

20. B. Wales *et al.*, *Nucl. Instrum. Methods Phys. Res. A* **667**, 11–15 (2012).
21. J. Hine, A. M. Dowell, J. E. Singley, *J. Am. Chem. Soc.* **78**, 479–482 (1956).
22. J. Ullrich *et al.*, *Rep. Prog. Phys.* **66**, 1463–1545 (2003).
23. O. Jagutski *et al.*, *IEEE Trans. Nucl. Sci.* **49**, 2477–2483 (2002).
24. Further details on the measurement principle, with six additional figures and four movies, are available in the supplementary materials on *Science Online*.

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Supplementary Materials

www.sciencemag.org/cgi/content/full/341/6150/1096/DC1
Supplementary Text
Figs. S1 to S7
Reference (25)
Movies S1 to S5
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Achieving the Convention on Biological Diversity's Goals for Plant Conservation

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Identifying which areas capture how many species is the first question in conservation planning. The Convention on Biological Diversity (CBD) aspires to formal protection of at least 17% of the terrestrial world and, through the Global Strategy for Plant Conservation, 60% of plant species. Are these targets of protecting area and species compatible? We show that 67% of plant species live entirely within regions that comprise 17% of the land surface. Moreover, these regions include most terrestrial vertebrates with small geographical ranges. However, the connections between the CBD targets of protecting area and species are complex. Achieving both targets will be difficult because regions with the most plant species have only slightly more land protected than do those with fewer.

Protected areas are broadly effective (1–6) and thus usually necessary, if not always sufficient, to protect species. Their effective allocation is vital to slow present extinction rates that are 100 to 1000 times faster than the natural background rate (7). The Convention on Biological Diversity's (CBD's) 20 Aichi Targets—agreed in October 2010 in Nagoya, Japan—extend to 2020 an international commitment to halt biodiversity loss (www.cbd.int/sp/targets/). Target 11 seeks formal protection of >17% of the terrestrial world. One can use the most taxonomically complete and spatially best-resolved data on species distributions (8)—birds (9), mammals (10), and amphibians (10)—to assess this target (11). Unfortunately, these are a taxonomically limited subset of ~23,000 terrestrial species from more than a million described animal species with many more as-yet unknown (12). This raises concerns about their representativeness for setting global conservation priorities. By contrast, plants form a large taxonomic sample with >350,000 described species and ~15% awaiting description (13). Important in themselves, plants influence the diversity of insects (14) and other animals. In 2010, the CBD updated the Global Strategy for Plant Conservation (GSPC) (11), seeking protection for 60% of plant species as a critical indicator

toward CBD goals. Are these targets of protecting area and species compatible?

Satisfying the joint aspirations of the CBD's Aichi Target 11 and the GSPC will be difficult. First, by 2009, the world had protected ~13% of global land area (15), but half of the world's major habitat divisions—ecoregions (16)—did not meet a target of 10% coverage. Some ~75% of them had <10% of their area strictly protected (15). Present conservation efforts bias toward lands that are high, cold, dry, or otherwise far from people—often a mismatch with where conservation needs are pressing (17). These statistics show that protected areas are not representative of terrestrial environments, but they do not address species targets directly.

Second, for plants, as for most taxa, unresolved issues of taxonomy generate uncertainties in how many species there are amid existing catalogs of described species and how many are still missing from them (13, 18). Target 1 of the GSPC is to complete “a widely accessible working list of all known plant species, as a step toward a complete world flora” (19). Major international botanical gardens responded in 2010 with “The Plant List” (www.theplantlist.org)—a working list of all known plant species. Here, we analyze a subset of ~109,000 species taken from the World Checklist of Selected Plant Families (WCSP) (20). For this subset, literature compilers and taxonomists have attempted a consensus overview of the current state of knowledge of select families, including correct names for currently accepted species and their synonyms. For this quarter of the world's plant species, we pre-

viously predicted where as-yet undescribed species likely live (18).

Third, species' distributional data are imperfect (21). Elsewhere, we map birds, mammals, and amphibians on a scale of 10 km by 10 km (8). We compare them to plant distributions below. The details of these animal distributions are exceptional; plant distributional data are coarser. Flowering plant species in the WCSP are tagged to one or more of the 369 countries or geographic regions delineated by the International Taxonomic Database Working Group (22). Further details on the species and regions are in the supplementary materials (23). Nonetheless, this spatial scale captures the essential first step of comparing targets of area protected to species protected.

More problematic is that plant distributional data are species lists from regions where the largest region is 2 million times the area of the smallest. For the biodiversity hotspots of Myers *et al.* (24), the ratio is ~130. The relationships of numbers of species (S) to area (A) are well described by $S = cA^z$; c and z are parameters. Because z is <1, species densities, S/A , generally decline with increasing area. This makes objective comparisons of areas—and the designation of conservation priorities—challenging. On the basis of species' totals alone, apparent priorities tend to be the largest regions; those based on species' densities, the smallest ones. Further complicating matters, z depends on circumstance: Islands, continuous areas within continents, and biogeographically unrelated regions have different characteristic values (25). This fact dashes hopes of a single, global correction of species' numbers by a simple function of area to permit regional comparisons.

We can address this issue directly, because our results fall from quantitative databases and not the expert opinions used by Myers *et al.*, which are impossible to replicate or update. Our solution uses a greedy algorithm to accumulate species found only within a progressively larger set of regions (“endemic densities”; Fig. 1 and table S1b). We scale our results to 100,000 plant species and to 1000 km².

Regions with the highest densities enter first, followed by those adding progressively fewer new species to the aggregated total. Thus, the first 43 regions to enter are all islands, followed by Costa Rica. In the data that we consider, Costa Rica has 791 endemics and adds all of these, reducing the accumulated endemic density to 29. Panama enters next. It has 775 endemics, but adds

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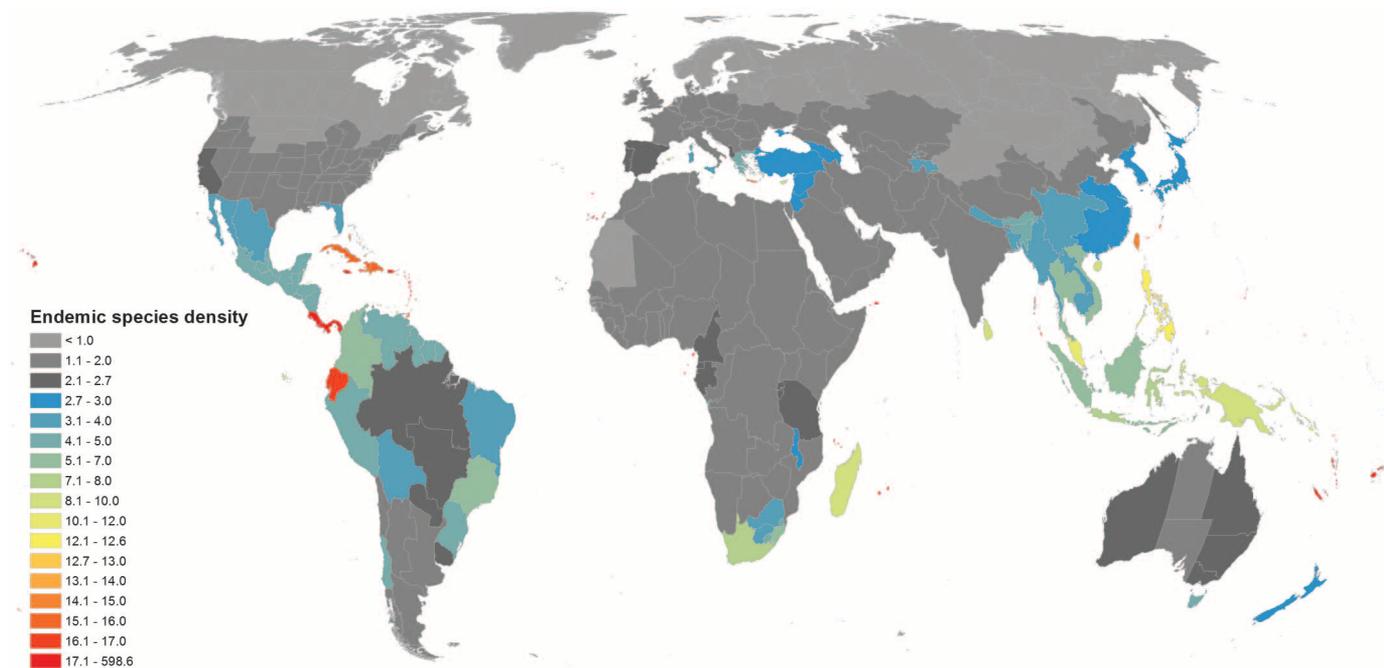


Fig. 1. Endemic accumulation map. Colors show the numbers of endemic species as they add to the total, given the inclusion of higher priority regions within the accumulated set scaled to 100,000 plant species and by 1000 km² of accumulated area.

1309 species to the accumulated total because additional species are endemic to Panama and Costa Rica combined. The accumulated endemic density of these 45 regions is now 25.

We obtain a broadly similar map when optimizing for species richness instead of number of endemic species (“richness densities”; fig. S1 and table S2).

As much as the discrete and variable areas of the plant regions permit, the advantage of greedy algorithms is that they create a continuous curve of increasing areas and species. Figure 2 shows the accumulation curve optimized to capture species only found within an accumulated set of regions (endemics) and those incidentally captured (all species) by this set.

Unlike the biodiversity hotspot approach in which areas and species are either included or not, our accumulations provide a continuous ranking on which the Aichi targets are entirely arbitrary benchmarks. Nonetheless, considering the 17% target—an area of ~24.3 million km²—allows useful comparisons.

First, the regions that we select encompass part of the ranges of 81% of the plant species and all of the ranges of 67%. We are not suggesting that we could protect all of these regions and nothing else, but this hypothetical 17% sets the bar for achieving the GSPC goal via CBD Target 11, as shown by the red crossed lines in Fig. 2. (By optimizing just for species richness, a similar set of regions captures 86% of species in the same total area; see fig. S2 and table S1a).

Second, for any benchmark, we must ask whether our greedy accumulation algorithm is optimal. Moreover, to what extent do other almost-

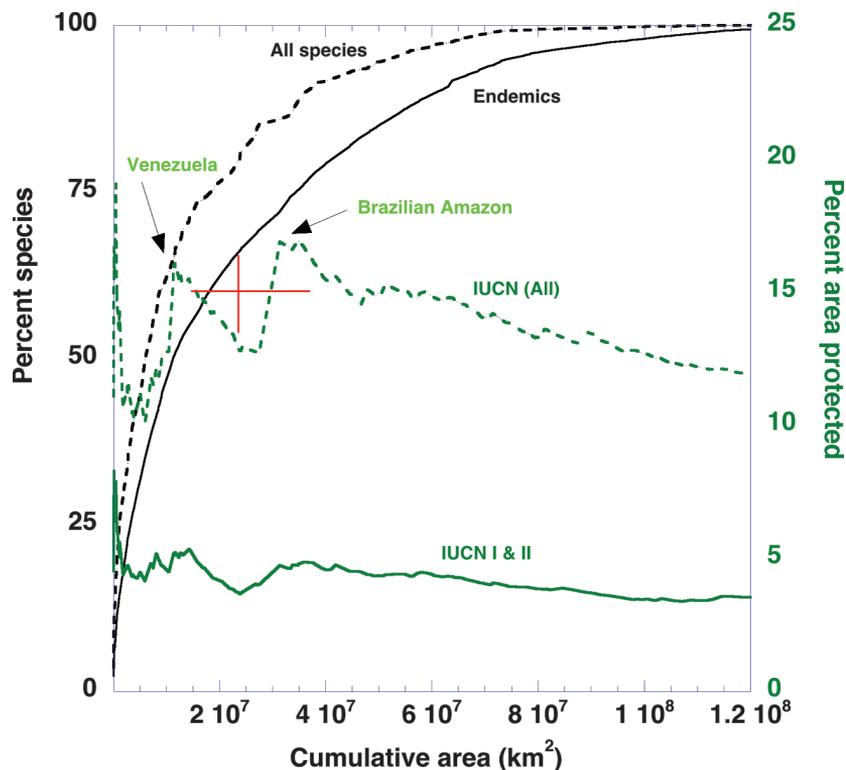


Fig. 2. Species and protected area accumulations. Black lines: species found within (dashed line) or only within (solid line) accumulating areas. The red cross shows targets of 60% species and 17% of land area protected. Green lines: the cumulative percentages of areas receiving some protection (dashed line, IUCN classes I to VI plus indigenous and other areas) and the greatest protection (solid line, IUCN classes I and II).

as-good solutions surround this optimum? The supplementary materials detail our use of a genetic algorithm to answer these questions.

Third, our selected regions are important for terrestrial vertebrates. We find that 89% of bird species, 80% of amphibians, and 74% of

mammals live within them. Percentages for species with ranges smaller than the median geographical size—those with a much higher risk of being threatened—are 88, 82, and 73%, respectively (Fig. 3).

Fourth, biodiversity hotspots cover only ~17.4 million km² and capture 44% of endemic species (24). Not surprisingly, our formal optimization performs better, capturing 59% in the

same amount of area. It also captures 74% of all plant species, a number Myers *et al.* could not estimate. What is notable is not the better performance of our approach, but the similarities and differences in the regions chosen between the two approaches (Fig. 4).

The areas that we omit have much to do with spatial resolution. Hotspots include montane forest of East Africa and the Western Ghats of

India, plus southwestern Australia, and the coastal moist forests of West and East Africa. These areas are not included in our selections because they are embedded in much larger regions. The finer-scale vertebrate data also show the importance of these regions, plus others including the forests along Australia's eastern seaboard (Fig. 3). Conversely, Myers *et al.* considered levels of habitat loss and so excluded

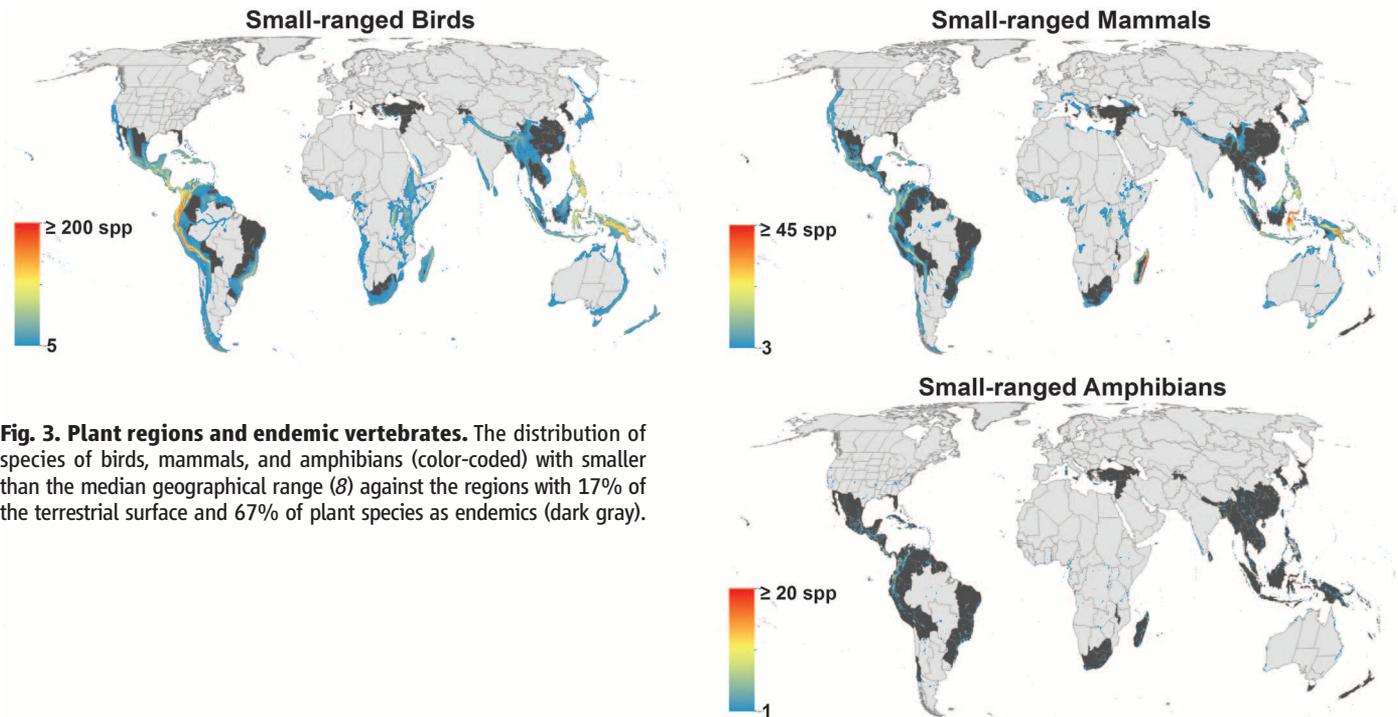


Fig. 3. Plant regions and endemic vertebrates. The distribution of species of birds, mammals, and amphibians (color-coded) with smaller than the median geographical range (β) against the regions with 17% of the terrestrial surface and 67% of plant species as endemics (dark gray).

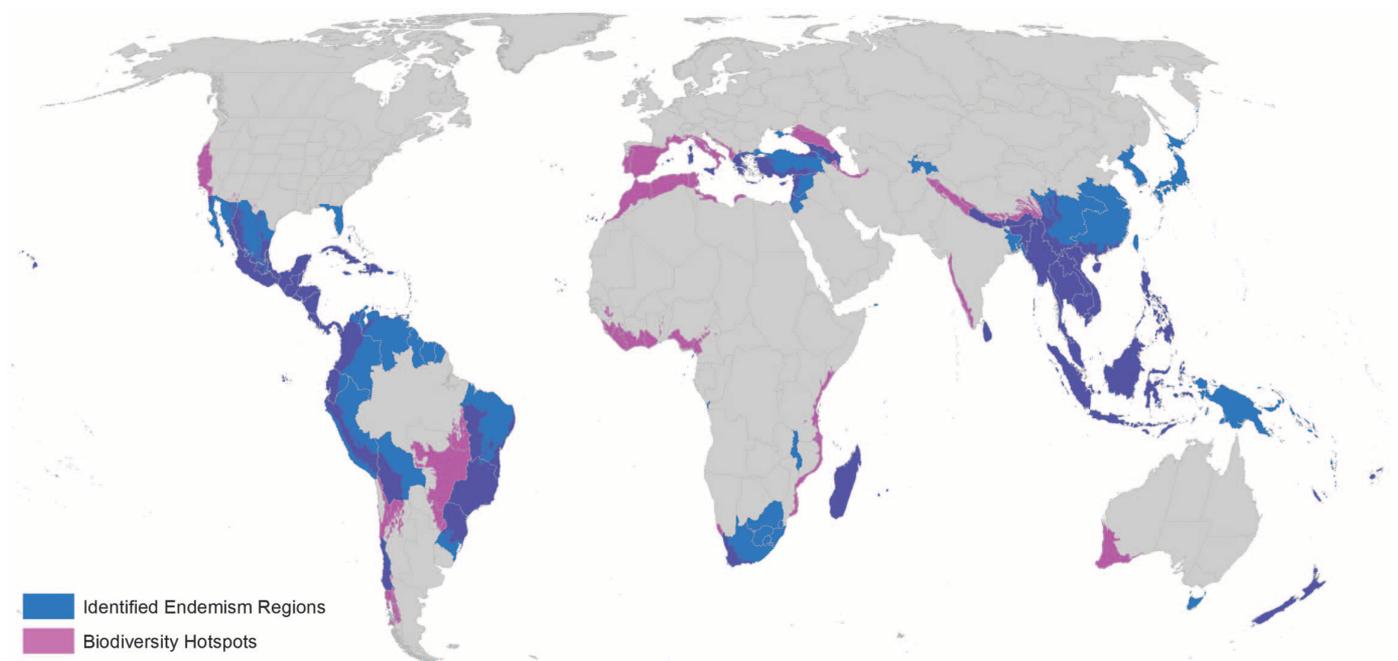


Fig. 4. A comparison of this paper's identified regions (blue) and biodiversity hotspots (24).

New Guinea, which we do not. Our inclusion of Turkey and the Middle East, Japan, Korea, and more of China, northern South America, and Southern Africa reflects our estimates of their numbers of endemic species.

Our results have five consequences.

1) Broadly, tropical and subtropical islands, moist tropical and subtropical forests (especially those in mountains), and Mediterranean ecosystems hold concentrations of plant endemics. The majority of as-yet undescribed plant species also live in these regions (18). Further discoveries would likely enhance their importance.

2) Our figures suggest the achievement of Aichi goals by concentrating protected areas in regions of highest endemism. Had nations already implemented this strategy, we would see proportionally greater protection rates where species densities are high. Figure 2 shows that, within the regions we select, strict protected areas [International Union for Conservation of Nature (IUCN) classes I and II (26)] occur at only slightly higher rates than in nonselected regions. The most important areas include Costa Rica and Panama, which have >10% of their land in IUCN classes I and II. This is a weak trend, however. When considering all the categories of protection (IUCN I to VI plus indigenous territories), the total protected is much higher, but the trend similar.

3) The ability of protected areas to protect depends upon the nature and location of threats (2, 5). For example, within our 17% set, 9.4% of plant species are endemic to a total of ~1.9 million km² of islands. Island plants suffer greatly from introduced species (27), something the establishment of protected areas does not completely address.

4) Figure 2 (and see table S1b) show a hitherto poorly appreciated effect of indigenous areas. In tropical South America, these protect large areas of tropical moist forest with high plant richness.

5) Overall, the global land area currently protected, ~13%, is close to Aichi's 17%. This seems encouraging. However, of the 17% that contains the entire range of 67% of the world's plant species, only 14% is protected in some way, barely more than the global average.

The total area protected imperfectly measures species' protection, however. Even with perfect data on species' distributions, the "Noah's Ark effect" (28) renders simple optimal allocation of priority areas meaningless. A small total area—a metaphorical "ark"—can capture many species but ignore long-term viability. Numerous protected areas of large aggregate size may house many species, but be individually too small to maintain viable populations. How small is "too small" depends on the species—tigers demand more area than tiger lilies—as well as the distribution of habitat fragments (29) and levels of threat (2, 5). How much area countries should protect—and where—are ecological questions. Political practicalities dominate actions, as the Aichi target of 17% testifies.

The spatial resolution of presently available data is inadequate to address this key concern at the spatial scales at which conservation actions are taken and protected areas established. Nonetheless, we show that how protected areas are allocated within and across regions constrains how efficiently plant diversity can be sustained. Understanding this is necessary to achieve the Convention on Biological Diversity's conservation goals.

References and Notes

- J. M. Adeney, N. L. Christensen, S. L. Pimm, *PLoS ONE* **4**, e5014 (2009).
- K. S. Andam, P. J. Ferraro, A. Pfaff, G. A. Sanchez-Azofeifa, J. A. Robalino, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 16089–16094 (2008).
- J. Geldmann *et al.*, *Biol. Conserv.* **161**, 230–238 (2013).
- L. N. Joppa, S. R. Loarie, S. L. Pimm, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 6673–6678 (2008).
- A. Nelson, K. M. Chomitz, *PLoS ONE* **6**, e22722 (2011).
- L. N. Joppa, A. Pfaff, *Proc. Biol. Sci.* **278**, 1633–1638 (2011).
- S. L. Pimm, G. J. Russell, J. L. Gittleman, T. M. Brooks, *Science* **269**, 347–350 (1995).
- C. N. Jenkins, S. L. Pimm, L. N. Joppa, *Proc. Natl. Acad. Sci. U.S.A.* **110**, E2602–E2610 (2013).
- BirdLife International, Bird species distribution maps of the world (BirdLife International, Cambridge, UK, 2011), vol. 2013; www.birdlife.org/datazone/info/spcdownload.
- International Union for the Conservation of Nature, IUCN Red List of Threatened Species. Version 2010.4 (2013); www.iucnredlist.org/technical-documents/spatial-data.
- L. Cantú-Salazar, C. D. L. Orme, P. C. Rasmussen, T. M. Blackburn, K. J. Gaston, *Biodivers. Conserv.* **22**, 1033–1047 (2013).
- B. R. Scheffers, L. N. Joppa, S. L. Pimm, W. F. Laurance, *Trends Ecol. Evol.* **27**, 501–510 (2012).
- L. N. Joppa, D. L. Roberts, S. L. Pimm, *Proc. R. Soc. B* **278**, 554–559 (2011).
- D. R. Strong, J. H. Lawton, S. R. Southwood, *Insects on Plants. Community Patterns and Mechanisms* (Blackwell Scientific Publications, Oxford, 1984).

- C. N. Jenkins, L. Joppa, *Biol. Conserv.* **142**, 2166–2174 (2009).
- D. M. Olson *et al.*, *Bioscience* **51**, 933 (2001).
- L. N. Joppa, A. Pfaff, *PLoS ONE* **4**, e8273 (2009).
- L. N. Joppa, D. L. Roberts, N. Myers, S. L. Pimm, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 13171–13176 (2011).
- A. Paton, E. Nic Lughadha, *Bot. J. Linn. Soc.* **166**, 250–260 (2011).
- WCSP 2008 World checklist of selected plant families. The Board of Trustees of the Royal Botanic Gardens, Kew. See www.kew.org/wcsp.
- C. N. Jenkins *et al.*, *Divers. Distrib.* **17**, 652–662 (2011).
- N. Brummitt, S. Bachman, J. Moat, *Endanger. Species Res.* **6**, 127–135 (2008).
- Materials and methods are available as supplementary materials on Science Online.
- N. Myers, R. A. Mittermeier, C. G. Mittermeier, G. A. da Fonseca, J. Kent, *Nature* **403**, 853–858 (2000).
- M. L. Rosenzweig, *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, 1995).
- International Union for the Conservation of Nature and United Nations Environment Programme, World Conservation Monitoring Centre, The World Database on Protected Areas (WDPA) July Release (Cambridge, UK, 2012); www.protectedplanet.net.
- D. F. Sax, S. D. Gaines, *Proc. Natl. Acad. Sci. U.S.A.* **105** (suppl. 1), 11490–11497 (2008).
- S. L. Pimm, J. H. Lawton, *Science* **279**, 2068–2069 (1998).
- J. K. Schnell, G. M. Harris, S. L. Pimm, G. J. Russell, *Conserv. Biol.* **27**, 520–530 (2013).

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Supplementary Materials

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Materials and Methods
Figs. S1 to S3
Table S1

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Caffeoyl Shikimate Esterase (CSE) Is an Enzyme in the Lignin Biosynthetic Pathway in *Arabidopsis*

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Lignin is a major component of plant secondary cell walls. Here we describe caffeoyl shikimate esterase (CSE) as an enzyme central to the lignin biosynthetic pathway. *Arabidopsis thaliana cse* mutants deposit less lignin than do wild-type plants, and the remaining lignin is enriched in *p*-hydroxyphenyl units. Phenolic metabolite profiling identified accumulation of the lignin pathway intermediate caffeoyl shikimate in *cse* mutants as compared to caffeoyl shikimate levels in the wild type, suggesting caffeoyl shikimate as a substrate for CSE. Accordingly, recombinant CSE hydrolyzed caffeoyl shikimate into caffeate. Associated with the changes in lignin, the conversion of cellulose to glucose in *cse* mutants increased up to fourfold as compared to that in the wild type upon saccharification without pretreatment. Collectively, these data necessitate the revision of currently accepted models of the lignin biosynthetic pathway.

The evolutionary emergence of lignin, a phenolic polymer deposited in the secondary cell wall, allowed the development of vas-

cular land plants. The hydrophobic and strengthening nature of lignin enables conducting xylem vessels to transport water and nutrients from the