selection. The stronger response of unpigmented daphnids apparently compensates for a weaker ultraviolet tolerance compared with that of their pigmented congeners. This implies that ultraviolet radiation is not only a proximate but, at the same time, is also an ultimate factor for the migration of zooplankton.

If ultraviolet radiation is both an ultimate and a proximate factor it could have had an initial role in the evolution of the predator-induced daytime sinking in DVM[24]. Perhaps the benefit for populations whose migration was originally ultraviolet-induced would have increased with the abundance of visually orienting predators. An extended migration amplitude would also have further contributed to the benefit of vertical migration, and then been evolutionarily established as predator-induced DVM in zooplankton. The depth necessary to avoid visually orienting predators[25] generally exceeds the depth to which damaging ultraviolet intensities penetrate[7], as visible light penetrates deeper into natural waters than does ultraviolet radiation[26], and fish are able to forage at very low light levels[27,28]. Owing to the abundance of fish in many lakes, ultraviolet protection would already be achieved by a predator-induced DVM. Nevertheless, if *Daphnia* can avoid being circulated to the surface by turbulent mixing in the epilimnion (circulating surface water), a migration into the hypolimnion (non-circulating, lower water layer) might even be advantageous in lakes where ultraviolet penetration is reduced by higher contents of DOC[18]. It follows that the impact of natural and anthropogenically increased ultraviolet radiation[29] on zooplankton DVM should have an involvement in aquatic environments with temporally or spatially low fish abundance, such as in high mountain lakes, arctic regions and in many marine areas. On the basis of our results we propose that pigmentation and migration are two alternative strategies to avoid harmful ultraviolet radiation and we expect pigmentation, as it increases visibility and thus susceptibility to visual predation, to be found in lakes without fish, and migration to be found in lakes with fish. Our study shows that depth-selection behaviour can be a multi-causal phenomenon. The additive benefits possibly increase the adaptive value and thus facilitate the evolution and persistence of such a complex behaviour. □

Methods
Cultures
Cultures of unpigmented *D. cucullata* originated from Lake Thalersee (Bavaria, Germany) and *D. rosea* with carotenoid body pigmentation originated from a fishless pond in the Bavarian alps (Germany). Two *D. pulex* clones, one an unpigmented clone and the other with a melanized carapace, were isolated from Churchill in arctic Canada.

Mesocosm experiments
For the experiments we constructed Perspex tube mesocosms (height 1 m; diameter 46 mm). For the laboratory experiments the mesocosms were irradiated from above by one Phillips TL12/40W ultraviolet-B fluorescent tube, two Osram L36/W/11 Lumilux daylight and two Salvina ES Standard F36W/129ST tubes giving a light spectrum that covered the ultraviolet and visible bandwidth of natural sunlight. Light was scattered by an opalescent ultraviolet-permeable Perspex sheet. We used acetate foil to eliminate ultravioloet-C radiation of the Phillips ultraviolet-B florescent tube. Ultraviolet radiation was excluded from controls by Mylar foil. Three control and three ultraviolet treatments were positioned in an alternating order and screened off from the others to prevent systematic errors. The total irradiation difference between ultraviolet and control treatments (wavelength (λ) > 400 nm) was less than 2%. Spectral irradiance was measured with a calibrated Bentham spectral radiometer. For the experiments with natural sunlight the system was transported to the roof of the institute, where it had been installed in a dark container allowing light to penetrate the Perspex tubes only from above.

The mesocosms were filled with filtered (0.45 µm) water from the eutrophic Lake Klostersee (Germany), which had been stored for more than a week to exclude the possible effects of algae and kairomones. Kd$_{310}$ (the diffuse attenuation coefficient for wavelength 310nm) in Lake Klostersee (measured in the lake) was 4.33 m^{-1}. Owing to the experimental geometry the attenuation was higher in the experimental columns: Kd$_{310}$(exp) = ~10 m^{-1}.

To obtain vertical gradients of radiation (Fig. 2e) we constructed Perspex tubes of each depth, sealed the bottom with ultraviolet-permeable acetate foil and measured the ultraviolet radiation that penetrated each water column. The system was cooled to 12 °C and heated from above by lamp irradiation to 20 °C, which resulted in a steep vertical temperature gradient (Fig. 2f). We optimized the system in a series of previous experiments to obtain not only directional, but also graded responses. We added 20 light-acclimated (20 mW m^{-2}) daphnids to each mesocosms. For the experiments with juveniles we used 3–4-day-old (3rd to 4th instar) daphnids; for the experiments with adults we used 10-day-old daphnids. On the basis of the results of pilot experiments, we counted the individuals after 2-h acclimation of the daphnids to the light (both with and without continuous ultraviolet radiation) and temperature conditions. We verified stabilization of the behaviour by counting five times (repeated measurement, time interval of 20 min). No significant shift of the median depth was detected during the 80 min of the measurement. For statistical analysis we compared the within treatment variation between the replicates with Kruskal–Wallis tests. Owing to the homogeneous conditions in our set-up we found no significant difference between replicates. This allowed us to pool the data and to compare the treatments with Mann–Whitney U-tests.

Measuring the protective effect of pigmentation
To verify the protective effect of melanin, we measured ultraviolet transmission directly at the exuviae. Five freshly moulted exuviae from transparent and melanized *D. pulex* were washed in H$_2$O-bidest and transferred on quartz glass covers slips. The centre of one side of the exuviae was positioned over a 100-µm diaphragm. The spectral irradiation of a 100-W quartz halogen calibration light bulb transmitting the cover slide with and without an exuviae was measured by a Bentham spectral radiometer between 280 nm and 780 nm at 1-nm steps. Transmission was calculated by the quotient of the spectral irradiance of an empty cover slide $\omega_{qu}(\lambda)$, and the spectral irradiance of a cover slide with exuviae $\omega_{ex}(\lambda)$: $T(\lambda) = \omega_{ex}(\lambda)\omega_{qu}(\lambda)^{-1}$.

1. Zaret, T. M. & Suffern, J. S. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.* **21,** 804–813 (1976).
2. Stich, H. B. & Lampert, W. Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature* **293,** 396–398 (1981).
3. Neill, W. E. Induced vertical migration in copepods as a defence against invertebrate predation. *Nature* **345,** 524–526 (1990).
4. De Meester, L., Weider, L. J. & Tollrian, R. Alternative antipredator defences and genetic polymorphism in a pelagic predator–prey system. *Nature* **378,** 483–485 (1995).
5. Williamson, C. E. *et al.* Ultraviolet radiation and zooplankton community structure following deglaciation in Glacier Bay, Alaska. *Ecology* (in the press).
6. Calkins, J. & Thordadottir, T. The ecological significance of solar UV radiation on aquatic organisms. *Nature* **283,** 563–566 (1980).
7. Williamson, C. E., Zagarese, H. E., Schulze, P. C., Hargreaves, B. R. & Seva, J. The impact of short-term exposure to UV-B radiation on zooplankton communities in north temperate lakes. *J. Plankton Res.* **16,** 205–218 (1994).
8. Siebeck, O. & Böhm, U. Challenges for an appraisal of UV-B effects upon planktonic crustaceans under natural radiation conditions with a non-migrating (*Daphnia pulex obtusa*) and a migrating cladoceran (*Daphnia galeata*). *Arch. Hydrobiol. Beih. Ergebn. Limnol.* **43,** 197–206 (1994).
9. Kerfoot, W. C. Adaptive value of vertical migration: comments on the predator hypothesis and some alternatives. *Contr. Mar. Sci. Suppl.* **27,** 91–113 (1985).
10. Hairston, N. G. Jr Photoprotection by carotenoid pigments in the copepod *Diaptomus nevadensis*. *Proc. Natl Acad. Sci. USA* **73,** 971–974 (1976).

71

11. Hebert, P. D. N. & Emery, C. J. The adaptive significance of cuticular pigmentation in *Daphnia*. *Funct. Ecol.* **4,** 703–710 (1990).

12. Lampert, W. The adaptive significance of diel vertical migration of zooplankton. *Funct. Ecol.* **3,** 21–27 (1989).

13. De Meester, L., Dawidowicz, P., van Gool, E. & Loose, C. J. in *The Ecology and Evolution of Inducible Defenses* (eds. Tollrian, R. & Harvell, C. D.) 160–176 (Princeton Univ. Press, Princeton, New Jersey, 1999).

14. Ringelberg, J. The positively phototactic reaction of *Daphnia magna* Strauss: a contribution to the understanding of diurnal vertical migration. *Neth. J. Sea Res.* **2,** 319–406 (1964).

15. Bollens, S. M., Frost, B. W. & Cordell, J. R. Chemical, mechanical and visual cues in the vertical migration behavior of the marine planktonic copepod *Acartia hudsonica*. *J. Plankton Res.* **16,** 555–564 (1994).

16. Loose, C. J. & Dawidowicz, P. Trade-offs in diel vertical migration by zooplankton: The costs of predator avoidance. *Ecology* **75,** 2255–2263 (1994).

17. Fleischmann, E. M. The measurement and penetration of ultraviolet radiation into tropical marine water. *Limnol. Oceanogr.* **34,** 1623–1629 (1989).

18. Morris, D. P. et al. The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnol. Oceanogr.* **40,** 1381–1391 (1995).

19. Smith, K. C. & Macagno, E. R. UV photoreception in the compound eye of *Daphnia magna* (Crustacea, Branchiopoda). A fourth spectral class in single ommatidia. *J. Comp. Physiol. A* **166,** 597–606 (1990).

20. Merker, E. Sehen die Daphnien ultraviolettes Licht? *Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere.* **48,** 277–348 (1930).

21. Hessen, D. O. *Daphnia* responses to UV-light. *Arch. Hydrobiol. Beih.* **43,** 85–195 (1994).

22. Storz, U. C. & Paul, R. J. Phototaxis in water fleas (*Daphnia magna*) is differently influenced by visible and UV light. *Comp. Physiol. A* **183,** 709–717 (1998).

23. Leech, D. M. & Williamson, C. E. *In situ* exposure to ultraviolet radiation alters the depth distribution of *Daphnia*. *Limnol. Oceanogr.* **46,** 416–420 (2001).

24. Damkaer, D. M. in *The Role of Solar Ultraviolet Radiation in Marine Ecosystems* (ed. Calkins, J.) 701–706 (Plenum, New York, 1982).

25. Dodson, S. I. Predicting diel vertical migration of zooplankton. *Limnol. Oceanogr.* **35,** 1195–1200 (1990).

26. Smith, R. C. & Baker, K. S. Optical properties of the clearest natural waters (200–800 nm). *Appl. Optics* **20,** 177–184 (1981).

27. Vinyard, G. L. & O'Brien, W. J. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). *J. Fish. Res. Bd. Can.* **33,** 2845–2849 (1976).

28. Confer, J. L. et al. Visual predation by planktivores. *Oikos* **31,** 27–37 (1978).

29. Madronich, S., McKenzie, R. L., Caldwell, M. M. & Bjorn, L. Changes in ultraviolet radiation reaching the earth's surface. *Ambio* **24,** 143–152 (1995).

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Partitioning selection and complementarity in biodiversity experiments

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The impact of biodiversity loss on the functioning of ecosystems and their ability to provide ecological services has become a central issue in ecology. Several experiments have provided evidence that reduced species diversity may impair ecosystem processes such as plant biomass production[1–5]. The interpretation of these experiments, however, has been controversial[6–12] because two types of mechanism may operate in combination[6,13–15]. In the 'selection effect', dominance by species with particular traits affects ecosystem processes. In the 'complementarity effect', resource partitioning or positive interactions lead to increased total resource use. Here we present a new approach to separate the two effects on the basis of an additive partitioning analogous to the

Price equation in evolutionary genetics[16–19]. Applying this method to data from the pan-European BIODEPTH experiment[4] reveals that the selection effect is zero on average and varies from negative to positive in different localities, depending on whether species with lower- or higher-than-average biomass dominate communities. In contrast, the complementarity effect is positive overall, supporting the hypothesis that plant diversity influences primary production in European grasslands through niche differentiation or facilitation.

Recent theoretical work has revealed that the observed responses of ecosystem processes to changes in species or functional-group diversity can be generated by a combination of different effects[13–15]. These biodiversity effects can be grouped into two classes. First, there are those that arise from niche differentiation or facilitation between species, and that can increase the performance of communities above that expected from the performance of individual species. Distinguishing the effects of niche differentiation and facilitation may often be difficult in practice; therefore, we refer to these mechanisms collectively as 'complementarity'. One common form of complementarity in plant communities (which involves both resource partitioning and facilitation) arises between legumes, which have the ability to fix atmospheric nitrogen, and other plants, which have access only to soil nitrogen.

The second class of biodiversity effects gives rise to relationships between biodiversity and ecosystem functioning through selective processes, such as interspecific competition, which cause dominance (high relative abundance) of species with particular traits. For example, in one model of the 'sampling effect'[6,13], higher-diversity plant mixtures assembled at random from a pool of species have a higher chance of containing and becoming dominated by the
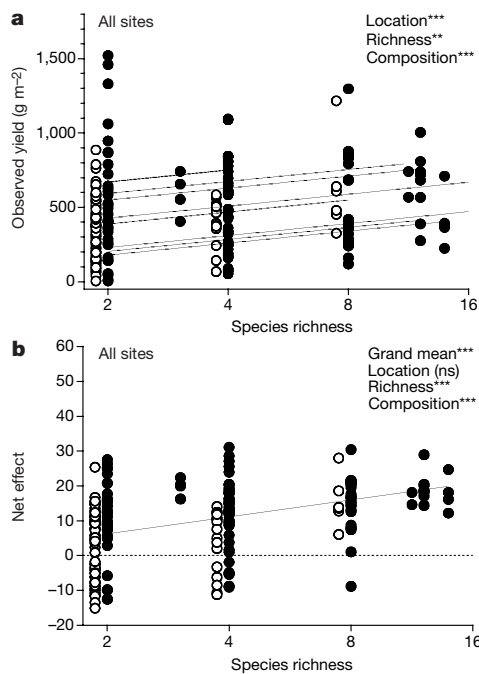

Figure 1 Observed yield Y_O and net biodiversity effect ΔY as functions of species richness across all localities in mixtures of the BIODEPTH experiment. **a**, Observed yield; **b**, net biodiversity effect. Open circles are plots that do not contain any legume species; filled circles are plots that contain legumes. Lines are slopes from the multiple regression model using species richness on a $\log_2$ scale. Lines in **a** from highest elevation to lowest are: Germany, Silwood, Sheffield, Switzerland, Ireland, Greece, Sweden and Portugal. Values of the biodiversity effect (in $g\,m^{-2}$) are square-root transformed to meet the assumptions of analyses but preserve the original positive and negative signs. (Single asterisk, $P < 0.05$; double asterisk, $P < 0.01$; triple asterisk, $P < 0.001$; ns: non-significant.)