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(4–6, 8) to contribute up to 80% to the primary OH formation in the continental PBL, is generally overestimated.

References and Notes

1. B. J. Finlayson-Pitts, J. N. Pitts, *Chemistry of the Upper and Lower Atmosphere: Theory, Experiments and Applications* (Academic Press, San Diego, 2000), first ed.
2. A. Hofzumahaus et al., *Science* **324**, 1702–1704 (2009).
3. U. Platt, D. Perner, G. W. Harris, A. M. Winer, J. N. Pitts Jr., *Nature* **285**, 312–314 (1980).
4. B. Alicke et al., *J. Geophys. Res.* **108**, (D4), 8247 (2003).
5. J. Kleffmann et al., *Geophys. Res. Lett.* **32**, L05818 (2005).
6. K. Acker et al., *Geophys. Res. Lett.* **33**, L02809 (2006).
7. P. S. Monks et al., *Atmos. Environ.* **43**, 5268–5350 (2009).
8. Y. F. Elshorbany et al., *Atmos. Environ.* **44**, 5383–5394 (2010).
9. A. Neftel, A. Blatter, R. Hesterberg, T. Staffelbach, *Atmos. Environ.* **30**, 3017–3025 (1996).
10. M. Sörgel et al., *Atmos. Chem. Phys.* **11**, 10433–10447 (2011).
11. X. Li et al., *Atmos. Chem. Phys.* **12**, 1497–1513 (2012).
12. K. W. Wong et al., *Atmos. Chem. Phys.* **12**, 635–652 (2012).
13. X. Zhou et al., *Geophys. Res. Lett.* **28**, 4087–4090 (2001).
14. K. Stemmler, M. Ammann, C. Donders, J. Kleffmann, C. George, *Nature* **440**, 195–198 (2006).
15. H. Su et al., *Science* **333**, 1616–1618 (2011).
16. R. Oswald et al., *Science* **341**, 1233–1235 (2013).
17. X. Zhou et al., *Nat. Geosci.* **4**, 440–443 (2011).
18. S. Li, J. Matthews, A. Sinha, *Science* **319**, 1657–1660 (2008).
19. I. Bejan et al., *Phys. Chem. Chem. Phys.* **8**, 2028–2035 (2006).
20. M. Ammann et al., *Nature* **395**, 157–160 (1998).
21. K. Stemmler et al., *Atmos. Chem. Phys.* **7**, 4237–4248 (2007).
22. R. Häselser, T. Brauers, F. Holland, A. Wahner, *Atmos. Meas. Tech. Discuss.* **2**, 2027–2054 (2009).
23. N. Zhang et al., *Geophys. Res. Lett.* **36**, L15820 (2009).
24. R. B. Stull, *An Introduction to Boundary Layer Meteorology* (Kluwer Academic Publishers, 1988).
25. R. Bröske, J. Kleffmann, P. Wiesen, *Atmos. Chem. Phys.* **3**, 469–474 (2003).
26. M. Ndour et al., *Geophys. Res. Lett.* **35**, L05812 (2008).
27. B. Zhang, F.-M. Tao, *Chem. Phys. Lett.* **489**, 143–147 (2010).
28. R. Simonaitis, J. Heicklen, *J. Phys. Chem.* **78**, 653–657 (1974).
29. S. Aloisio, J. S. Francisco, *J. Phys. Chem. A* **104**, 6212–6217 (2000).
30. S. P. Sander, M. E. Peterson, *J. Phys. Chem.* **88**, 1566–1571 (1984).

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Supplementary Materials

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Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss

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The extent to which biodiversity change in local assemblages contributes to global biodiversity loss is poorly understood. We analyzed 100 time series from biomes across Earth to ask how diversity within assemblages is changing through time. We quantified patterns of temporal α diversity, measured as change in local diversity, and temporal β diversity, measured as change in community composition. Contrary to our expectations, we did not detect systematic loss of α diversity. However, community composition changed systematically through time, in excess of predictions from null models. Heterogeneous rates of environmental change, species range shifts associated with climate change, and biotic homogenization may explain the different patterns of temporal α and β diversity. Monitoring and understanding change in species composition should be a conservation priority.

Habitat destruction, pollution, and overharvesting, as well as climate change and invasive species, have led to conspicuous reductions in biological diversity (1). Globally, increasing numbers of species are under threat (2), populations of vulnerable taxa are declining (3), and ecosystem function is changing as a result (4). Although these large-scale patterns emerge from processes that are based on local community structure, as yet there is no comprehensive analysis of how temporal change in ecological assemblages contributes to this global picture. Because the implementation of conservation and

management decisions is typically at the scale of local to regional ecosystems (5, 6), knowledge of biodiversity change within assemblages is essential to inform policy. A comparative analysis of change across taxa, biomes, and geographic regions also provides insights into the mechanisms involved. Here, we use a definition of biodiversity that includes components of species richness, composition, and relative abundance of species. We use standardized biodiversity monitoring of assemblages over years and decades to assess global patterns of temporal change in species diversity.

We quantified change in biodiversity through time by two measures: temporal trends in α diversity and temporal β diversity (7). Temporal α diversity is a measure of diversity within a sample. It can be measured as species richness or with related diversity metrics that take species abundances into account. To measure temporal change in α diversity, we calculated, for each time series,

the slope of the long-term relationship between diversity and time. Typically, β diversity is used to compare the composition of different communities in space, but it can also be used to compare the composition of a single community through time. Temporal β diversity (temporal turnover) quantifies differences in species composition between two (or more) samples separated in time. Temporal turnover can be measured with metrics of similarity to track changes in species identities (and sometimes their abundances) through time, either by comparing adjacent sampling periods or with reference to a single baseline sample or time period. Because turnover metrics incorporate shifts in species composition, they potentially provide a more sensitive indicator of community change (8) than does α diversity.

Given widespread evidence of habitat change (9), abnormally high extinction rates (10), and documented declines of many species (2, 3), we predicted that most assemblages would exhibit a decrease in α diversity through time, although the pattern and extent of change may differ among taxonomic groups, climatic regions, and marine or terrestrial realms and with spatial scale (11). For example, there is no evidence of consistent loss of biodiversity among terrestrial plants (12). Similarly, as a consequence of long-term changes in species composition, we expected increases in temporal β diversity measured relative to an early baseline sample.

To quantify biodiversity change, we gathered all data sets we could find that met a priori quality criteria (13) for standardized, long-term quantitative sampling. This collection includes more than 6.1 million species occurrence records from 100 individual time series. There are 35,613 species represented, encompassing mammals, birds, fish, invertebrates, and plants. The geographical distribution of study locations is global, and includes marine, freshwater, and terrestrial biomes, extending from the polar regions to the tropics in

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both hemispheres (Fig. 1). The collective time interval represented by these data is from 1874 to the present, although most data series are concentrated in the past 40 years (Fig. 2). (See table S1 for a full description of the data sets used in the analysis and their sources.) We measured temporal α diversity with 10 metrics, including species richness, and temporal β diversity with four metrics, including the Jaccard similarity in-

dex. A strength of our analysis is that we calculate all metrics from the original data, rather than relying on published summary statistics, and thus are able to standardize sampling effort within each time series. Details of statistical standardization of data sets, choice of α diversity metrics, and null distributions for β diversity metrics based on Markov chain Monte Carlo (MCMC) methods and neutral model analyses are described in (13).

Surprisingly, we did not detect a consistent negative trend in species richness (Fig. 2A) or in any of the other metrics of α diversity (fig. S1). The overall slope (estimated by allowing each study to have a different intercept, but constraining all studies to have the same slope) is statistically indistinguishable from zero (Fig. 2). However, not all data sets have constant species richness. In a mixed model in which both the

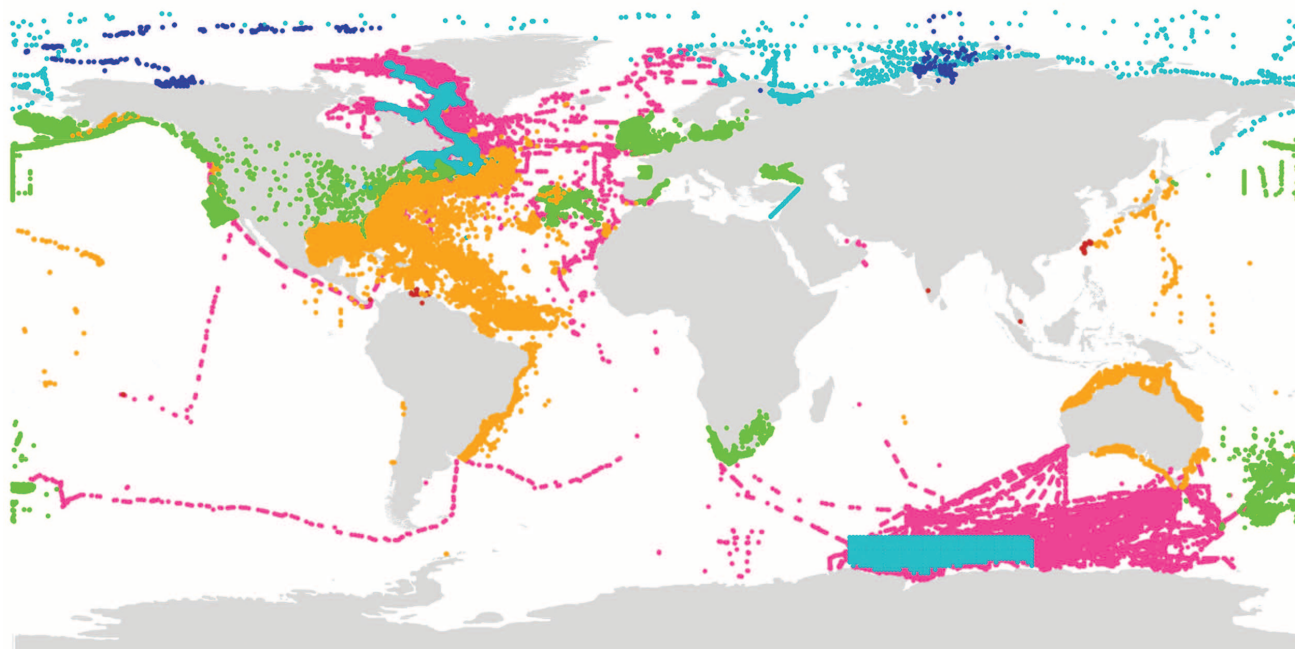


Fig. 1. Distribution of the survey sites included in our analysis. Data sets are color-coded to reflect their climatic region: pink, global; royal blue, polar; turquoise, polar-temperate; green, temperate; gold, temperate-tropical; red, tropical. See table S1 for details and sources of the data sets.

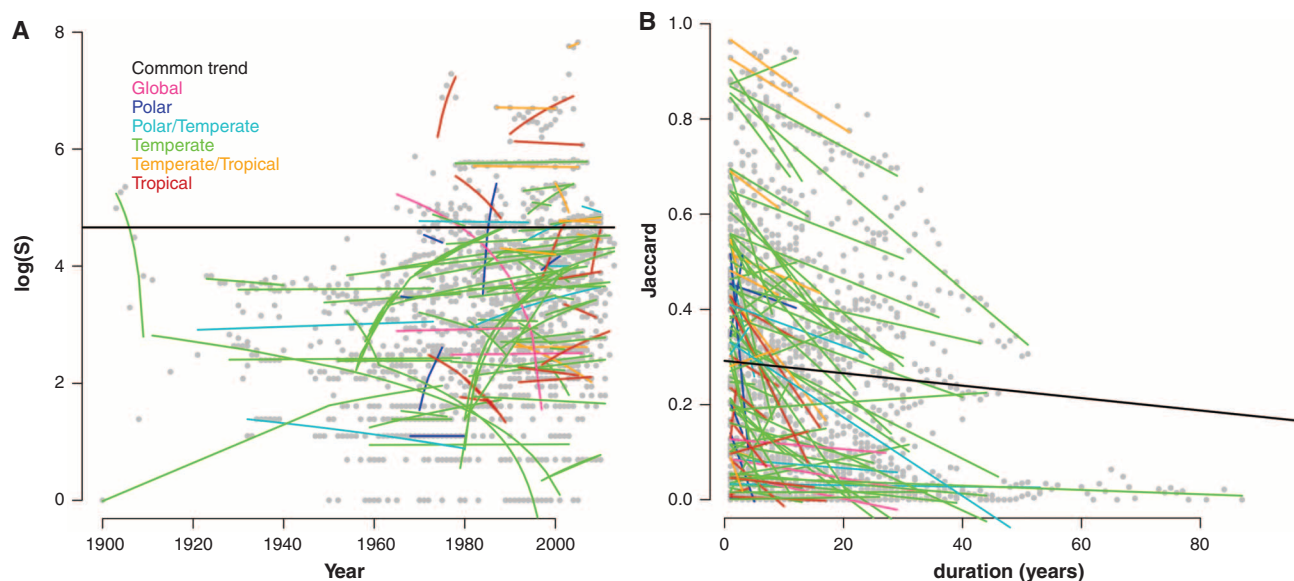


Fig. 2. Temporal change in α diversity and temporal β diversity. (A and B) Temporal change in species richness (A) and species composition (B) as measured by Jaccard similarity between each sample and the first sample in the time series. Data points are represented by gray circles and models fitted by solid lines. The black line corresponds to a model in which a single slope, but

different intercepts, were fitted to all the time series, and is represented here with the mean intercept. The colored lines correspond to a model where each time series had a different slope and intercept. Color coding corresponds to Fig. 1. Figure S10 presents a similar analysis for a different approach to rarefaction.

slope and the intercept are allowed to vary for each time series, slopes for species richness differ among assemblages, but do not exhibit systematic deviations. The variation cancels out because there are approximately equal numbers of negative and positive slopes (41 and 59, respectively), and the distribution of slopes is centered around zero, with the majority of slopes being statistically very close to zero (65 of 100 time series; Fig. 3A). This pattern was also observed for short-term changes rather than long-term linear trends: Of 1557 measurements of species richness in two consecutive times, 629 (40%) increased, 624 (40%) decreased, and 304 (20%) did not change (fig. S2). Collectively, these analyses reveal local variation in temporal α diversity but no evidence for a consistent or even an average negative trend.

The variability in slopes of α diversity could be explained by spatial, temporal, and biological attributes of each of the time series. However, for all measures of α diversity, slope is not a significant function of total species richness, extent of the spatial distribution of samples, starting date, or duration of the time series (figs. S3 and S4). Average slopes estimated for the marine and terrestrial time series are not significantly different from zero (fig. S5). Time series for terrestrial plants exhibit, on average, a positive slope for species richness, in contrast to Vellend *et al.* (12), who found no consistent change. There are no significant patterns for other taxonomic groups. An analysis of slopes by climatic regions reveals that temperate time series have a significantly positive trend, and time series sampled at a global scale show a significantly negative trend (fig. S5). Tropical time series also have a negative slope, but it is not significantly different from zero.

In contrast to species richness and other measures of α diversity, species temporal turnover as

measured by the Jaccard similarity index and other measures of β diversity (fig. S6) exhibits consistent long-term changes (Figs. 2B and 3B). Specifically, community similarity measured as Jaccard's index between an ensuing year and the first year of sampling (the time-series baseline) decreases in 79 out of 100 the time series, with a slope of -0.01 on average. Because Jaccard's similarity is bounded between 0 and 1, a 0.01 slope means change in community composition per decade of 10% of the species (Fig. 2B). This result is robust if the last census point is used as the baseline (fig. S7). A model with constant overall slope and different intercept for each time series (and with the time axis rescaled relative to each time-series baseline) is also negative. Turnover slopes are therefore almost uniformly negative, which is indicative of systematic change in community composition since the initial census point.

Even in a stochastic time series, some degree of turnover is to be expected because of temporal autocorrelation. However, the patterns of turnover in these time series are more pronounced and negative than what would be expected from simple temporal autocorrelation. Specifically, MCMC simulations of species-specific extinction and colonization produce slopes in turnover of -0.00013 on average, with confidence intervals straddling zero, and an approximately 50-50 distribution of positive and negative slopes (13) (fig. S8). Similarly, neutral model simulations incorporating species abundance show change in similarity two orders of magnitude lower than we observed (13) (fig. S9). The decrease in community similarity observed in our analysis is therefore not a simple consequence of drift and autocorrelation caused by a colonization-extinction Markov model or by a model of neutral dynamics.

These time series collectively exhibit no systematic change in temporal α diversity, although temperate assemblages show, on average, a positive trend in α diversity, whereas at the global scale we detected a negative trend. Moreover, across all climatic regions, realms, and taxonomic groups, temporal β diversity is increasing relative to the baseline (initial) sample. There are several reasons why α diversity may remain constant while temporal β diversity is consistently increasing.

One potential driver is that intensification of trade and transport, combined with the rapid increase in invasions of exotic taxa, is leading to the homogenization of species composition at local scales (14). Although homogenization may lead to a global loss of species, α diversity at local scales may stay constant or even increase as invaders replace residents and β diversity changes through time (11). This was the mechanism that Elton highlighted when he first voiced concerns about global biodiversity loss (15). Additional forces that might contribute to these contrasting patterns of α and β diversity include poleward shifts in geographic ranges as species respond to climate change (16). Moreover, contemporary habitat destruction and species loss is higher in tropical versus temperate regions (9), which is consistent with assessments of change in temporal α diversity in terrestrial plants (12) and population trends of vertebrates (17).

Our results suggest that local and regional assemblages are experiencing a substitution of their taxa, rather than systematic loss. This outcome may in part reflect the fact that most of the available data are from the past 40 years, which highlights concerns over the problem of a "shifting baseline" in diversity monitoring (18). Nonetheless, we show that at these temporal and spatial scales there is no evidence of consistent or accelerating

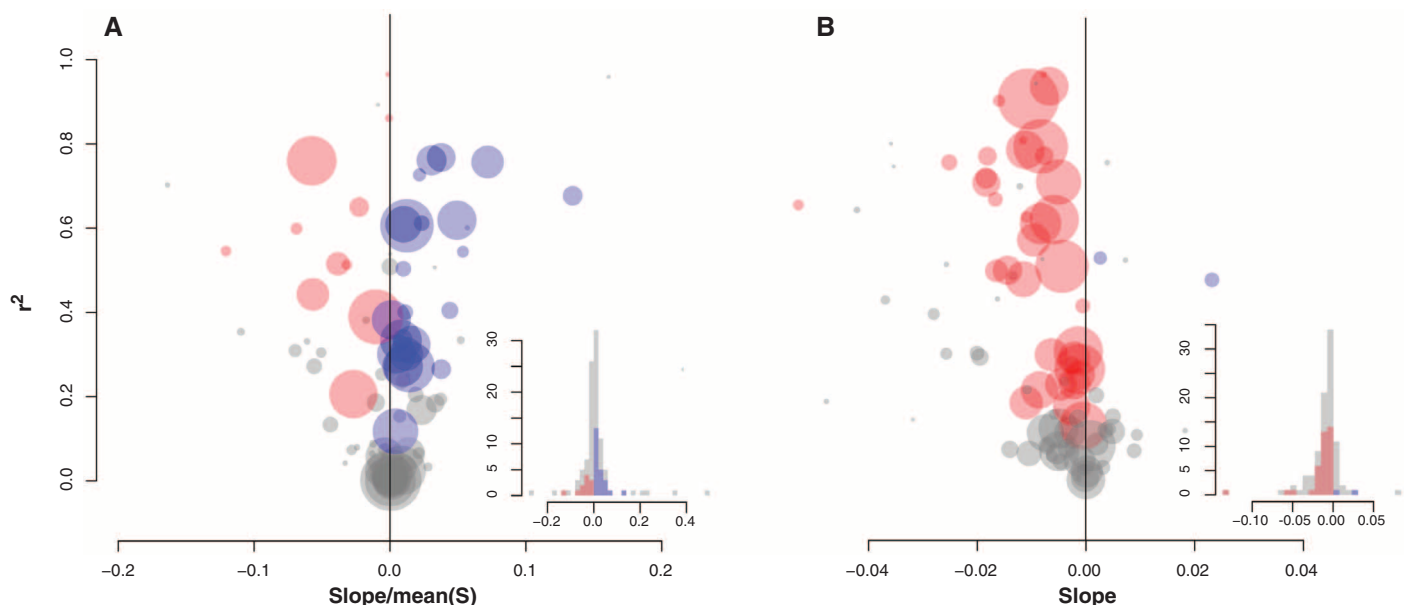


Fig. 3. Trends in α diversity and temporal β diversity. (A and B) Slope estimate distributions for species richness (A) and Jaccard similarity (B). Slope estimates (horizontal axis), coefficient of determination r^2 (vertical axis), and

number of data points in time series (bubble size) are shown for each of the data sets. Bubbles are color-coded as blue (positive slope), red (negative slope), and gray (nonsignificantly different from 0) (13).

loss of α diversity. Most important, changes in species composition usually do not result in a substitution of like with like, and can lead to the development of novel ecosystems (19). For example, disturbed coral reefs can be replaced by assemblages dominated by macroalgae (20) or different coral species (21); these novel marine assemblages may not necessarily deliver the same ecosystem services (such as fisheries, tourism, and coastal protection) that were provided by the original coral reef (22).

Our core result—that assemblages are undergoing biodiversity change but not systematic biodiversity loss (Figs. 2 and 3)—does not negate previous findings that many taxa are at risk, or that key habitats and ecosystems are under grave threat. Neither is it inconsistent with an unfolding mass extinction, which occurs at a global scale and over a much longer temporal scale. The changing composition of communities that we document may be driven by many factors, including ongoing climate change and the expanding distributions of invasive and anthropophilic species. The absence of systematic change in temporal α diversity we report here is not a cause for complacency, but rather highlights the need to address changes in assemblage composition, which have been widespread over at least the past 40 years. Robust analyses that acknowledge the complexity and heterogeneity of outcomes at different locations and scales provide the strongest case for policy action. There is a need to expand the focus of research and planning from biodiversity loss to biodiversity change.

References and Notes

- Millennium Ecosystem Assessment, *Ecosystems and Human Well-being: Synthesis* (2006); www.millenniumassessment.org/documents/document.356.aspx.pdf.
- S. H. M. Butchart *et al.*, *Philos. Trans. R. Soc. London Ser. B* **360**, 255–268 (2005).
- J. Loh *et al.*, *Philos. Trans. R. Soc. London Ser. B* **360**, 289–295 (2005).
- B. J. Cardinale *et al.*, *Nature* **486**, 59–67 (2012).
- B. F. Erasmus, S. Freitag, K. J. Gaston, B. H. Erasmus, A. S. van Jaarsveld, *Proc. R. Soc. London Ser. B* **266**, 315–319 (1999).
- S. Ferrier *et al.*, *Bioscience* **54**, 1101–1109 (2004).
- R. H. Whittaker, *Ecol. Monogr.* **30**, 279–338 (1960).
- A. E. Magurran, P. A. Henderson, *Philos. Trans. R. Soc. London Ser. B* **365**, 3611–3620 (2010).
- E. C. Ellis *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **110**, 7978–7985 (2013).
- A. D. Barnosky *et al.*, *Nature* **471**, 51–57 (2011).
- D. F. Sax, S. D. Gaines, *Trends Ecol. Evol.* **18**, 561–566 (2003).
- M. Vellend *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **110**, 19456–19459 (2013).
- See supplementary materials on Science Online.
- F. J. Rahel, *Annu. Rev. Ecol. Syst.* **33**, 291–315 (2002).
- C. S. Elton, *The Ecology of Invasion by Animals and Plants* (Univ. of Chicago Press, Chicago, 1958).
- C. Parmesan, *Annu. Rev. Ecol. Syst.* **37**, 637–669 (2006).
- B. Collen *et al.*, *Conserv. Biol.* **23**, 317–327 (2009).
- D. Pauly, *Trends Ecol. Evol.* **10**, 430 (1995).
- R. J. Hobbs *et al.*, *Glob. Ecol. Biogeogr.* **15**, 1–7 (2006).
- T. P. Hughes, *Science* **265**, 1547–1551 (1994).
- J. M. Pandolfi, S. R. Connolly, D. J. Marshall, A. L. Cohen, *Science* **333**, 418–422 (2011).
- N. A. J. Graham, J. E. Cinner, A. V. Norström, M. Nyström, *Curr. Opin. Environ. Sustain.* **7**, 9–14 (2014).

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Supplementary Materials

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Materials and Methods

Figs. S1 to S10

Table S1

Databases S1 and S2

References (23–160)

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Structural Basis for Assembly and Function of a Heterodimeric Plant Immune Receptor

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Cytoplasmic plant immune receptors recognize specific pathogen effector proteins and initiate effector-triggered immunity. In *Arabidopsis*, the immune receptors RPS4 and RRS1 are both required to activate defense to three different pathogens. We show that RPS4 and RRS1 physically associate. Crystal structures of the N-terminal Toll–interleukin-1 receptor/resistance (TIR) domains of RPS4 and RRS1, individually and as a heterodimeric complex (respectively at 2.05, 1.75, and 2.65 angstrom resolution), reveal a conserved TIR/TIR interaction interface. We show that TIR domain heterodimerization is required to form a functional RRS1/RPS4 effector recognition complex. The RPS4 TIR domain activates effector-independent defense, which is inhibited by the RRS1 TIR domain through the heterodimerization interface. Thus, RPS4 and RRS1 function as a receptor complex in which the two components play distinct roles in recognition and signaling.

Plant immune receptors contain nucleotide-binding and leucine-rich repeat domains and resemble mammalian nucleotide-binding

oligomerization domain (NOD)–like receptor (NLR) proteins (1). During infection, plant NLR proteins activate effector-triggered immunity upon recognition of corresponding pathogen effectors (2, 3). NLR protein activation of defense mechanisms is adenosine triphosphate dependent, causes defense gene induction, and often culminates in the hypersensitive cell death response (hereafter referred to as cell death) (4–6).

In some cases, plant and animal NLRs function in pairs to mediate immune recognition (7). For instance, both *RPS4* (resistance to *Pseudomonas syringae* 4) and *RRS1* (resistance to *Ralstonia solanacearum* 1) NLRs are required in *Arabidopsis* to recognize bacterial effectors AvrRps4 from *P. syringae* pv. *ptisi* and PopP2 from *R. solanacearum* and also the fungal pathogen *Colletotrichum higginsianum* (8, 9). Several NLR gene pairs in rice also function cooperatively to provide resistance to the fungus *Magnaporthe oryzae* (10–14). Similarly,

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