BIODIVERSITY

# Community-level regulation of temporal trends in biodiversity

Nicholas J. Gotelli,[1]* Hideyasu Shimadzu,[2,3] Maria Dornelas,[3] Brian McGill,[4] Faye Moyes,[3]

Box 1. Definitions.

ADF test. A statistical test for detecting regulation in a time series of observations (11). The test fits an autoregressive (AR) time series model with a lag of one time step (AR1) to a data series. The coefficient $\varphi$ in the AR1 model reflects the degree of regulation. The extreme cases are $\varphi = 0$, which represents a white noise (Gaussian) distribution that shows strong regulation following a perturbation, and $\varphi = 1$, which represents an unregulated random walk that does not recover or return to a central value following a perturbation. The ADF test estimates the probability that the fitted value of $|\varphi| < 1$, which corresponds to a regulated process. The null hypothesis is that the time series represents a random walk with $\varphi = 1$.

AR time series model. A statistical model for a variable (such as abundance or species richness) that changes through time. In any AR model, the system has a “memory”

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## DISCUSSION

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## SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/7/e1700315/DC1

Supplementary Text

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fig. S2. Time series of uncorrelated white noise with a linear temporal trend.
fig. S3. Time series of uncorrelated white noise with a one-time perturbation.
fig. S4. Time series of random walk.
fig. S5. Time series of a random walk with a linear temporal trend.
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## REFERENCES AND NOTES


1. R. M. Sibly, J. Hone, Population growth rate and its determinants: An overview. Philos. Trans. R. Soc. London Ser. B 357, 1153–1170 (2002).
2. H. Leirs, N. C. Stenseth, J. D. Nichols, J. E. Hines, R. Verhagen, W. Verheyen, Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. Nature 389, 176–180 (1997).
3. S. A. Levin, Ecosystems and the biosphere as complex adaptive systems. Ecosystems 1, 431–436 (1998).
4. B. C. Patten, E. P. Odum, The cybernetic nature of ecosystems. Am. Nat. 118, 886–895 (1981).
5. R. E. Ulanowicz, Aristotelean causalities in ecosystem development. Oikos 57, 42–48 (1990).
6. J. H. Brown, S. K. M. Ernest, J. M. Parody, J. P. Haskell, Regulation of diversity: Maintenance of species richness in changing environments. Oecologia 126, 321–332 (2001).
7. S. K. M. Ernest, J. H. Brown, K. M. Thibault, E. P. White, J. R. Goheen, Zero sum, the niche, and metacommunities: Long-term dynamics of community assembly. Am. Nat. 172, E257–E269 (2008).
8. A. Gonzalez, M. Loreau, The causes and consequences of compensatory dynamics in ecological communities. Annu. Rev. Ecol. Evol. Syst. 40, 393–414 (2009).
9. S. D. Connell, G. Ghedini, Resisting regime-shifts: The stabilising effect of compensatory processes. Trends Ecol. Evol. 30, 513–515 (2015).
10. P. Turchin, Complex Population Dynamics: A Theoretical/Empirical Synthesis (Princeton Univ. Press, 2003), 456 pp.
11. S. E. Said, D. A. Dickey, Testing for unit roots in autoregressive-moving average models of unknown order. Biometrika 71, 599–607 (1984).
12. W. H. Green, Econometric Analysis (Prentice Hall, ed. 5, 2002).
13. L. Van Valen, A new evolutionary law. Evol. Theor. 1, 1–30 (1973).
14. D. H. Wright, Species-energy theory: An extension of species-area theory. Oikos 41, 496–506 (1983).
15. D. L. Rabosky, A. H. Hurlbert, Species richness at continental scales is dominated by ecological limits. Am. Nat. 185, 572–583 (2015).
16. J. HilleRisLambers, P. B. Adler, W. S. Harpole, J. M. Levine, M. M. Mayfield, Rethinking community assembly through the lens of coexistence theory. Annu. Rev. Ecol. Evol. Syst. 43, 227–248 (2012).
17. D. Tilman, Biodiversity: Population versus ecosystem stability. Ecology 77, 350–363 (1996).
18. O. Allouche, R. Kadmon, A general frame1Tf6.5001006.5001222.23628Tf3.0701ough f diversity:

41. J. Wu, O. L. Loucks, From balance of nature to hierarchical patch dynamics: A paradigm shift in ecology. Quart. Rev. Biol. 70, 439–466 (1995).
42. S. L. Pimm, A. Redfearn, The variability of population-densities. Nature 334, 613–614 (1988).
43. W. Dodds, Laws, Theories, and Patterns in Ecology (University of California Press, 2011).
44. S. M. Scheiner, M. R. Willig, The Theory of Ecology (University of Chicago Press, 2011).
45. C. F. Dormann, O. Schweiger, P. Arens, I. Augenstein, S. Aviron, D. Bailey, J. Baudry, R. Billeter, R. Bugter, R. Bukácek, F. Burel, M. Cerny, R. De Cock, G. De Blust, R. DeFilippi, T. Diekötter, J. Dirksen, W. Durka, P. J. Edwards, M. Frenzel, R. Hamersky, F. Hendrickx, F. Herzog, S. Klotz, B. Koolstra, A. Lausch, D. Le Coeur, J. Liira, J. P. Maelfait, P. Opdam, M. Roubalova, A. Schermann-Legionnet, N. Schermann, T. Schmidt, M. J. M. Smulders,

96. P. A. Henderson, A. E. Magurran, Direct evidence that density-dependent regulation underpins the temporal stability of abundant species in a diverse animal community. Proc. Biol. Sci. 281, 20141336 (2014).
97. E. Woehler, "Seabirds of the Southern and South Indian Ocean - Australian Antarctic Data Centre"; www.iobis.org [accessed 2012].
98. R. Ostler, "Marine Nature Conservation Review (MNCR) and associated benthic marine data held and managed by JNCC - EurOBIS," Joint Nature Conservation Committee, Centre for Ecology and hydrology, Aberdeenshire, UK; www.emodnet-biology.eu/data-catalog?module=dataset&dasid=621 [accessed 2012].
99. Southeast Fisheries Science Center, National Oceanic and Atmospheric Administration. NOAA Southeast Fishery Science Center (SEFSC) Fisheries Log Book System (FLS) Commercial Pelagic Logbook Data; www.iobis.org [accessed 2012].
100. P. Pugh, "Discovery Collections Midwater Database," National Oceanography Centre, Southampton, UK (2000); https://gcmd.nasa.gov/KeywordSearch/Metadata.do?Portal=GCMD&MetadataView=Full&EntryId=OBIS.Discovery.Collections.Midwater [accessed 2012].
101. "South Western Pacific Regional OBIS Data Asteroid Subset," NIWA (National Institute of Water and Atmospheric Research - New Zealand) MBIS (Marine Biodata Information System) accessed through South Western Pacific OBIS; www.iobis.org [accessed 2012].
102. D. Clark, B. Branton, "DFO Maritimes Research Vessel Trawl Surveys, OBIS Canada Digital Collections," Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada, OBIS Canada (2007); www.iobis.org [accessed 2012].
103. M. Reichert, "MARMAP Chevron Trap Survey 1990-2009," SCDNR/NOAA MARMAP Program, SCDNR MARMAP Aggregate Data Surveys, The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program, Marine Resources Research Institute, South Carolina Department of Natural Resources (2009); www.usgs.gov/obis-usa/data_search_and_access/participants.html [accessed 2012].
104. "Previous_fisheries_REVIZEE_Program," Tropical and Subtropical Western South Pacific OBIS; www.iobis.org [accessed 2012].
105. "South Western Pacific Regional OBIS Data Bryozoan Subset," South Western Pacific OBIS; www.iobis.org [accessed 2012].
106. "South Western Pacific Regional OBIS Data provider for the NIWA Marine Biodata Information System," NIWA (National Institute of Water and Atmospheric Research - New Zealand) MBIS (Marine Biodata Information System), South Western Pacific OBIS; www.iobis.org [accessed 2012].
107. "CMarZ (Census of Marine Zooplankton)-Asia Database," OBIS-SCAR-MarBIN; www.scarmarbin.be [accessed 2012].
108. "EPA's EMAP Database," U.S. Environmental Protection Agency, Environmental Monitoring and Assessment Program (EMAP); www.iobis.org [accessed 2012].
109. "The Observer Program database," OBIS-USA North Pacific Groundfish Observer (North Pacific Research Board); www.iobis.org [accessed 2012].
110. P. N. Halpin, A. J. Read, E. Fujioka, B. D. Best, B. Donnelly, L. J. Hazen, C. Kot, K. Urian, E. Labrecque, A. Dimatteo, J. Cleary, C. Good, L. B. Crowder, K. D. Hyrenbach, OBIS-SEAMAP: The world data center for marine mammal, sea bird, and sea turtle distributions. Oceanography 22, 104–115 (2009).
111. R. G. B. Brown, D. N. Nettleship, P. Germain, C. E. Tull, T. Davis, Atlas of Eastern Canadian Seabirds (Canadian Wildlife Service, 1975).
112. A. W. Diamond, A. J. Gaston, R. G. B. Brown, Converting PIROP counts of seabirds at sea to absolute densities. Can. Wildl. Serv. Progr. 164, 21 (1986).
113. F. Huettmann, An ecological GIS research application for the northern Atlantic—The PIROP database software, environmental data sets and the role of the internet/WWW, in Hypermedia im Umweltschutz Proceedings of Deutsche Gesellschaft für Informatik (GI) and Forschungsinstitut für anwendungsorientierte Wissensverarbeitung (FAW) Ulm, W.-F. Riekert, K. Tochtermann, Eds. (Umwelt-Informatik aktuell, Bd.17, Metropolis Verlag, 1998), pp. 213–217.
114. "PIROP Northwest Atlantic 1965–1992 - OBIS SEAMAP"; www.iobis.org [accessed 2012].
115. A. J. Read, P. N. Halpin, L. B. Crowder, B. D. Best, E. Fujioka, Eds., "OBIS-SEAMAP: Mapping marine mammals, birds and turtles" (2011); http://seamap.env.duke.edu [accessed 2012].
116. P. P. W. Yen, W. J. Sydeman, S. J. Bograd, K. D. Hyrenbach, Spring-time distributions of migratory marine birds in the southern California Current: Oceanic eddy associations and coastal habitat hotspots over 17 years. Deep Sea Res. Part 2 Oceanogr. Res. Pap. 53, 399–418 (2006).
117. J. Jahncke, C. Rintoul, "CalCOFI and NMFS Seabird and Marine Mammal Observation Data, 1987-2006," California Cooperative Oceanic Fisheries Investigations (CalCOFI) and National Marine Fisheries Service (NMFS) cruises, 1987–2006 - OBIS SEAMAP (2006); www.iobis.org [accessed 2012].
118. C. Rintoul, B. Schlagenhauf-Langabeer, K. D. Hyrenbach, K. H. Morgan, W. J. Sydeman, Atlas of California Current Marine Birds and Mammals: Version 1 (unpublished report, PRBO Conservation Science, 2006).
119. P. P. W. Yen, W. J. Sydeman, K. D. Hyrenbach, Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: Implications for trophic transfer and conservation. J. Mar. Syst. 50, 79–99 (2004).
120. "Bahamas Marine Mammal Research Organisation Opportunistic Sightings - OBIS SEAMAP"; www.iobis.org [accessed 2012].
121. M. Machete, R. S. Santos, Azores Fisheries Observer Program (POPA): A case study of the multidisciplinary use of observer data, in Proceedings of the 5th International Fisheries Observer Conference, Victoria, Canada, T. A. McVea, S. J. Kennelly, Eds. (2007).
122. T. Morato, D. A. Varkey, C. Damaso, M. Machete, M. Santos, R. Prieto, R. S. Santos, T. J. Pitcher, Evidence of a seamount effect on aggregating visitors. Mar. Ecol. Prog. Ser. 357, 23–32 (2008).
123. P. Amorim, M. Figueiredo, M. Machete, T. Morato, A. Martins, R. S. Santos, Spatial variability of seabird distribution associated with environmental factors: A case study of marine important bird areas in the Azores. ICES J. Mar. Sci. 66, 29–40 (2009).
124. "POPA cetacean, seabird, and sea turtle sightings in the Azores area 1998–2009 - OBIS SEAMAP"; www.iobis.org [accessed 2012].
125. "Marine Biological Sample Database, JAMSTEC," OBIS_JAPAN; www.godac.jamstec.go.