between ORC binding and nucleosome turnover, suggesting that turnover facilitates ORC binding. In contrast, other chromatin features that would be expected for open or dynamic chromatin, including nucleosome density, mononucleosome/oligonucleosome ratio (a measure of micrococcal nuclease accessibility), H2Av (an H2A.Z histone variant enriched in active chromatin), and salt-soluble nucleosomes, show little if any dependence on ORC abundance (Fig. 3, H to P). Our findings support the hypothesis that replication origins are determined by chromatin, not by sequence features (*20*, *21*). The better quantitative correspondence of ORC to CATCH-IT data than to other chromatin measurements implies that the ORC occupies DNA that is made accessible by nucleosome turnover. In support of this interpretation, we note that very similar correspondences are seen when CATCH-IT data are aligned with GAF sites (fig. S9) and that GAF directs nucleosome turnover in vivo (*22*, *23*).

Our direct strategy for measuring the kinetics of nucleosome turnover does not rely on transgenes or antibodies but rather uses native histones and generic reagents. Thus, CATCH-IT provides a general tool for studying activities that influence nucleosome turnover. With use of CATCH-IT, we found direct evidence that epigenetic maintenance involves nucleosome turnover, a process that erases histone modifications (*10*). The fact that EZ is responsible for di- and trimethylation of H3K27, but the nucleosomes that it modifies turn over faster than a cell cycle, argues against proposals that histone modifications required for cellular memory themselves transmit epigenetic information (*24*). Rather, by simply increasing or decreasing accessibility of DNA to sequence-specific binding proteins, regulated nucleosome turnover may perpetuate active or silent gene expression states and facilitate initiation of replication.

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25. We thank T. Furuyama for suggesting this approach, members of our lab for helpful discussions, and the Hutchinson Center Genomics Shared Resource for microarray processing. This work was supported by NIH grant 1R21DA025758 to S.H. and NIH Postdoctoral Fellowship 1F32GM083449 to R.B.D. All data sets can be found in GEO: GSE19788.

Supporting Online Material

www.sciencemag.org/cgi/content/full/328/5982/1161/DC1
Materials and Methods
Figs. S1 to S9
Table S1
References

7 January 2010; accepted 1 April 2010
10.1126/science.1186777

Global Biodiversity: Indicators of Recent Declines

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In 2002, world leaders committed, through the Convention on Biological Diversity, to achieve a significant reduction in the rate of biodiversity loss by 2010. We compiled 31 indicators to report on progress toward this target. Most indicators of the state of biodiversity (covering species' population trends, extinction risk, habitat extent and condition, and community composition) showed declines, with no significant recent reductions in rate, whereas indicators of pressures on biodiversity (including resource consumption, invasive alien species, nitrogen pollution, overexploitation, and climate change impacts) showed increases. Despite some local successes and increasing responses (including extent and biodiversity coverage of protected areas, sustainable forest management, policy responses to invasive alien species, and biodiversity-related aid), the rate of biodiversity loss does not appear to be slowing.

In 2002, world leaders committed, through the Convention on Biological Diversity (CBD), "to achieve by 2010 a significant reduction of the current rate of biodiversity loss" (*1*), and this "2010 target" has been incorporated into the United Nations Millennium Development Goals in recognition of the impact of biodiversity loss on human well-being (*2*). The CBD created a framework of indicators to measure biodiversity loss at the level of genes, populations, species, and ecosystems (*3*, *4*). Although a minority have been published individually (*5*), hitherto they have not been synthesized to provide an integrated outcome. Despite suggestions that the target is unlikely to be (*6*–*8*), or has not been (*4*, *9*, *10*), met, we test this empirically using a broad suite of biodiversity indicators.

To evaluate achievement of the 2010 target, we (i) determined the trend, and timing and direction of significant inflections in trend for individual indicators (*11*) and (ii) calculated aggregated indices relating to the state of biodiversity, pressures upon it, policy and management responses, and the state of benefits (ecosystem services) that people derive from biodiversity, using the best available sources. To calculate aggregate indices, we first scaled each of 24 indicators (out of 31) with available trend information to a value of 1 in the first year with data from 1970 onward (only eight indicators had earlier trends) and calculated annual proportional change from this first year. Then we used a generalized additive modeling framework (*5*, *12*, *13*) and determined significant inflections (*12*). Although absolute values are difficult to interpret because they aggregate different elements of biodiversity, this approach permits a synthetic interpretation of rate changes across the elements measured: For example, the aggregated state index should show positive inflections if biodiversity loss has been significantly reduced.

Our analyses suggest that biodiversity has continued to decline over the past four decades, with most (8 out of 10) state indicators showing negative trends (Fig. 1 and Table 1). There have been declines in population trends of (i) vertebrates (*13*) and (ii) habitat specialist birds; (iii) shorebird populations worldwide; extent of (iv) forest (*14*, *15*); (v) mangroves; (vi) seagrass beds; and (vii) the condition of coral reefs. None show significant recent reductions in the rate of decline (Table 1), which is either fluctuating (i), stable (ii), based on too few data to test significance (iii to vi), or stable after a deceleration two decades ago (vii). Two indicators, freshwater quality and trophic integrity in the marine ecosystem, show stable and marginally improving trends, respectively, which are likely explained by geographic biases in data availability for the former and spatial expansion of fisheries for the latter (*5*). Aggregated trends across state indicators have declined, with no significant recent reduction in rate: The most recent inflection in the index (in 1972) was negative (Fig. 2). Because there were fewer indicators with trend data in the 1970s, we recalculated the index from 1980, which also showed accelerating biodiversity loss: The most recent inflection (2004) was negative. Finally, aggregated species' extinction risk (i.e., biodiversity loss at the species level) has accelerated: The International Union for Conservation of Nature (IUCN) Red List Index (RLI), measuring rate of change (*16*, *17*), shows negative trends.

The majority of indicators of pressures on biodiversity show increasing trends over recent decades (Fig. 1 and Table 1), with increases in (i) aggregate human consumption of the planet's ecological assets, (ii) deposition of reactive nitrogen, (iii) number of alien species in Europe, (iv) proportion of fish stocks overharvested, and (v) impact of climate change on European bird population trends (*18*). In no case was there a significant reduction in the rate of increase (Table 1), which was stable (i, iii, and v), fluctuating (iv), or based on too few data to test significance (ii), although growth in global nitrogen deposition may have slowed, and this may explain why the most recent inflection in aggregated trends (in 2006) was negative (Fig. 2) (*5*). Global trends for habitat fragmentation are unavailable, but it is probably increasing; for example, 80% of remaining Atlantic Forest fragments are <0.5 km^2 in size (*19*), and 59% of large river systems are moderately or strongly fragmented by dams and reservoirs (*20*).

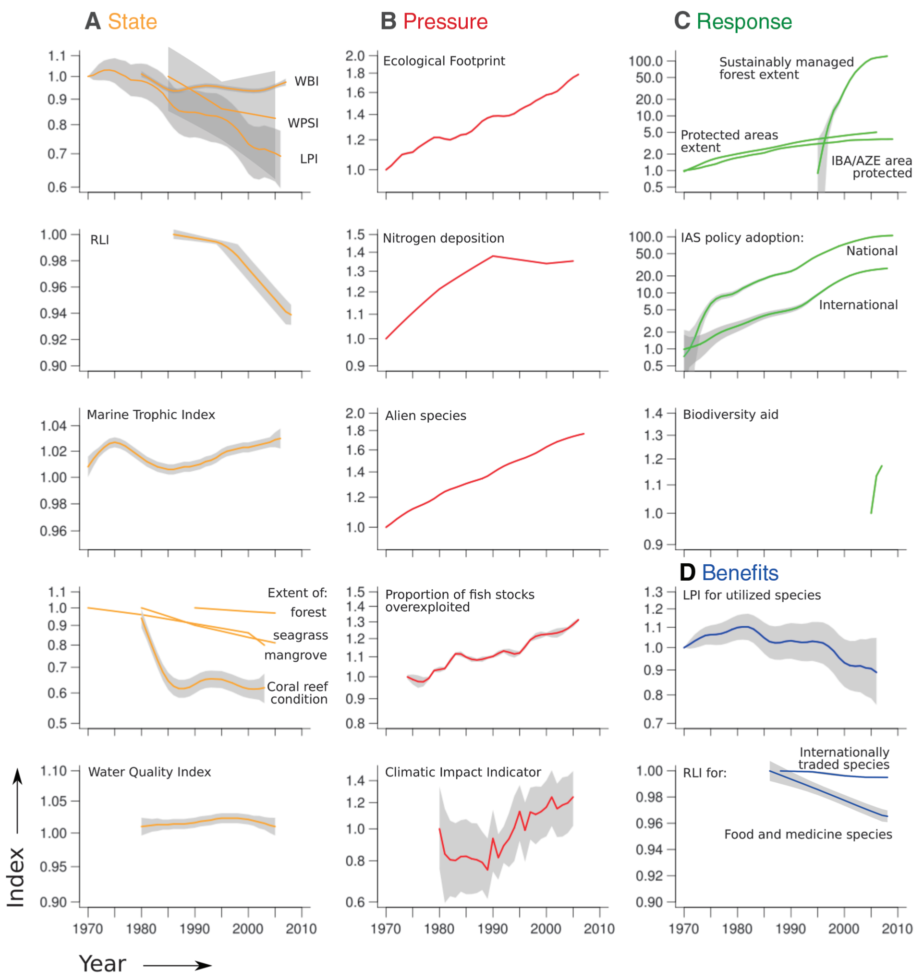

Fig. 1. Indicator trends for (**A**) the state of biodiversity, (**B**) pressures upon it, (**C**) responses to address its loss, and (**D**) the benefits humans derive from it. Data scaled to 1 in 1970 (or for first year of data if >1970), modeled (if >13 data points; see Table 1), and plotted on a logarithmic ordinate axis. Shading shows 95% confidence intervals except where unavailable (i.e., mangrove, seagrass, and forest extent, nitrogen deposition, and biodiversity aid). WBI, Wild Bird Index; WPSI, Waterbird Population Status Index; LPI, Living Planet Index; RLI, Red List Index; IBA, Important Bird Area; AZE, Alliance for Zero Extinction site; IAS, invasive alien species.

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Table 1. Summary of global biodiversity indicator trends.

Indicator	Data availability (years)†	% Change since 1970‡	Mean annual % change§					Trends in rate of change‖
			1970s	1980s	1990s	2000s	Since 1970	
		State						
Living Planet Index (LPI) (mean population trends of vertebrates)	1970–2006	−31*	−0.2	−1.4	−1.4	−0.9	−1.0	F
Wild Bird Index [mean population trends of habitat specialists in Europe and North America, disaggregated for terrestrial (t) and wetland (w) species]	1980–2007	−2.6*		−0.6	−0.2	+0.6	−0.1	S
		−16*(t)		−1.3	−0.7	+0.3	−0.7	D 1982–2007
		+40*(w)		+1.1	+1.3	+1.1	+1.2	S
Waterbird Population Status Index (% shorebird populations increasing, stable, or decreasing)	1985–2005†	−33		−1.4	−2.0	−2.4	−2.0	A?
Red List Index (RLI) (extinction risk of mammals, birds, amphibians, and corals)	1986–2008	−6.1*		−0.1	−0.2	−0.5	−0.3	A
Marine Trophic Index (shift in fishing catch from top predators to lower trophic levels)	1950–2006	+3.0*	+0.1	−0.1	+0.1	+0.1	+0.1	S
Forest extent	1990–2005†	−3.1			−0.2	−0.2	−0.2	S?
Mangrove extent	1980–2005†	−19		−1.0	−0.7	−0.7	−0.8	S?
Seagrass extent	1930–2003†	−20	−0.4	−0.5	−0.5	−2.4	−0.7	A?
Coral reef condition (live hard coral cover)	1980–2004	−38*		−3.9	−0.3	+0.2	−1.8	D 1985–1988
Water Quality Index (physical/chemical quality of freshwater)	1980–2005	0		+0.1	+0.0	−0.2	+0	S
Number of state indicators declining			**2/3**	**8/9**	**8/10**	**7/10**	**8/10**	
		Pressures						
Ecological footprint (humanity's aggregate resource-consumption)	1961–2006	+78*	+2.0	+1.3	+1.3	+2.1	+1.6	S
Nitrogen deposition rate (annual reactive N deposited)	1850–2005†	+35	+2.0	+1.3	−0.3	+0.2	+0.9	D?
No. alien species in Europe (Mediterranean marine, mammal, and freshwater)	1970–2007	+76*	+2.0	+1.4	+1.6	+1.1	+1.5	S
Exploitation of fish stocks (% overexploited, fully exploited, or depleted)	1974–2006	+31*	+0.6	+0.6	+1.1	+1.2	+0.9	F
Climatic Impact Indicator (degree to which European bird population trends have responded in the direction expected from climate change)	1980–2005	+23*		−0.8	+3.2	+1.2	+1.2	S
Number of pressure indicators increasing			**4/4**	**4/5**	**4/5**	**5/5**	**5/5**	
		Responses						
Extent of Protected Areas (PAs)	1888–2006	+400*	+7.6	+4.5	+3.4	+2.4	+4.7	S
Coverage by PAs of Important Bird Areas and Alliance for Zero Extinction sites	1888–2009	+360*	+5.6	+4.6	+2.6	+0.8	+3.4	D 1999–2008
Area of forest under sustainable management (FSC certified)	1995–2008	+12,000*			+100	+20	+46	D 2006
International IAS policy adoption (no. signatories to conventions with provision for tackling IAS)	1952–2008	+2700*	+10	+6.9	+14	+5.1	+9.1	S
National IAS policy adoption (% countries with relevant legislation)	1964–2009	+10,000*	+30	+8.7	+12	+4.1	+13	D 2004–2009
Official development assistance (US$ per year provided in support of CBD)	2005–2007†	+17				+8.4	+8.3	D?
Number of response indicators increasing			**4/4**	**4/4**	**5/5**	**6/6**	**6/6**	
		Benefits						
LPI for utilized vertebrate populations	1970–2006	−15*	+1.0	−0.3	−1.3	−1.7	−0.4	A 1972–2006
RLI for species used for food and medicine	1986–2008	−3.5*		−0.2	−0.2	−0.2	−0.2	A
RLI for bird species in international trade	1988–2008	−0.5*		−0.01	−0.03	−0.02	−0.03	A
Number of benefits indicators declining			**0/1**	**3/3**	**3/3**	**3/3**	**3/3**	

*Significant trends ($P < 0.05$). †Identifies indicators with insufficient data to test significance of post-1970 trends, usually because annual estimates are unavailable. ‡Since earliest date with data if this is post-1970. §Because the indicators measure different parameters, some comparisons of mean annual % change between indicators are less meaningful than comparisons between decades for the same indicator. ‖Rate of change decelerating (D), accelerating (A), stable (S, i.e., no years with significant changes), fluctuating (F, i.e., a sequence of significant positive and negative changes), or with too few data points to test significance (?); years indicate periods in which second derivatives differed significantly from zero ($P < 0.05$).

All indicators of policy and management responses show increasing trends (Fig. 1 and Table 1), with increases in (i) extent of protected areas (PAs) (Table 2); (ii) coverage by PAs of two subsets of Key Biodiversity Areas (*21*) [39% of the area of 10,993 Important Bird Areas and 42% of the area of 561 Alliance for Zero Extinction sites (*22*) by 2009]; (iii) area of sustainably managed forests [1.6 million km^2 under Forest Stewardship Council (FSC) certification by 2007]; (iv) proportion of eligible countries signing international agreements relevant to tackling invasive alien species (IAS) [reaching 82% by 2008 (*23*)]; (v) proportion of countries with national legislation to control and/or limit the spread and impact of IAS [reaching 55% by 2009 (*23*)]; and (vi) biodiversity-related aid (reaching US$3.13 billion in 2007). The rate of increase was stable (i and iv), slowing (ii, iii, and v), or based on too few data to test significance (vi) (Table 1). The last three inflections in aggregated trends (2002, 2004, and 2008) were all negative (Fig. 2), indicating that the rate of improvement has slowed. Two other indicators have only baseline estimates: Management effectiveness was "sound" for 22% of PAs ("basic" for 65% and "clearly inadequate" for 13%), and the proportion of genetic diversity for 200 to 300 important crop species conserved ex situ in gene banks was estimated to be 70% (*24*).

Only three indicators address trends in the benefits humans derive from biodiversity (Fig. 1 and Table 1): (i) population trends of utilized vertebrates have declined by 15% since 1970, and aggregate species' extinction risk has increased

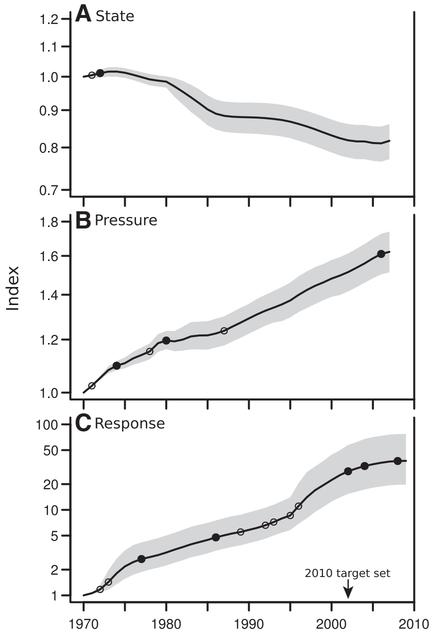

Fig. 2. Aggregated indices of (**A**) the state of biodiversity based on nine indicators of species' population trends, habitat extent and condition, and community composition; (**B**) pressures on biodiversity based on five indicators of ecological footprint, nitrogen deposition, numbers of alien species, overexploitation, and climatic impacts; and (**C**) responses for biodiversity based on six indicators of protected area extent and biodiversity coverage, policy responses to invasive alien species, sustainable forest management, and biodiversity-related aid. Values in 1970 set to 1. Shading shows 95% confidence intervals derived from 1000 bootstraps. Significant positive/upward (open circles) and negative/downward (filled circles) inflections are indicated.

Table 2. Examples of successes and positive trends relevant to the 2010 target (*5*).

Indicator	Successes and positive trends
	State
Living Planet Index of Palearctic vertebrate populations	Increased by 43% since 1970 (e.g., Eurasian beaver and common buzzard)
Waterbird populations in North America and Europe	Increased by 44% since 1980 owing to wetland protection and sustainable management (but populations remain below historic levels).
Species downlisted on the IUCN Red List	Species qualifying for downlisting to lower categories of extinction risk owing to successful conservation action include 33 birds since 1988 (e.g., Lear's macaw), 25 mammals since 1996 (e.g., European bison), and 5 amphibians since 1980 (e.g., Mallorcan midwife toad).
Wild Bird Index and Red List Index for species listed on the European Union Birds Directive	Annex 1–listed species' population trends have improved in EU countries (*27*) and extinction risk reduced (RLI increased 0.46% during 1994–2004) owing to designation of Special Protected Areas and implementation of Species Action Plans under the directive (e.g., white-tailed eagle).
Extinctions prevented	At least 16 bird species extinctions were prevented by conservation actions during 1994–2004, e.g., black stilt (*28*).
Water Quality Index in Asia	Improved by 7.4% since 1970.
	Pressures
Deforestation in Amazonian Brazil	Slowed from 2.8 million ha in 2003–2004 to 1.3 million ha in 2007–2008, but it is uncertain to what extent this was driven by improved enforcement of legislation versus reduced demand owing to economic slowdown.
	Responses
National biodiversity strategies and action plans (NBSAPs)	87% of countries have now developed NBSAPs and therefore have outlined coherent plans for tackling biodiversity loss at the national scale.
Protected areas (PAs)	Nearly 133,000 PAs designated, now covering 25.8 million km^2: 12% of the terrestrial surface (but only 0.5% of oceans and 5.9% of territorial seas), e.g., Juruena National Park, Brazil, designated in 2006, covering 19,700 km^2 of Amazon/cerrado habitat.
Invasive alien species (IAS) policy, eradication, and control	82% of eligible countries have signed international agreements relevant to preventing the spread and promoting the control/eradication of IAS. Successful eradications/control of IAS include pigs on Clipperton Atoll, France (benefiting seabirds and land crabs), cats, goats and sheep on Natividad, Mexico (benefiting black-vented shearwater), and red fox in southwest Australia (benefiting western brush wallaby).
Official development assistance for biodiversity	Increased to at least US$3.13 billion in 2007.

at an accelerating rate (as shown by the RLI) for (ii) mammals, birds, and amphibian species used for food and medicine (with 23 to 36% of such species threatened with extinction) and (iii) birds that are internationally traded (principally for the pet trade; 8% threatened). Trends are not yet available for plants and other important utilized animal groups. Three other indicators, which lack trend data, show (iv) 21% of domesticated animal breeds are at risk of extinction (and 9% are already extinct); (v) languages spoken by fewer than 1000 people (22% of the current 6900 languages) have lost speakers over the past 40 years and are in danger of disappearing within this century (loss of linguistic diversity being a proxy for loss of indigenous biodiversity knowledge); and (vi) more than 100 million poor people live in remote areas within threatened ecoregions and are therefore likely to be particularly dependent upon biodiversity and the ecosystem services it provides.

Indicator development has progressed substantially since the 2010 target was set. However, there are considerable gaps and heterogeneity in geographic, taxonomic, and temporal coverage of existing indicators, with fewer data for developing countries, for nonvertebrates, and from before 1980 and after 2005 (*4*, *5*, *25*). Interlinkages between indicators and the degree to which they are representative are incompletely understood. In addition, there are gaps for several key aspects of state, pressures, responses, and especially benefits (*4*, *5*, *7*, *26*).

Despite these challenges, there are sufficient data on key dimensions of biodiversity to conclude that at the global scale it is highly unlikely that the 2010 target has been met. Neither individual nor aggregated indicators of the state of biodiversity showed significant reductions in their rates of decline, apart from coral reef condition, for which there has been no further deceleration in decline since the mid-1980s. Furthermore, all pressure indicators showed increasing trends, with none significantly decelerating. Some local system-specific exceptions with positive trends for particular populations, taxa, and habitats (Table 2) suggest that, with political will and adequate resources, biodiversity loss can be reduced or reversed. More generally, individual and aggregated response indicators showed increasing trends, albeit at a decelerating rate (and with little direct information on whether such actions are effective). Overall, efforts to stem biodiversity loss have clearly been inadequate, with a growing mismatch between increasing pressures and slowing responses.

Our results show that, despite a few encouraging achievements, efforts to address the loss of biodiversity need to be substantially strengthened by reversing detrimental policies, fully integrating biodiversity into broad-scale land-use planning, incorporating its economic value adequately into decision making, and sufficiently targeting, funding and implementing policies that tackle biodiversity loss, among other measures. Sustained investment in coherent global biodiversity monitoring and indicators is essential to track and improve the effectiveness of these responses.

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29. We are grateful for comments, data, or help from R. Akçakaya, L. Alvarez-Filip, A. Angulo, L. Bennun, L. Coad, N. Cox, M. Dubé, C. Estreguil, M. Evans, B. Galil, V. Gaveau, F. Gherardi, S. Goldfinger, R. Green, A. Grigg, P. Herkenrath, C. Hilton-Taylor, M. Hoffmann, E. Kleynhans, J. Lamoreux, S. Livingstone, E. Marais, P. Martin, I. May, A. Milam, K. Noonan-Mooney, H. Pavese, B. Polidoro, C. Pollock, D. Pritchard, J. Schipper, F. Schutyser, V. Shutte, S. Simons, J. Škorpilová, A. Stattersfield, P. Voříšek, R. Wright, M. Wackernagel, and M. Waycott. We acknowledge support from the Global Environment Facility to the 2010 Biodiversity Indicators Partnership; Shell Foundation; European Commission; the Sea Around Us Project (University of British Columbia/Pew Environment Group) to D.P. and R.W.; World Wildlife Fund, The Nature Conservancy, and the University of Queensland to M.H. and F.L.; T. Haas and the New Hampshire Charitable Foundation to K.E.C.; and the National Science Foundation (NSF) to J.-F.L. Opinions and findings expressed here do not necessarily reflect the views of the NSF or other funding bodies.

Supporting Online Material

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Data File 1

26 January 2010; accepted 8 April 2010
Published online 29 April 2010;
10.1126/science.1187512
Include this information when citing this paper.

Plectasin, a Fungal Defensin, Targets the Bacterial Cell Wall Precursor Lipid II

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Host defense peptides such as defensins are components of innate immunity and have retained antibiotic activity throughout evolution. Their activity is thought to be due to amphipathic structures, which enable binding and disruption of microbial cytoplasmic membranes. Contrary to this, we show that plectasin, a fungal defensin, acts by directly binding the bacterial cell-wall precursor Lipid II. A wide range of genetic and biochemical approaches identify cell-wall biosynthesis as the pathway targeted by plectasin. In vitro assays for cell-wall synthesis identified Lipid II as the specific cellular target. Consistently, binding studies confirmed the formation of an equimolar stoichiometric complex between Lipid II and plectasin. Furthermore, key residues in plectasin involved in complex formation were identified using nuclear magnetic resonance spectroscopy and computational modeling.

Plectasin is a 40–amino acid residue fungal defensin produced by the saprophytic ascomycete *Pseudoplectania nigrella* (*1*). Plectasin shares primary structural features with defensins from spiders, scorpions, dragonflies and mussels and folds into a cystine-stabilized alpha-

Science

Global Biodiversity: Indicators of Recent Declines

Stuart H. M. Butchart, Matt Walpole, Ben Collen, Arco van Strien, Jörn P. W. Scharlemann, Rosamunde E. A. Almond, Jonathan E. M. Baillie, Bastian Bomhard, Claire Brown, John Bruno, Kent E. Carpenter, Geneviève M. Carr, Janice Chanson, Anna M. Chenery, Jorge Csirke, Nick C. Davidson, Frank Dentener, Matt Foster, Alessandro Galli, James N. Galloway, Piero Genovesi, Richard D. Gregory, Marc Hockings, Valerie Kapos, Jean-Francois Lamarque, Fiona Leverington, Jonathan Loh, Melodie A. McGeoch, Louise McRae, Anahit Minasyan, Monica Hernández Morcillo, Thomasina E. E. Oldfield, Daniel Pauly, Suhel Quader, Carmen Revenga, John R. Sauer, Benjamin Skolnik, Dian Spear, Damon Stanwell-Smith, Simon N. Stuart, Andy Symes, Megan Tierney, Tristan D. Tyrrell, Jean-Christophe Vié and Reg Watson

Science **328** (5982), 1164-1168.
DOI: 10.1126/science.1187512originally published online April 29, 2010

Global Biodiversity Target Missed
In 2002, the Convention on Biological Diversity (CBD) committed to a significant reduction in the rate of biodiversity loss by 2010. There has been widespread conjecture that this target has not been met. **Butchart *et al.*** (p. 1164, published online 29 April) analyzed over 30 indicators developed within the CBD's framework. These indicators include the condition or state of biodiversity (e.g., species numbers, population sizes), the pressures on biodiversity (e.g., deforestation), and the responses to maintain biodiversity (e.g., protected areas) and were assessed between about 1970 and 2005. Taken together, the results confirm that we have indeed failed to meet the 2010 targets.