

Moreover, the direct link of the ALVZ to the basal detachment under the eastern plateau margin, as well as its correlation with the extent of the entire shortened plateau upper crust (Fig. 2), strongly supports its relevance to the tectonic shortening process. The mechanical weakness of the mid-crustal ALVZ and the Eastern Cordillera basal detachment, as inferred from the presence of melts and fluids, probably separates crustal shortening in an upper-crust imbricate belt<sup>7–9</sup> from a deeper crust with an unknown mode of internal deformation. The continuity of the deep crustal structure across the entire plateau suggests a single crustal thickening process, namely tectonic shortening, rather than important additional contributions from other processes that involve the mantle<sup>23</sup>. As a consequence, bulk crustal shortening from surface observations may have been substantially underestimated.

Our interpretation of the ALVZ is similar, in its tectonic aspect, to the interpretation of the low-velocity zone in Tibet—which has remarkably similar depth, thickness and lateral extent<sup>24,25</sup>. Moreover, as documented by a study of xenoliths<sup>26</sup>, the middle crust (30–50 km depth) of the northern Tibetan plateau consists of hot and dry refractory rocks similar to those we expect below TRAC2. The existence of analogous low-velocity zones below the Earth's two highest plateaux suggests their fundamental role in the plateau-building process, possibly as decoupling zones that partition crustal shortening into a largely brittle upper-crust domain and ductile deep crust. □

Received 15 October 1999; accepted 12 October 2000.

1. DeMets, C., Gordon, R. G., Argus, D. F. & Stein, S. Current plate motions. *Geophys. J. Int.* **101**, 425–478 (1990).
2. Isacks, B. L. Uplift of the central Andean plateau and bending of the Bolivian orocline. *J. Geophys. Res.* **93**, 3211–3231 (1988).
3. James, D. E. Andean crustal and upper mantle structure. *J. Geophys. Res.* **76**, 3246–3271 (1971).
4. Wigger, P. J. *et al.* in *Tectonics of the Southern Central Andes* (eds Reutter, K. -J., Scheuber, E. & Wigger, P. J.) 23–48 (Springer, Berlin, 1994).
5. Zandt, G., Velasco, A. A. & Beck, S. L. Composition and thickness of the southern Altiplano crust, Bolivia. *Geology* **22**, 1003–1006 (1994).
6. Beck, S. L. *et al.* Crustal thickness variations in the Central Andes. *Geology* **24**, 407–410 (1996).
7. Allmendinger, R. W. & Gubbels, T. Pure and simple shear plateau uplift, Altiplano-Puna, Argentina and Bolivia. *Tectonophysics* **259**, 1–13 (1996).
8. Kley, J. & Monaldi, C. R. Tectonic shortening and crustal thickness in the central Andes: how good is the correlation? *Geology* **26**, 723–726 (1998).
9. Lamb, S., Hoke, L., Kennan, L. & Dewey, J. in *Orogeny Through Time* (eds Burg, J. P. & Ford, M.) 237–264 (Special Publication 121, Geological Society, London, 1997).
10. Allmendinger, R. W., Jordan, T. E., Kay, S. M. & Isacks, B. L. The evolution of the Altiplano-Puna Plateau of the Central Andes. *Annu. Rev. Earth Planet. Sci.* **26**, 139–174 (1997).
11. Owens, T. J., Zandt, G. & Taylor, S. R. Seismic evidence for an ancient rift beneath the Cumberland Plateau, Tennessee: A detailed analysis of broadband teleseismic P waveforms. *J. Geophys. Res.* **89**, 7783–7795 (1984).
12. Yuan, X., Ni, J., Kind, R., Mechie, J. & Sandvol, E. Lithospheric and upper mantle structure of southern Tibet from a seismological passive source experiment. *J. Geophys. Res.* **102**, 27491–27500 (1997).
13. Jones, C. H. & Phinney, R. A. Seismic structure of the lithosphere from teleseismic converted arrivals observed at small arrays in the southern Sierra Nevada and vicinity, California. *J. Geophys. Res.* **103**, 10065–10090 (1998).
14. Kosarev, G. *et al.* Seismic evidence for a detached Indian lithospheric mantle beneath Tibet. *Science* **283**, 1306–1309 (1999).
15. Kay, R. W. & Kay, S. M. Delamination and delamination magmatism. *Tectonophysics* **219**, 177–189 (1993).
16. Cassidy, J. F. Numerical experiments in broadband receiver function analysis. *Bull. Seismol. Soc. Am.* **82**, 1453–1474 (1992).
17. Sobolev, S. V. & Babeyko, A. Yu. Modelling of mineralogical composition, density and elastic wave velocities in the unhydrous rocks. *Surv. Geophys.* **15**, 515–544 (1994).
18. Peacock, S. M. The importance of blueschist - eclogite dehydration reactions in subducting oceanic crust. *Geol. Soc. Am. Bull.* **105**, 684–694 (1993).
19. Kirby, S., Engdahl, E. R. & Denlinger, R. in *Subduction Top to Bottom* (eds Bebout, G. E., Scholl, D. W., Kirby, S. H. & Platt, J. P.) 195–214 (Geophysical Monograph 96, American Geophysical Union, Washington DC, 1996).
20. ANCORP Working Group. Seismic reflection image of Andean subduction zone revealing offset of intermediate-depth seismicity into oceanic mantle. *Nature* **397**, 341–344 (1999).
21. Lucassen, F., Lewerenz, S. & Franz, G. Metamorphism, isotopic ages and composition of lower crustal granulite xenoliths from the Cretaceous Salta Rift, Argentina. *Contrib. Mineral. Petrol.* **134**, 325–341 (1999).
22. Chmielewski, J., Zandt, G. & Haberland, C. The central Andean Altiplano-Puna Magma body. *Geophys. Res. Lett.* **26**, 783–786 (1999).
23. Giese, P., Scheuber, E., Schilling, F., Schmitz, M. & Wigger, P. Crustal thickening processes in the Central Andes and the different natures of the Moho-discontinuity. *J. S. Am. Earth Sci.* **12**, 201–220 (1999).
24. Nelson, K. D. *et al.* Partially molten middle crust beneath southern Tibet: Synthesis of project INDEPTH results. *Science* **274**, 1684–1688 (1996).

25. Kind, R. *et al.* Evidence from earthquake data for a partially molten crustal layer in southern Tibet. *Science* **274**, 1692–1694 (1996).
26. Hacker, B. R. *et al.* Hot and dry deep crustal xenoliths from Tibet. *Science* **287**, 2463–2466 (2000).
27. Cahill, T. A. & Isacks, B. L. Seismicity and shape of the subducted Nazca Plate. *J. Geophys. Res.* **97**, 17503–17529 (1992).
28. Graeber, F. & Asch, G. Three dimensional models of P wave velocity and P to S velocity ratio in the southern central Andes by simultaneous inversion of local earthquake data. *J. Geophys. Res.* **104**, 20237–20256 (1999).
29. Engdahl, E. R., van der Hilst, R. D. & Buland, R. Global teleseismic earthquake relocation with improved travel times and procedures for depth determination. *Bull. Seismol. Soc. Am.* **88**, 722–743 (1998).

Supplementary information is available on Nature's World-Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature.

**Acknowledgements**

We thank R. Trumbull and F. Lucassen for discussions, J. Mechie and D. Harlov for comments on the manuscript, and G. Chong and M. Wilke for supporting the experiments. The field experiments were supported by the Collaborative Research Center (SFB) 267 of the Deutsche Forschungsgemeinschaft, the GeoForschungsZentrum Potsdam, the Freie Universität Berlin, the US National Science Foundation, the PASSCAL project, the Universidad de Chile (Santiago) and the Universidad Catolica del Norte (Antofagasta).

Correspondence and requests for materials should be addressed to R.K. (e-mail: kind@gfz-potsdam.de).

.....  
**Disturbance and diversity in experimental microcosms**

**Angus Buckling\*, Rees Kassen†, Graham Bell‡ & Paul B. Rainey\***

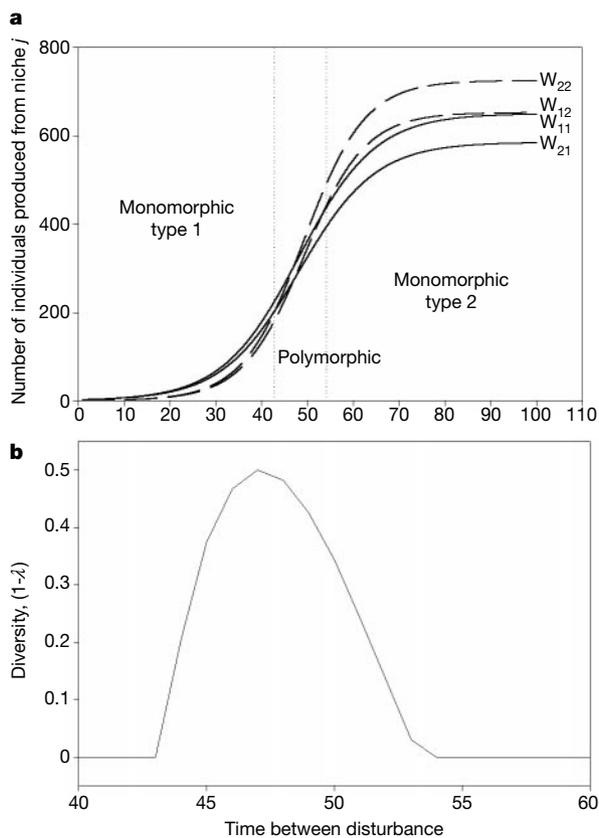
\* Department of Plant Sciences, University of Oxford, Oxford OX1 3RB, UK  
 † Department of Biology, McGill University, Montreal H3A 1B1, Quebec, Canada  
 ‡ Redpath Museum, McGill University, Montreal H3A 2K6, Quebec, Canada

.....  
**External agents of mortality (disturbances) occur over a wide range of scales of space and time, and are believed to have large effects on species diversity. The “intermediate disturbance hypothesis”<sup>1–3</sup>, which proposes maximum diversity at intermediate frequencies of disturbance, has received support from both field<sup>4,5</sup> and laboratory<sup>6,7</sup> studies. Coexistence of species at intermediate frequencies of disturbance is thought to require trade-offs between competitive ability and disturbance tolerance<sup>8</sup>, and a metapopulation structure, with disturbance affecting only a few patches at any given time<sup>9–11</sup>. However, a unimodal relationship can also be generated by global disturbances that affect all patches simultaneously, provided that the environment contains spatial niches to which different species are adapted<sup>12</sup>. Here we report the results of tests of this model using both isogenic and diverse populations of the bacterium *Pseudomonas fluorescens*. In both cases, a unimodal relationship between diversity and disturbance frequency was generated in heterogeneous, but not in homogeneous, environments. The cause of this relationship is competition among niche-specialist genotypes, which maintains diversity at intermediate disturbance, but not at high or low disturbance. Our results show that disturbance can modulate the effect of spatial heterogeneity on biological diversity in natural environments.**

Selection in heterogeneous environments may act to maintain diversity<sup>13–15</sup>, and the conditions under which this can occur have recently been derived<sup>16</sup> using a modification of the classic Levene model<sup>17</sup>. There are two key requirements. First, each species must be fitter than the other in one of the two niches, so that selection is antagonistic. Second, each niche must contribute approximately equal numbers of individuals to the global population. If one niche contributes many more individuals to the community than the

other, the type that is better adapted to this niche will become fixed, even if it is greatly inferior in the less productive niche. We have previously shown how productivity affects diversity through its effect on the relative production of niches<sup>16</sup>. We now show that disturbance can be treated in a similar way.

The frequency of disturbance is likely to affect diversity in a heterogeneous environment because the production of individuals from each niche will be a function of time since the last disturbance. Consider a population growing logistically<sup>18</sup> with an initial time lag during which the individuals adjust physiologically to local conditions but do not reproduce. If disturbance is very frequent, the niche associated with the smaller time lag will produce the most individuals, and at equilibrium the community will be dominated by the type better adapted to this niche (Figs 1a and 2a). Conversely, if disturbance is very infrequent the niche with the greater carrying capacity will contribute more individuals to the global population, and the type adapted to this niche will dominate (Figs 1a and 2a). At intermediate levels of disturbance, the number of individuals emerging from each niche becomes approximately equal, which permits the two types to coexist. This generates a unimodal



**Figure 1** The effect of disturbance frequency on diversity, in the case where competitive ability and disturbance tolerance are negatively related. **a**, The number of individuals of type *j* produced from niche *j* as a function of time between disturbance follows the logistic model:

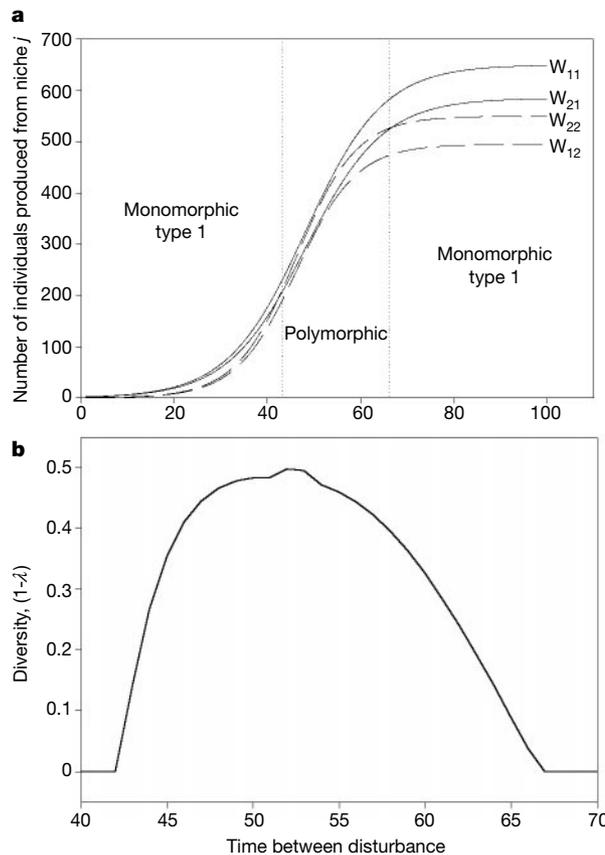
$$N_j(t) = \frac{K_j}{1 + a_j e^{-r_j(t-T_j)}} \quad (1)$$

where *K* is the carrying capacity of a given niche, *a<sub>j</sub>* is a constant defined as  $[(K_j - N_j(0))/N_j(0)]$ , where *N*(0) is density at time 0, *r* is the limiting rate of growth, *t* is time, and *T* is the lag or acclimation period that elapses before growth begins again. Parameter values are: type 1 in niche 1 (*W*<sub>11</sub>), *r* = 0.12, *K* = 650, *T* = 0; type 2 in niche 2 (*W*<sub>22</sub>), *r* = 0.15, *K* = 725, *T* = 10; *N*<sub>0</sub> = 2 in all cases. The less fit type in each niche had a fitness equal to 90% of that of the more fit type at all time points. **b**, The behaviour of the diversity index, 1 - λ, at equilibrium.

relationship between diversity and disturbance frequency (Figs 1b and 2b). Depending on parameter values, this may involve either the steady replacement of one type by another along a disturbance gradient (Fig. 1b) or dominance of the same type at both high and low disturbance frequency (Fig. 2b). We note that it is possible to obtain a similar relationship between disturbance frequency and diversity without including a time lag, although the conditions under which this occurs are more restrictive.

To test the hypothesis that diversity is unimodally related to the frequency of global disturbance in heterogeneous, but not homogeneous, environments we used populations of the bacterium *P. fluorescens*<sup>19,20</sup>. In a spatially heterogeneous environment (a static glass microcosm containing nutrient broth medium) *P. fluorescens* populations rapidly diversify, generating a range of specialist genotypes that are readily distinguished by their colony morphologies on agar plates<sup>15</sup>. Three main classes of specialist are readily distinguishable: smooth (SM) morphs, resembling the ancestral genotype, which inhabit the liquid phase; wrinkly-spreading (WS) morphs, which colonize the air–broth interface; and fuzzy-spreader (FS) morphs, which colonize the bottom of the vial. Within each main category substantial variation exists. Populations evolving in spatially homogeneous environments (continuously shaken microcosms) show little evidence of diversification and are predominantly of the SM type<sup>15</sup>. Because reproduction is entirely asexual, these variants are analogous to species<sup>16</sup>.

Two experiments differing in the amount of diversity present in the founding populations were conducted simultaneously. In the first, microcosms were founded by populations that had previously

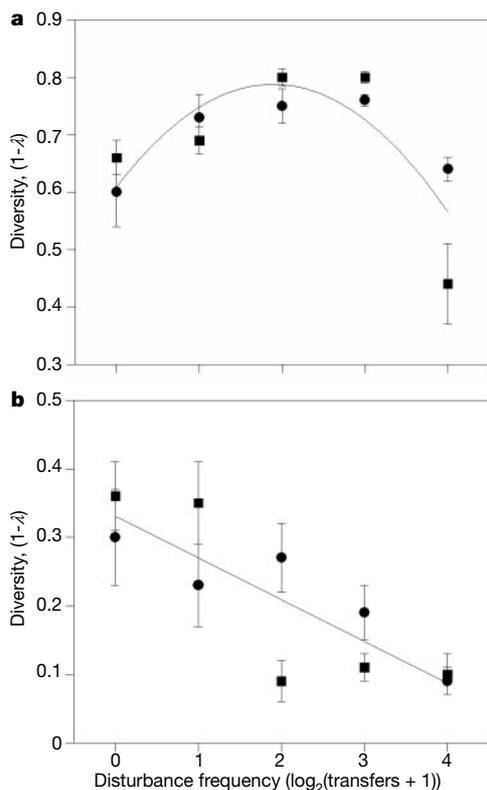


**Figure 2** The effect of disturbance frequency on diversity, in the case where competitive ability and disturbance tolerance are positively related. Parameter values are: type 1 in niche 1 (*W*<sub>11</sub>), *r* = 0.12, *K* = 650, *T* = 0; type 2 in niche 2 (*W*<sub>22</sub>), *r* = 0.155, *K* = 550, *T* = 10. **a**, The number of individuals of type *j* produced from niche *j* as a function of time between disturbance. **b**, The behaviour of (1 - λ) at equilibrium.

been allowed to diversify, whereas in the second the founding populations were genetically uniform, comprising a single ancestral SM genotype. Disturbances were nonspecific mass mortality events: after thorough homogenization, 99.9% of the culture was discarded and the remaining 0.1% ( $\sim 10^7$  bacteria) transferred to fresh media-filled microcosms. The populations thus went through a minimum of 10 generations ( $\log_2(1,000)$ ) between disturbances. Experiments were performed over a 16-day period in both shaken (homogeneous) and static (heterogeneous) microcosms under five different disturbance regimes: daily, every second day, fourth day, eighth day, or not at all during the course of 16 days. After 16 days, cultures were plated onto agar and diversity determined by scoring the frequency of colony morphologies.

Under all disturbance conditions, diversity was two to three times greater in the static than in the shaken environment (Fig. 3), supporting the main result of previous work—that spatial heterogeneity is crucial both to the emergence and to the maintenance of diversity<sup>15</sup>. Intermediate frequencies of disturbance caused a further 30% increase in diversity in the heterogeneous microcosms, resulting in a unimodal relationship between diversity and transfer frequency (Fig. 3a, linear term,  $F_{1,78} = 0.84$ ,  $P > 0.1$ ; negative quadratic term,  $F_{1,77} = 44.68$ ,  $P < 0.001$ ). This was not the case in the homogenous microcosms, where this relationship was negative and monotonic (Fig. 3b, linear term,  $F_{1,77} = 29.7$ ,  $P < 0.001$ ; quadratic term,  $F_{1,76} = 0.19$ ,  $P > 0.1$ ). In both heterogeneous and homogeneous microcosms the relationship between diversity and disturbance frequency was the same, whether the founding cultures were initially uniform or diverse ( $P > 0.1$  for the interaction between disturbance frequency and base population).

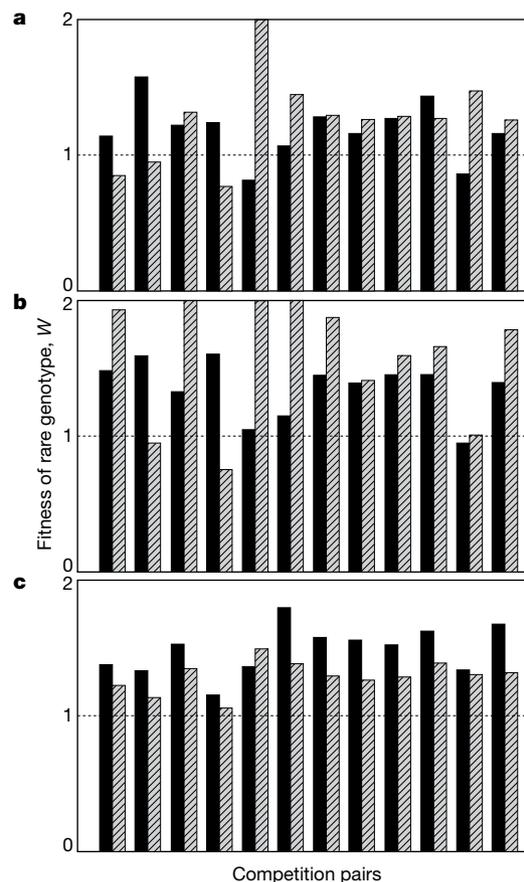
Heterogeneous microcosms all contained variants of both the broth-colonizing SM and air–broth interface-colonizing WS



**Figure 3** Mean diversity ( $1 - \lambda$ ) at different frequencies of disturbance in heterogeneous and homogeneous environments, after 16 days. Values of the mean are given as  $\pm 1$  s.e.m.,  $n = 8$ . **a**, Heterogeneous environment; **b**, homogeneous environment. Cultures were initiated with either isogenic (circles) or diverse (squares) base populations.

morphs; some contained a small proportion ( $< 1\%$ ) of FS morphs. Cultures disturbed at intermediate frequencies contained approximately equal numbers of SM and WS morphs, whereas at high or low disturbance SM or WS morphs dominated in different replicates. Only variants of the ancestral-like SM morph were present in the homogeneous microcosms. The negative relationship between diversity and disturbance frequency in these microcosms (Fig. 3b) is probably an effect of the number of generations and hence the opportunity for periodic selection to purge transient variation. Asexual populations in homogeneous environments are characterized by periodic selective sweeps<sup>21,22</sup>, therefore clonal replacement would occur more slowly in undisturbed populations (fewer generations) revealing more diversity.

Differently adapted specialists can coexist if each has greater fitness than the other when rare (negative frequency-dependent selection)<sup>23,24</sup>. If stable coexistence is more likely at intermediate disturbance frequencies, then competing WS and SM genotypes should both be more likely to invade a population dominated by the other type under this regime. To test this, 12 independent pairs of SM and WS genotypes, with opposing genetic markers, were cultured as mixtures. The frequency of the rare genotype was 0.01 in each case, and populations were cultured for 16 days under high, medium and low disturbance frequencies (daily, 4-daily and no disturbance over a 16-day period, respectively). The frequencies of genotypes were scored on agar plates and used to calculate relative fitness. Before conducting this experiment we confirmed that diversity in the paired SM–WS populations was indeed greatest at



**Figure 4** Relative fitness ( $W$ ) of WS (solid bars) and SM (hatched bars) genotypes after 16 days when initiated at a ratio of 1:100. Each pair of bars shows the fitness when rare of the WS and SM genotypes in each of the 12 competition pairs. The same genotype pairs were competed under daily transfer (**a**), no transfer (**b**) and 4-daily transfer (**c**) conditions. The horizontal line across each graph indicates equal fitness of the rare and common genotypes in each competition ( $W = 1$ ).

intermediate disturbance ( $F_{2,33} = 5.20, P < 0.01$ ), and that diversity at high and low disturbance were comparable (effect of combining high and low disturbance treatments:  $F_{1,33} = 1.18, P > 0.1$ ).

Under the intermediate disturbance regime the rare genotype increased in frequency relative to the common genotype in every instance (Fig. 4). However, in populations subjected to either high or low disturbance only certain genotypes were able to invade when rare. We failed to observe the operation of negative frequency-dependent selection in five populations subjected to high disturbance and in three populations subjected to low disturbance (Fig. 4). Moreover, the mean variance in fitness of each WS and SM pair was significantly lower under intermediate (0.03), than high (0.11) or low (0.16), disturbance frequencies (intermediate versus high:  $F_{2,2} = 3.67, P < 0.05$ ; Fig. 4).

The original formulation of the intermediate disturbance hypothesis requires a trade-off between competitive ability and disturbance tolerance<sup>8</sup>. Although this is not a requirement of our model, such a trade-off might have affected diversity in our experimental microcosms. We investigated this possibility by calculating genetic correlations for fitness of the WS and SM morphs under the high and low disturbance regimes. In 10 of the 12 populations, the same genotype in each pair was fittest under both the high and low disturbance regimes (sign test of correlation coefficients:  $P < 0.05$ ; Fig. 4a and b) showing that no general trade-off between disturbance tolerance and competitive ability was expressed.

Explanations for the unimodal relationship between disturbance and diversity are typically cast in terms of local patch dynamics, and there is good evidence from field studies<sup>4,5</sup> that this is often an appropriate interpretation. Many natural ecosystems are subject to disturbances that act more or less uniformly over large areas, such as grazing or fires. It has long been known that grazing may change the species composition of the community<sup>25</sup>, and in many cases grazed areas have higher species diversity<sup>26</sup>. Moreover, experimental removal of tissue by mowing causes an increase in diversity similar to that associated with grazing by either exotic<sup>27</sup> or native<sup>28</sup> herbivores. The mechanism we have identified here may explain why such uniform disturbances can lead to increased diversity. Disturbance, like productivity, can modulate the effect of environmental heterogeneity by changing the relative production<sup>16</sup> of different niches. □

## Methods

### Disturbance in heterogeneous and homogeneous environments

Cultures were initiated with  $10^7$  cells from either an isogenic or diverse population of *P. fluorescens* strain SBW25 (ref. 15), and cultured at 28 °C in 25-ml glass universals with loose plastic lids, containing 6 ml of King's Medium B (KB). An isogenic population was produced by growing ancestral SBW25 for 18 h under shaken conditions. Two diverse populations were created by culturing ancestral SBW25 for 4 d under shaken and static conditions. The shaken and static diverse populations were used to initiate experimental cultures subsequently exposed to shaken and static conditions, respectively. Five disturbance frequencies were used: 6  $\mu$ l of culture was transferred to fresh medium every day, every second, fourth and eighth day, and not at all, during a 16-day period. Four isogenic and 4 diverse replicate populations were established for each treatment in each environment (shaken and static). The experiment was replicated, but with different starting populations. Diversity was measured as the complement of Simpson's index of concentration ( $1 - \lambda$ ), calculated from approximately 100 colonies grown on KB agar plates:  $\lambda = \sum p_i^2$ , where  $p_i$  is the proportion of the *i*th morph<sup>29</sup>.

### Competition experiments

Six SM and 6 WS genotypes were isolated from 4-day-old cultures grown in static tubes established from both the wild type and an SBW25 pantothenate-requiring auxotroph<sup>15</sup>. Each SM genotype was competed against an independent WS genotype with a different genetic background at 100:1 and 1:100 ratios (a total of  $10^5$  cells per ml starting populations) under the three disturbance regimes in static tubes containing 6 ml KB medium supplemented with 0.0024% pantothenic acid, negating any fitness cost of the panB mutation<sup>15</sup>. Diversity ( $1 - \lambda$ ) was calculated from the frequency of wild-type and panB genotypes, and averaged across the two reciprocal competition cultures. Relative fitness ( $W$ ; Fig. 4) was calculated from the ratio of the estimated malthusian parameters

( $m$ ) of the rare: common genotypes<sup>20</sup>,  $m = \ln(N_f/N_0)$ , where  $N_0$  is the starting density and  $N_f$  the final density (determined by counting at least 2,000 and 200 colonies, respectively grown on vitamin-free KB agar supplemented with  $4.8 \times 10^{-6}\%$  pantothenic acid—on this medium the pantothenate marked strain is readily distinguished by its greatly reduced size).

### Statistical analyses

Analyses were performed by stepwise deletion from full statistical models using GLIM 4; non-significant terms ( $P > 0.1$ ) were included in the error variance when calculating test statistics of remaining terms<sup>30</sup>. The effect of disturbance frequency on (logit-transformed) diversity in Fig. 3 was analysed separately for cultures in the shaken and non-shaken environments. Experiment number (1 or 2) and base population (isogenic or diverse) were fitted as 2-level factors, and  $\log_2(\text{transfer rate} + 1)$  fitted as both a linear and quadratic covariate. For (logit-transformed) diversity in the competition cultures, both disturbance frequency (high, low and intermediate) and genotype pair were fitted as factors. Orthogonal contrasts were performed to determine whether diversity under high and low disturbance differed<sup>30</sup>.

Received 14 August; accepted 23 October 2000.

- Grime, J. P. Control of species diversity in herbaceous vegetation. *J. Environ. Mgmt* **1**, 151–167 (1973).
- Connell, J. H. Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310 (1978).
- Huston, M. A. *Biological Diversity* (Cambridge Univ. Press, Cambridge, 1994).
- Floder, S. & Sommer, U. Diversity in planktonic communities: An experimental test of the intermediate disturbance hypothesis. *Limnol. Oceanogr.* **44**, 1114–1119 (1999).
- Sousa, W. P. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* **60**, 1225–1239 (1979).
- Gaedeke, A. & Sommer, U. The influence of the frequency of periodic disturbances on the maintenance of phytoplankton diversity. *Oecologia* **71**, 25–28 (1986).
- Weider, L. J. Disturbance, competition and the maintenance of clonal diversity in *Daphnia pulex*. *J. Evol. Biol.* **5**, 505–522 (1992).
- Petraitis, P. S., Latham, R. E. & Niesenbaum, R. A. The maintenance of species diversity by disturbance. *Q. Rev. Biol.* **64**, 393–418 (1989).
- Rosenzweig, M. L. *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, 1995).
- Slatkin, M. Competition and regional coexistence. *Ecology* **55**, 128–134 (1974).
- Levin, S. A. & Paine, R. T. Disturbance, patch formation, and community structure. *Proc. Natl Acad. Sci. USA* **71**, 2744–2747 (1974).
- Chesson, P. & Huntly, N. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.* **150**, 519–553 (1997).
- Korona, R., Nakatsu, C. H., Forney, L. J. & Lenski, R. E. Evidence for multiple adaptive peaks from populations of bacteria evolving in a structured habitat. *Proc. Natl Acad. Sci. USA* **91**, 9037–9041 (1994).
- Bell, G. A. C. Experimental evolution in *Chlamydomonas*. 1. Short-term selection in uniform and diverse environments. *Heredity* **78**, 490–497 (1997).
- Rainey, P. B. & Travisano, M. Adaptive radiation in a heterogeneous environment. *Nature* **394**, 69–72 (1998).
- Kassen, R., Buckling, A., Bell, G. & Rainey, P. B. Diversity peaks at intermediate productivity in experimental microcosms. *Nature* **406**, 508–512 (2000).
- Levene, H. Genetic polymorphism when more than one ecological niche is available. *Am. Nat.* **87**, 331–333 (1953).
- Gause, G. F. *The Struggle for Existence* (Williams and Wilkins, Baltimore, 1934).
- Rainey, P. B., Buckling, A., Kassen, R. & Travisano, M. The emergence and maintenance of diversity: Insights from experimental bacterial populations. *Trends Ecol. Evol.* **15**, 243–247 (2000).
- Lenski, R. E., Rose, M. R., Simpson, S. C. & Tadler, S. C. Long-term experimental evolution in *Escherichia coli*. 1. Adaptation and divergence during 2,000 generations. *Am. Nat.* **138**, 1315–1341 (1991).
- Atwood, K. C., Schneider, L. K. & Ryan, F. J. Selective mechanisms in bacteria. *Cold Spring Harb. Symp. Quant. Biol.* **16**, 345–354 (1952).
- Elena, S. F., Cooper, V. S. & Lenski, R. E. Punctuated evolution caused by selection of rare beneficial mutations. *Science* **272**, 1802–1804 (1996).
- Haldane, J. B. S. *The Causes of Evolution* (Harper, New York, 1932).
- Ayala, F. J. & Campbell, C. A. Frequency-dependent selection. *Annu. Rev. Ecol. Syst.* **5**, 115–138 (1974).
- Milton, W. E. J. & Davies, R. O. The yield, botanical and chemical composition of natural hill herbage under manuring, controlled grazing and hay conditions. *J. Ecol.* **35**, 65–95 (1947).
- Milchunas, D. G. & Lauenroth, W. K. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol. Monogr.* **63**, 327–366 (1993).
- Collins, S. L. Interaction of disturbances in tallgrass prairie: a field experiment. *Ecology* **68**, 1243–1250 (1987).
- Collins, S. L., Knapp, A. K., Briggs, J. M., Blair, J. M. & Steinauer, E. M. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* **280**, 745–747 (1998).
- Simpson, E. H. Measurement of diversity. *Nature* **163**, 688 (1949).
- Crawley, M. J. *GLIM for Ecologists* (Blackwell Science, Oxford, 1993).

### Acknowledgements

We thank J. Pannell, N. Colegrave, K. McCann and M. Brockhurst for comments and discussion. This work was supported by the UK NERC and BBSRC (A.B. and P.B.R.), the Canadian NSERC (G.B. and R.K.) and the British Council.

Correspondence and requests for materials should be addressed to A.B. (e-mail: angus.buckling@plant-sciences.ox.ac.uk).