# Science

29. B. Yang, A. Sugio, F. F. White, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 10503 (2006).
30. M. Yuan, Z. Chu, X. Li, C. Xu, S. Wang, *Plant Cell Physiol.* **50**, 947 (2009).
31. Z. Chu *et al.*, *Genes Dev.* **20**, 1250 (2006).
32. A. Lundby, H. Mutoh, D. Dimitrov, W. Akemann, T. Knöpfel, *PLoS ONE* **3**, e2514 (2008).
33. K. Ataka, V. A. Pieribone, *Biophys. J.* **82**, 509 (2002).

# Changes in Wind Pattern Alter Albatross Distribution and Life-History Traits

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Westerly winds in the Southern Ocean have increased in intensity and moved poleward. Using long-term demographic and foraging records, we show that foraging range in wandering albatrosses has shifted poleward in conjunction with these changes in wind pattern, while their rates of travel and flight speeds have increased. Consequently, the duration of foraging trips has decreased, breeding success has improved, and birds have increased in mass by more than 1 kilogram. These positive consequences of climate change may be temporary if patterns of wind in the southern westerlies follow predicted climate change scenarios. This study stresses the importance of foraging performance as the key link between environmental changes and population processes.

The vast majority of studies of the effects of changing environments on species biology have been conducted in terrestrial ecosystems and temperature and rainfall have been the main environmental factors considered (*1*, *2*), potentially ignoring other key climatic variables. In marine systems, wind is a major component of the environment, and climate change–induced alterations in oceanic wind regimes and strength have already occurred (*3*) and are predicted to increase (*4*). For example, over the past 50 years, Southern Hemisphere westerlies have shifted poleward and increased in intensity following movement of the Southern Annular Mode (SAM, characterized as increased pressure between 40° and 65°S) into a positive phase (*5*, *6*). Such changes in wind regime may affect the movement or distribution of wind-dependent species, such as migratory land birds (*7*) or pelagic seabirds (*8–10*). Pelagic seabirds, in particular, are wide-ranging predators that rely extensively on wind to move at low costs between breeding and foraging sites (*8*, *11*), suggesting that they may be highly affected by wind pattern changes.

Here, we investigate whether changes in wind conditions over the Southern Ocean have influenced the foraging ecology and life-history traits of the wandering albatross (*Diomedea exulans*), one of the most wide-ranging pelagic seabirds. We aimed to assess whether the foraging performance of albatrosses has changed over the past few decades in relation to wind conditions and to understand the possible consequences of such change on life history (i.e., breeding performance and condition). We combine data on the duration of foraging trips and breeding success collected over nearly 40 years, from 1966 to 2010, as well as foraging performance and body mass (1989 to 2010) of breeders from Crozet Islands, located in the windiest area of the Southern Ocean.

In the western Indian Ocean sector of the Southern Ocean, wind speeds have increased in the center of the westerly flow (Fig. 1), as well as locally at Crozet (Fig. 2B), as a result of the shift of the global SAM index into a positive phase (Fig. 2A). No changes occurred in subtropical waters, whereas wind speed increased in sub-Antarctic waters, especially south of Crozet (table S1 and Fig. 1). When decomposing wind into its two components—zonal wind from west to east, and meridional wind from north to south (Fig. 1)—the most pronounced changes have occurred for the latter. The meridional component has strongly increased and shifted poleward, whereas these trends were not as strong for the zonal component (Figs. 1 and 2, C and D).

Crozet wandering albatrosses foraged from subtropical to Antarctic waters at a maximum range of more than 3500 km (Fig. 1, upper panels). Although both sexes overlap in the latitudinal band of 40° to 50°S, males prefer colder waters at the latitude of Crozet or to the south (down to 60°S), whereas females favor warmer waters to the north as far as 30°S (Fig. 1, lower panels). Foraging parameters estimated from tracking data have changed over the past 20 years in parallel to changes in wind conditions. The northern range (the most northerly latitude attained during a foraging trip) of wandering albatrosses was strongly influenced by meridional winds and shifted extensively poleward in females and to a smaller extent in males (Table 1 and Fig. 3), whereas there was no significant trend over time for the southern range (Table 1). Concurrently, there was a significant decrease in the maximum distance from the colony (Table 1, foraging range).

As shown by earlier studies (*8*, *11*), wind strongly influenced albatross flight speed. We found that the meridional component best explained the increase in flight speed during a foraging trip (Table 1). Flight speeds increased until 2008, whereas the last value of the time series (2010) was characterized by very low wind speeds, comparable to those in the early 1990s (Figs. 2 and 3). Travel speed (daily distance covered) increased in both sexes, in relation to wind speed, whereas total distance covered did not change (Table 1 and Fig. 3). Females spent a higher proportion of the overall foraging time in flight than males (Fig. 3). Thus, the increase in the daily distance covered was due, for females, to an increase in flight speed with a concomitant shift in distribution poleward into more windy conditions, whereas for males it was due to shorter time periods spent sitting on the water.

Even though the total distance covered did not increase over years, the duration of foraging trips decreased due to increasing meridional winds (Table 1). This decrease in the duration of trips was confirmed over a longer period (during the past 4 decades; in 1970, 1989, 1999, and 2008) from an independent large data set: The mean duration of foraging trips was highly variable (2 to 35 days), similar between sexes, and decreased by 22% between 1970 and 2008 (from $12.4 \pm 6.8$ to $9.7 \pm 5.5$ days; fig. S1, mixed effect analysis of variance, year effect $F_{3,724} = 11.3$, $P < 0.001$). Finally, the angle between flight direction and wind direction shifted by 10° from 1989 to 2010, with birds tending to use tail winds to a larger extent in the 1990s than in the 2000s (fig. S2).

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**Fig. 1.** Foraging trips (**Upper panels**), and frequency distribution according to latitude of locations (**Lower two left panels**) of breeding male and female wandering albatrosses during incubation period (January to February 1989 to 2010). (**Lower three right panels**) Changes in wind speed (S wind), and zonal and meridional winds according to latitudes during two periods (1990 to 1995 and 2000 to 2005). Green dots (upper panels) and dotted line (lower panels) indicate position of Crozet Islands
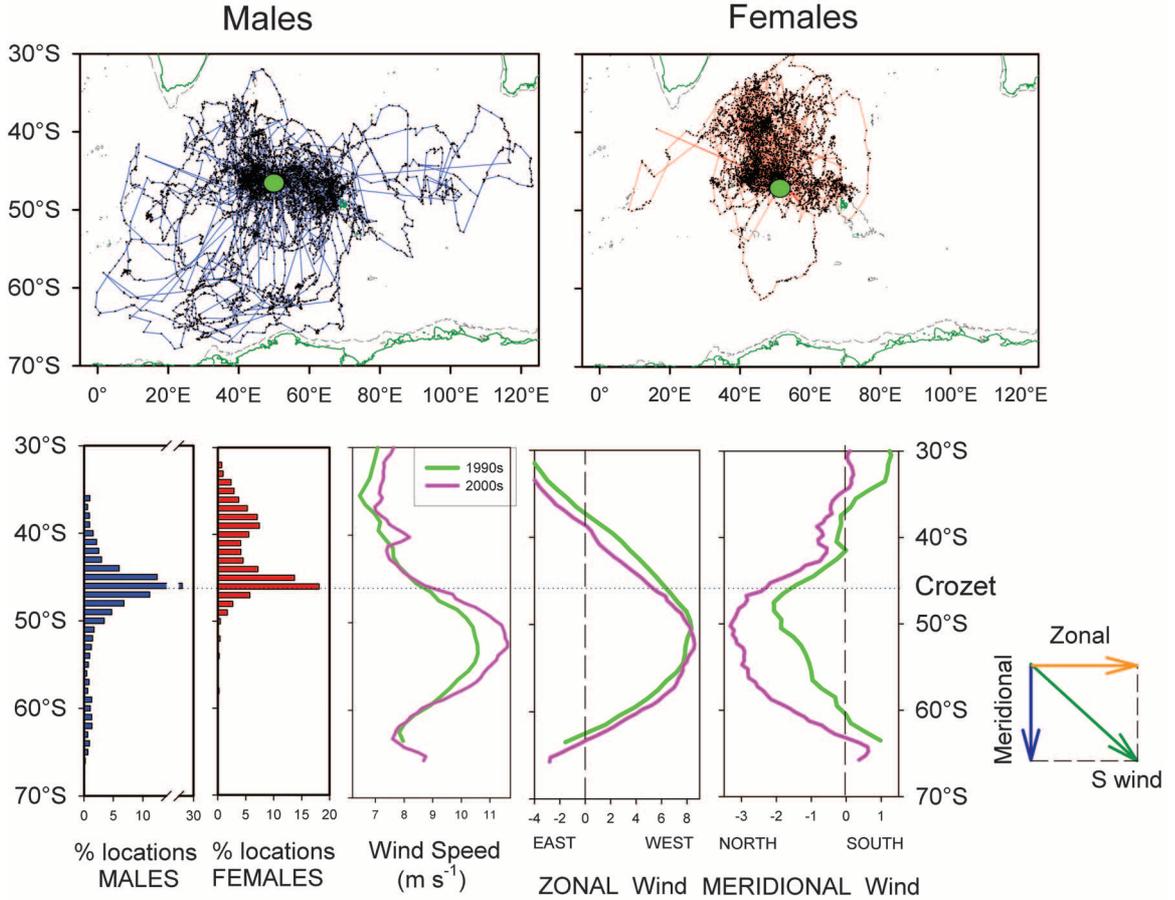


The breeding success of wandering albatrosses was on average $76.0 \pm 6.5\%$ and increased over the past 40 years (Fig. 4A). Breeding success is the result of failures that mainly occur during incubation ($81.7 \pm 9.1\%$ of total failures, $n = 18$ years). We found that failures during incubation were explained by the foraging trip duration (generalized linear models, $F_{1,310} = 5.7$, $P = 0.018$). Specifically, the probability of breeding failure increased with the duration of foraging trips. In parallel, the body mass of incubating males and females increased significantly over the past 20 years by 1 kg, i.e., by 10 to 12% of the body mass ($F_{8,519} = 12.3$, $P < 0.0001$ and $F_{8,498} = 17.2$, $P < 0.0001$, respectively; Fig. 4B). This increase in body mass was not related to changes in body size (no change in the length of the beak length was recorded over the same period; males: $F_{9,424} = 1.5$, $P = 0.143$; females: $F_{9,402} = 1.46$, $P = 0.158$).

Wandering albatrosses appear so far to have benefited from wind changes occurring in the Southern Ocean, with higher speeds allowing for more rapid travel. In wandering albatrosses, the probability of prey encounter and capture is related to the daily distances individuals are able to cover (12). In the 2000s, birds moved quicker than in the 1990s and thus were able to cover similar distances during shorter bouts at sea. Simultaneously, tracked birds shifted their
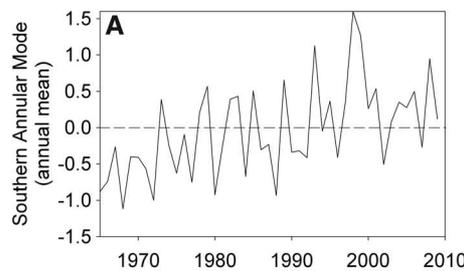
**Fig. 2.** Changes over time in (**A**) the Southern Annular Mode (SAM), as well as in wind parameters in January to February at the Crozet islands (from 1989 to 2010); (**B**) average speed ($y = 0.0572 \times year - 105.1$, $r^2 = 0.34$, $P = 0.0034$); (**C**) zonal component [west-east, positive values indicate westerly flow, negative values easterly flow ($y = 0.0447 \times year + 86.8$, $r^2 = 0.23$, $P = 0.032$)]; and (**D**) meridional component (north-south, positive values indicate southerly winds, negative values northerly wind [$y = -0.0485 \times year - 89.8$, $r^2 = 0.23$, $P = 0.030$)].
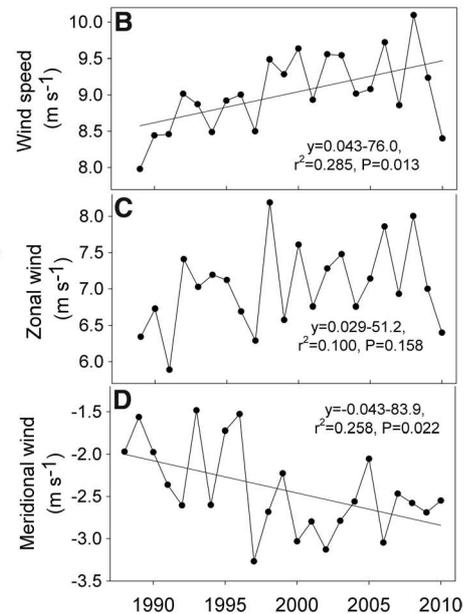


range southward (Fig. 3), a trend also documented from line transects in the southwestern Indian Ocean over the past 30 years (13). Females have shifted poleward their northern range to a larger extent than males. This southward shift of the northern range allows females to fly at

higher speeds in windier areas, as well as in waters less distant from the colonies, and thus to further reduce foraging time. Because males and females share incubation duties (14), the reduction of foraging time resulted in shorter incubation shifts and thus a lower probability

**Table 1.** Estimated parameters (±SE) of retained models of the stepwise procedure using the Akaike Information Criteria (AIC) scores to explain foraging parameters of wandering albatrosses.

| Parameter | Final model | Sex | Year | | Wind speed (WS) | | Meridional wind (MW) | | AIC |
|---|---|---|---|---|---|---|---|---|---|
| | | P-value | Estimate (±SE) | P-value | Estimate (±SE) | P-value | Estimate (±SE) | P-value | |
| Trip duration | ~Year + MW + sex:year | | −0.029 ± 0.087 | 0.017 | | | +0.615 ± 0.195 | 0.002 | 512.4 |
| Total distance covered | ~WS | | | | −465 ± 169 | 0.007 | | | 2674.9 |
| Maximum range | ~Year + WS | | −19.7 ± 8.0 | 0.025 | −136.2 ± 40 | 0.001 | | | 2297.7 |
| Travel speed | ~Sex + year + WS | F > M 0.004 | 0.128 ± 0.029 | <0.001 | 0.271 ± 0.138 | 0.052 | | | 296.3 |
| Flight speed | ~MW | | | | | | -0.207 ± 0.09 | 0.023 | 196.1 |
| Percent time on water | ~Sex + year + MW + sex:MW | M > F <0.001 | −0.741 ± 0.219 | <0.001 | | | 2.10 ± 0.751 | 0.007 | 492.5 |
| Northern range | ~Sex + MW | F > M <0.001 | | | | | 0.221 ± 0.162 | 0.013 | 451.6 |
| Southern range | ~Sex + WS | F > M <0.001 | | | 0.623 ± 0.249 | 0.013 | | | 504.1 |
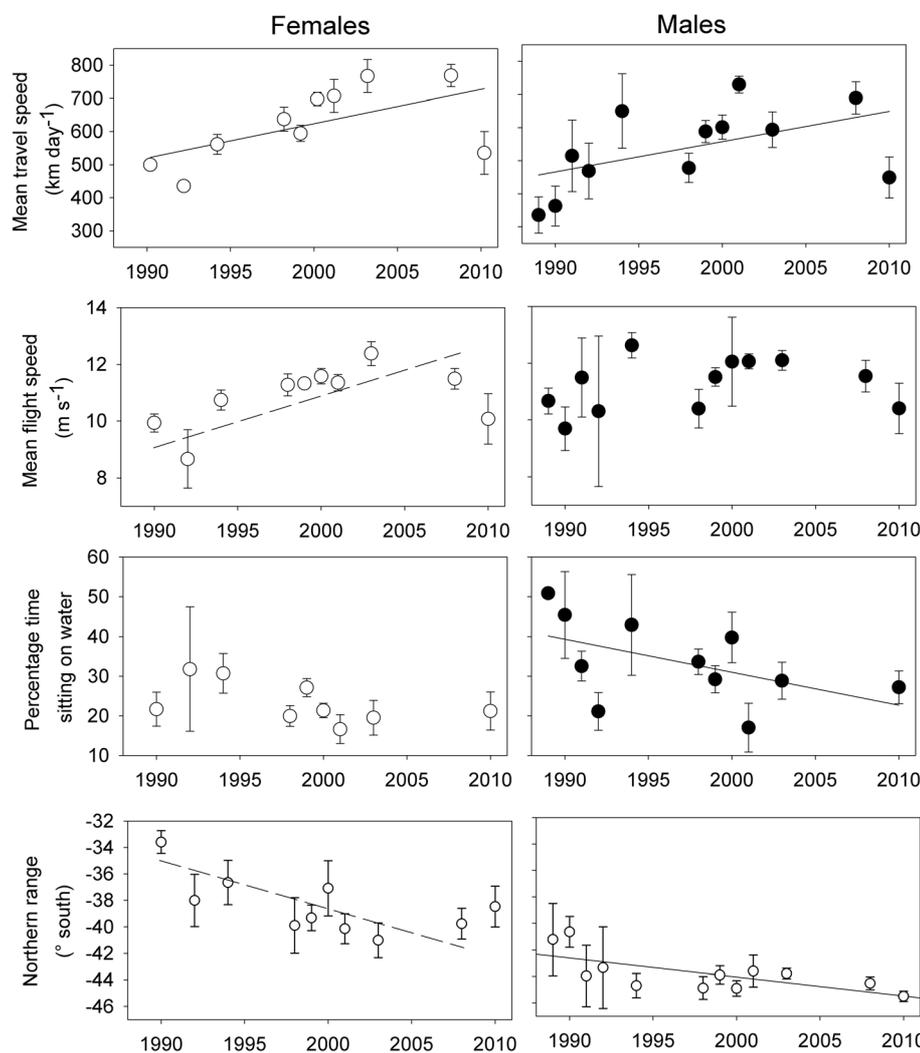


**Fig. 3.** Changes between 1989 and 2010 in four foraging parameters of male and female Crozet wandering albatrosses (mean ± 1 SD). Continuous lines indicate significant trends over time. (Dotted lines indicate significant trends over years when the atypical 2010 year is excluded from analysis.)

of breeding failure. Our results indicate that shorter foraging trips and fasts of incubating birds on the nest likely account for the increase in breeding success. The observed southward shift of the northern range of females may also have positive consequences in terms of conservation. The wandering albatross Crozet population has decreased as a result of adult mortality, especially in females, due to longline fishing targeting tuna in subtropical waters (*15*, *16*). If the range of breeding females moves southward due to environmental changes, they will be less likely to overlap with tuna longliners, whose effort has not shifted southward during the past 50 years (*17*).

One of the most unexpected changes we observed over the past 20 years was a considerable increase of both males and females by more than 1 kg in body mass. Such an increase in mass for a similar structural size has important implications for flight performance because it results in an increase in wing loading (*18*). Higher wing loading allows albatrosses using dynamic soaring flight to exploit windier zones, because stronger winds increase airspeeds and lift required by high wing loading (*19*). Thus, increased mass may not only be the result of increased body stores due to shorter fasts of birds on the nest but may also constitute an adaptive response to windier conditions.

So far, past climate changes have affected positively the foraging efficiency and foraging range of wandering albatrosses, ultimately improving breeding success and reducing mortality risks, respectively. However, these positive effects may not last in the future. Indeed, the shift to positive values of the SAM during the past half century is projected to carry on, with westerlies continuing to move poleward and increase in intensity (fig. S3). By 2080, wind speed, as well as meridional and zonal winds, should be higher south of Crozet, but lower to the north, with a reversing of zonal and meridional wind at the extremes of the range of wandering albatrosses (fig. S3) with several potential consequences for the Crozet population. Travel and flight speeds will not respond linearly to the increase in wind speed, and too strong gales winds become unfavorable for dynamic soaring flights (*20*). In addition, the poleward shift of westerlies to an increasing distance to the south of the colonies will likely make the location of Crozet less optimal for central-place foraging birds. In addition, if the present trend in the use of tail to side winds continues, costs of foraging should increase with increasing head winds and more distant favorable winds (*8*). Similarly to
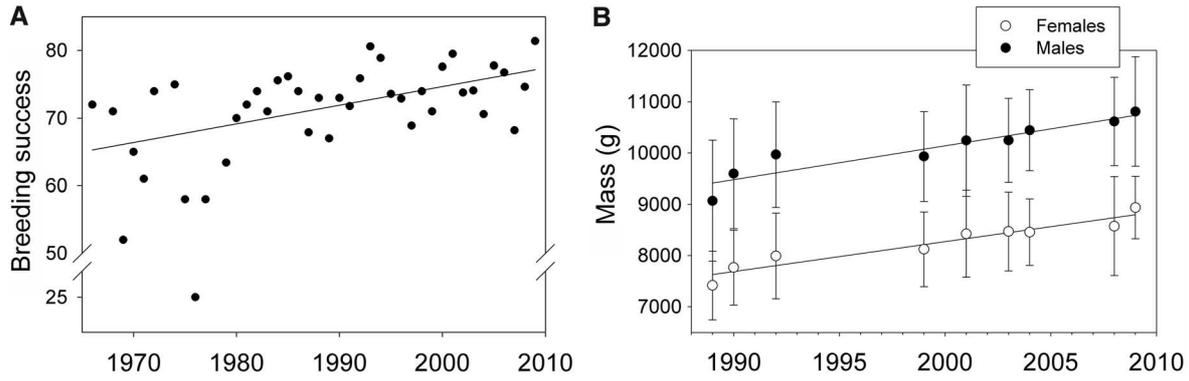
**Fig. 4. (A)** Changes in breeding success over the past 40 years ($r^2 = 0.30$, $P = 0.0003$). From 1988 to 2009 only, $r^2 = 0.19$, $P = 0.048$. **(B)** Changes over the past 20 years in the mass of breeding wandering albatrosses in January to February.

wandering albatrosses, the movements of many other species of albatrosses and petrels are strongly constrained by wind conditions (*8*, *21*), and species richness of Procellariiformes is positively associated to wind speed (*22*). Thus, future research should consider wind fields as an important driver of the distribution and migration of these oceanic species.

**References and Notes**

1. C. Parmesan, *Annu. Rev. Ecol. Syst.* **37**, 637 (2006).
2. G.-R. Walther *et al.*, *Nature* **416**, 389 (2002).
3. I. R. Young, S. Zieger, A. V. Babanin, *Science* **332**, 451 (2011).
4. S. Solomon, *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge Univ. Press, Cambridge, 2007).
5. N. P. Gillett, D. W. Thompson, *Science* **302**, 273 (2003).
6. D. W. Thompson, S. Solomon, *Science* **296**, 895 (2002).
7. T. Alerstam, D. Christie, A. Ulfstrand, *Bird Migration* (Cambridge Univ. Press, Cambridge, 1993).
8. H. Weimerskirch, T. Guionnet, J. Martin, S. A. Shaffer, D. P. Costa, *Proc. Biol. Sci.* **267**, 1869 (2000).
9. A. M. Felicísimo, J. Muñoz, J. González-Solis, *PLoS ONE* **3**, e2928 (2008).
10. R. M. Suryan *et al.*, *PLoS ONE* **3**, e4016 (2008).
11. E. Wakefield *et al.*, *Ecol. Monogr.* **79**, 663 (2009).
12. H. Weimerskirch, A. Gault, Y. Cherel, *Ecology* **86**, 2611 (2005).
13. C. Péron *et al.*, *Glob. Change Biol.* **16**, 1895 (2010).
14. H. Weimerskirch, *Oecologia* **102**, 37 (1995).
15. H. Weimerskirch, N. Brothers, P. Jouventin, *Biol. Conserv.* **79**, 257 (1997).
16. G. N. Tuck, T. Polacheck, J. P. Croxall, H. Weimerskirch, *J. Appl. Ecol.* **38**, 1182 (2001).
17. G. N. Tuck, T. Polacheck, C. M. Bulman, *Biol. Conserv.* **114**, 1 (2003).
18. C. Pennycuick, *Bird Flight Performance: A Practical Calculation Manual* (Oxford Univ. Press, Oxford, 1989).
19. S. A. Shaffer, H. Weimerskirch, D. Costa, *Funct. Ecol.* **15**, 203 (2001).
20. T. Alerstam, G. A. Gudmundsson, B. Larsson, *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **340**, 55 (1993).
21. J. González-Solís *et al.*, *Mar. Ecol. Prog. Ser.* **391**, 221 (2009).
22. R. Davies, U. Irlich, S. Chown, K. Gaston, *Glob. Ecol. Biogeogr.* **19**, 98 (2009).

# Plant Species Richness and Ecosystem Multifunctionality in Global Drylands

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Experiments suggest that biodiversity enhances the ability of ecosystems to maintain multiple functions, such as carbon storage, productivity, and the buildup of nutrient pools (multifunctionality). However, the relationship between biodiversity and multifunctionality has never been assessed globally in natural ecosystems. We report here on a global empirical study relating plant species richness and abiotic factors to multifunctionality in drylands, which collectively cover 41% of Earth's land surface and support over 38% of the human population. Multifunctionality was positively and significantly related to species richness. The best-fitting models accounted for over 55% of the variation in multifunctionality and always included species richness as a predictor variable. Our results suggest that the preservation of plant biodiversity is crucial to buffer negative effects of climate change and desertification in drylands.

Two decades of research have revealed causal linkages between biodiversity and univariate measures of ecosystem functioning, such as primary productivity or nitrogen accumulation, in many terrestrial and aquatic habitats (*1–4*). These relationships suggest that the loss of biodiversity may impair the functioning of natural ecosystems and thus diminish