

## A critique for meta-analyses and the productivity–diversity relationship

HELMUT HILLEBRAND<sup>1,3</sup> AND BRADLEY J. CARDINALE<sup>2</sup>

<sup>1</sup>*Institute for Chemistry and Biology of the Marine Environment, Carl-von-Ossietzky University Oldenburg, Schleusenstrasse 1, 26382 Wilhelmshaven, Germany*

<sup>2</sup>*Department of Ecology, Evolution and Marine Biology, University of California–Santa Barbara, Santa Barbara, California 93106 USA*

It is an exciting time to be an ecologist. Over the past several decades, our discipline has matured from one focused on the assembly of case studies based on natural history, to one that has seen improved conceptual frameworks and mathematical models that help explain ecological phenomena from species coexistence to elemental cycling. The maturation of our discipline has been fostered by many things, including improved technology, increased availability of data, and emergent methods for analyzing large data sets. One factor that has played a central role in the modern synthesis is meta-analyses. Gurevitch et al. (1992) introduced meta-analyses to ecologists and catalyzed their entrance into the ecological literature as a powerful statistical means to assess the generality of pattern and process. Soon after, the U.S. National Science Foundation established the National Center for Ecological Analysis and Synthesis (NCEAS) whose mission it is to bring together ecological data sets so that we could synthesize pattern and process using meta-analysis and many other analytical tools. NCEAS was so successful that it was soon after mimicked by other scientific disciplines (e.g., NESCent, the National Evolutionary Synthesis Center).

However, when our initial honeymoon with “synthesis” was over, criticisms began to surface, exposing the inherent warts and flaws of a growing discipline. Some argued that data sets were now being analyzed, and syntheses performed, by researchers who knew little about (or perhaps had never even seen) the systems they were trying to understand. Such “remote ecology” reduces an appreciation for natural history, and may lead to incorrect conclusions because one doesn’t understand the intricacies and contingencies of each system that reveal how pattern is linked to process. Some argued that meta-analyses were proliferating more rapidly than the methods needed for quality control, and that the concatenation of data sets was leading to a propagation of errors.

These are essentially the arguments levied by Whittaker (2010, from now on W2010). W2010 strongly criticizes the use of meta-analyses in ecology, and uses three syntheses of a fundamentally important ecological pattern (the productivity-diversity relationship, PDR) to illustrate why he believes there are flaws in the use of this tool. He especially criticizes the first of these analyses by Mittelbach et al. (2001) (from now on M2001). He argues that these meta-analyses have lacked stringent and transparent criteria in study selection, have ignored important correlates of the relevant independent and response variables (e.g., spatial scale), and have been inconsistent in their categorization of studies to the extent that the authors of the different syntheses have reached divergent conclusions.

We agree with certain elements of Whittaker’s criticism, including the need for improved quality control and transparency in the selection and analysis of data. We also agree with W2010’s general sentiment that those who are performing meta-analyses have an obligation to read each paper included in their analyses carefully and to understand the unique features of a study that might influence one’s conclusions. There is no substitute for thoroughly understanding the natural history of the system(s) from which one is drawing inference, and no substitute for characterizing the unique and shared features of the studies included in a synthesis (for example, see Foster et al. 2006’s response to Halpern et al.’s 2006 meta-analysis, or the comments on Worm et al. 2006, including those by Holker et al. 2007, Jaenike 2007, and Wilberg and Miller 2007). We detail comments on these points in the section *Quality issues in meta-analysis*.

However, beyond his relatively straight-forward call to improve the way we conduct meta-analyses, there is little in W2010 that we agree with. We are especially worried that W2010 proposes that we throw out the baby with the bathwater, calling for a halt in meta-analyses so that we can refocus attention on the intricacies of each case study. This proposition thoroughly neglects the many improvements in the handling and analyses of data that have been developed for meta-analyses over the last 15 years (see accompanying

Manuscript received 14 January 2009; revised 17 July 2009; accepted 28 July 2009. Corresponding Editor: D. R. Strong. For reprints of this Forum, see footnote 1, p. 2534.

<sup>3</sup> E-mail: hillebrand@icbm.de

comments by Ellison [2010] and Gurevitch and Mengersen [2010]). It also suggests that ecological patterns and processes are so highly system specific that it is difficult, perhaps impossible, to extract general trends amid the background of natural variation. We couldn't disagree more, and we are generally enthusiastic that ecology as a discipline has moved beyond the case studies and contingencies of individual systems to seek generality (see *A general critique for meta-analysis*).

In our final section, *Moving beyond patterns*, we add to W2010's commentary by suggesting that much of the confusion and disparity in conclusions among those seeking to synthesize the PDR stems from a lack of clear mechanistic thinking. Summarizing patterns without a clear mechanistic understanding of theoretically plausible relationships does nothing other than lead to confusion, no matter how rigorous and technically sound a meta-analysis might be. Therefore, we end with an appeal to those who might perform further meta-analyses to think more deeply about what should, according to ecological theory, be the dependent and independent variables behind the productivity–diversity relationship.

#### QUALITY ISSUES IN META-ANALYSES

Objective and clear criteria for data inclusion are the cornerstone of any endeavor to synthesize data. A meta-analysis has to be based on the most comprising and unbiased set of studies affiliated with the research question at hand. W2010 is justified in stating that those performing meta-analyses sometimes do not do a very good job in stating their search and inclusion criteria. Based on the “Methods” section in a meta-analysis, a researcher should be able to redo the entire analysis starting with the literature search and database build-up, proceeding with the statistical analysis, and finally coming to the same conclusions. Of course, these criteria are no different than the standards that should be imposed by reviewers on any publishable research.

W2010 details what he believes are flaws in the three analyses investigated by him, and goes on to propose seven “improved” criteria for the inclusion of studies in future meta-analyses. We do not take issue with his claim about flaws: for example, that authors have selected and categorized data in different ways that are sometimes not transparent and repeatable, and that authors have occasionally made mistakes or double entries into their data sets, which have led researchers to divergent conclusions. Moreover, subsequent papers criticized the original meta-analysis for flaws not only in the database, but also that the statistical models used to analyze the data were inappropriate. Such issues are clearly important to resolve. We agree that there needs to be improved standards for quality control in meta-analytic data sets. This is an issue that has been discussed at length (Osenberg et al. 1997, Englund et al. 1999, Gurevitch and Hedges 1999, LaJeunesse and Forbes 2003, Rosenberg 2005), and there are ongoing

attempts to develop the cyber-infrastructure needed to improve the management, sharing, and analysis of data in the next century (for example, the International Knowledge Network for Biocomplexity and accompanying management software Morpho). We also believe that debate over the nature and validity of different analyses is a normal, healthy part of the scientific process, and that this debate gradually leads to an improvement in conclusions. As such, W2010's comment helps promote a worthwhile debate.

However, we think it would be a tragedy to adopt W2010's strict criteria for how to overcome these problems. It generally strikes us as dangerous and naïve when a researcher suggests there is a single best, or optimal way to gain knowledge. Rather than trying to force researchers into a narrow mold, we believe that the primary constraints on a meta-analysis should be (1) *clarity*, researchers need to clearly state how the data is being used and why; (2) *transparency*, researchers to make abundantly clear how the data were collected, which data were included, and why; (3) *technical accuracy*, researchers need to be sure that the assumptions of their statistical tools match the structure of the data; and (4) *availability*, researchers need to make all data and technical code from their analyses available along with the published results so that the accuracy, reliability, and repeatability of the data set can be checked.

Although we have no doubt that W2010's comment was written in an attempt to promote clarity, accuracy, transparency and availability, his proposed criteria overshoot this aim by restricting analyses to very narrow grounds at the expense of the larger picture potentially gained by meta-analyses. For example, in criterion 1 W2010 argues that plant species richness is the only reasonable response variable that should be used as a measure of diversity. Although we agree that richness is the focus of many theories about productivity–diversity relationships, and although we agree that researchers should take great care to measure variables that are mechanistically consistent with ecological theory, there is no reason to believe species richness is the sole aspect of diversity that should be related to productivity. Not only is species richness itself a proxy for how other aspects of biodiversity are packaged (e.g., genetic or evolutionary divergence), several of the mechanisms by which productivity is thought to influence richness occur through changes in species evenness (Hillebrand et al. 2007), spatial turnover of taxa ( $\beta$  diversity; Chase and Leibold 2002, Gross and Cardinale 2007), or changes in functional group dominance (Declerck et al. 2007). Rather than argue that ecologists focus narrowly on just one response variable, it would be more constructive to emphasize that the focal variable should be motivated by the question, and that the question itself should be constructed so that there is a clear mechanistic underpinning or theoretical justification for expecting the response variable to change with productivity.

In criteria 2 and 5, W2010 argues that the studies included in an analysis should be completely homogeneous with respect to the scales at which they are performed, and with respect to the wide variety of potentially confounding variables that might influence species richness and productivity. Aside from the fact that this demand is incredibly unrealistic and would prevent us from summarizing more than a handful of studies at any one time, this argument ignores the fact that it is often a far more powerful approach in synthesis efforts to maximize variation among studies so that one can determine which co-varying factors actually “matter” in a way that they alter conclusions about the form of productivity-diversity relationships. A meta-analysis is especially useful if it reveals that a conclusion holds across a broad variety of empirical approaches or, alternatively, if it shows how a process or pattern is altered by a certain co-varying factor. It would be tragic to ignore or lose these new insights, as would happen if we adopted W2010’s criteria.

In criterion 6, W2010 proposes a cutoff for the number of observations along an  $x$ -axis needed to differentiate linear from nonlinear relationships. We agree that one’s ability to differentiate linear from nonlinear relationships can be an important issue when trying to understand productivity–diversity relationships. Detecting unimodality compared to a monotonically increasing relationship requires the occurrence of significant estimates of linear and quadratic regression terms, the detection of an internal maximum in the regression (e.g., Mitchell-Olds and Shaw 1987), and tests of whether the quadratic regression is a more parsimonious model than the simple linear one (e.g., by using Akaike information criteria, AIC, or log-likelihood methods; Burnham and Andersson 2002). However, we disagree with the need to impose some arbitrary cutoff for the number of observations needed to make a study useful. This criterion ignores the fact that meta-analytical techniques allow one to weight or reduce the impact of a study that is not well replicated, or to assign levels of confidence to studies that may be data poor (Gurevitch and Hedges 2001).

It becomes obvious from W2010 that the meta-analyses on productivity diversity relationships (PDR) by M2001 and others can be critically evaluated for including (or not including) certain studies or using certain methods. However, these problems remain unresolved by a very arbitrary list of “quality” criteria. Instead, the discussion should be by reanalysis of these data and the existence of this forum section reflects such a scientific progress. Although we share some points of criticism with W2010 on the lack of rigor in conducting these meta-analyses, we remain convinced that M2001 contributed much to the debate of PDR, as their analysis showed that the paradigm-like statement of a single universal hump-shaped PDR (Rosenzweig and Abramsky 1993) lacks empirical evidence. We do not

expect a reanalysis of the M2001 database to change this general outcome.

#### A GENERAL CRITIQUE FOR META-ANALYSIS

Aside from the detailed arguments about the criteria that should be used to guide meta-analyses, our strongest point of dissent with W2010 is with his calling for a halt in conducting meta-analyses. It almost goes without saying that ecological data tend to be highly contingent on scaling issues, on seasonal and other intra-annual patterns, on inter-annual differences in abiotic constraints, on the type of experimental or observational approach, the chosen measure for a certain biological variable, and so on. But those who focus all their attention on such contingencies will inevitably miss the forest for the trees, and fail to see generality in ecological phenomena (Lawton 1999).

Meta-analyses are the remote-sensing tools of ecology. They allow us to step back from small-scale contingencies and see a broader, albeit less detailed, overview of how a system operates. A meta-analysis can give a baseline result for a certain process (e.g., the impact of grazing on plant biomass) to which new experimental studies can be compared. A meta-analysis can give a central tendency for a process, pattern or effect, which is debated in the literature and in cases show why results are different between studies. In the best cases, meta-analyses create new research hypotheses by showing what we do not know. It is immanent in this kind of analysis that peculiarities of certain ecosystems and organisms are not reflected. However, the goal of meta-analyses is to reveal pattern and process of the whole forest, not to show what’s happening on the individual trees.

W2010 claims there are a number of technical shortcomings in three analyses of the PDR. His claims suggest that reevaluation and improvement of these meta-analyses might be useful. However, his suggestion that we halt meta-analyses is, in our opinion, short sighted. Not only does it neglect the power and usefulness of this tool, it ignores the many improvements of meta-analytical approaches achieved during the last decade. Ecologists have adopted different types of effect sizes (Osenberg et al. 1997, Gurevitch and Hedges 2001, LaJeunesse and Forbes 2003), have analyzed the statistical properties of these effect sizes (Hedges et al. 1999), and have improved their criteria for the inclusion of data (Englund et al. 1999). There is also increased awareness about the interdependency of data derived from one study and the importance of weighted meta-analyses. If these “best techniques” are not used correctly or reproducibly, then commenting on analyses and reanalyzing data is an integral part of the scientific process. However, calling for a halt in meta-analyses is like calling for cessation of cancer research simply because one drug didn’t live up to everyone’s expectations.

## MOVING BEYOND PATTERN

W2010 discussed what he sees as limitations of the different meta-analyses on PDR. While we accept his argument that there have been shortcomings and flaws in meta-analyses that require a second look, we have disagreed with his vision for how synthesis via meta-analyses should proceed. We also believe that W2010 misses an important point in his comment that, in our opinion, is one of the primary limitations with research on PDR, that is, the lack of focus on the mechanisms that are presumed to generate PDR. With the possible exception of the debate over how diversity is related to stability (see Ives and Carpenter 2008), few discussions in ecology are in a worse state of understanding mechanisms than the discussion on PDR. There are numerous reasons for this. Here we discuss just two.

First, empiricists have used a plethora of different variables to represent “diversity” and “productivity.” For example, consider that estimates of “productivity” range from variables as divergent as direct estimates of the rate of carbon flux through plants or animals, to the standing stock biomass of these same organisms, to the standing stock availability of resources used by these organisms, to the rates at which those resources are supplied, to highly derived covariates of resources or biomass such as latitude, depth, or elevation (M2001). Researchers often assume that the aforementioned variables are all mechanistically interchangeable, and that they operate consistently across varied trophic levels. Yet, the ecological theories on which predictions of PDR are often based suggest that species richness should be a function of (1) the supply rate of limiting resources that regulates species population sizes and stochastic rates of extinction (i.e., species–energy theory; see Wright 1983, Abrams 1995, Srivastava and Lawton 1998) and/or (2) the relative ratios of different resources that mediate competitive interactions and coexistence among species that share resources in a local community (resource-ratio theory; Tilman 1977, 1982). Empiricists tend to measure production and biomass as proxies for resource supply, which assumes there is a linear relationship between the availability of resources (what one might call the “potential” productivity of a system) and the conversion of those resources into new biomass (that is, the “actual” production of biomass). This may, at times and in some systems, be a legitimate assumption. However, it frequently is not: otherwise, why would we study things like Type-II functional response curves, compensatory feeding, assimilation efficiencies, and so on?

A second problem is that there is considerable confusion about whether productivity is the cause or the consequence of species diversity. Obviously, the supply rate of limiting resources, and the ratios at which different limiting resources are supplied, influence both the amount of biomass that can be achieved by a local community as well as the number of species it can support. As a result, species richness and productivity

are often associated with one another. However, as discussed in the last paragraph, theory argues it is the supply rate of one or more resources, not productivity per se, that is the direct proximate cause of species richness. Plants don't generally consume or compete for their own tissue, and as such, theory doesn't predict a direct causal link from biomass or production of plants to species richness of plants. If anything, the causal link between richness and production goes in the opposite direction. Over the past two decades, there has been a wealth of experiments that have manipulated the richness of primary producers in terrestrial, marine, and freshwater ecosystems and shown that more species-rich communities capture limited inorganic resources more efficiently (reviewed in Balvanera et al. 2006, Cardinale et al. 2006). As a result, diverse communities tend to achieve higher biomass because species use limiting resources in ways that are complementary in space or time (see meta-analysis of Cardinale et al. 2007).

The contrast between the perspective that productivity-drives-diversity vs. the perspective that diversity-drives-productivity has led several authors to propose conceptual frameworks (Loreau et al. 2001, Schmid 2002, Cardinale et al. 2009) and mathematical models (Gross and Cardinale 2007) to explain how these views can be merged. These models share the common feature that the rates and/or ratios of resource supply (i.e., potential productivity) are what directly limit species richness in a local community. However, it is species richness that regulates the efficiency by which resources are captured and converted into new tissue. Importantly, these frameworks have also shown that when pathways of causality are mixed up, or biomass and resource supply are assumed to be interchangeable, one can observe spurious relationships between species richness and biomass that change as a function of spatial scale (Gross and Cardinale 2007). The key point here is that, if one is not careful to correctly identify the proximate causal and response variables, you can get a totally different picture of what the species richness–productivity relationship (SRPR) looks like.

Perhaps it is no surprise that ecologists have yet to produce a consensus view on the qualitative nature of SRPR. In our opinion, one of the primary contributions of M2001 was to illustrate the lack of a dominant and generalizable pattern of SRPR, which overturned a paradigm of a single unimodal PDR applying to all kinds of organisms and ecosystems (Rosenzweig and Abramsky 1993). This lack of generality almost certainly reflects to one degree or another the widespread use of proxies and lack of direct causal mechanisms linking the measured variables that have hampered our understanding.

If the M2001 analysis can be improved by quantifying studies more rigorously, then this would be a useful part of the normal scientific process. But this does not justify suggesting to throw the baby out with the bathwater by

halting meta-analyses on PDR or other important issues in ecology. Before any researcher undertakes a new synthesis of PDR, we hope s/he will think deeply about what direct proximate causal and response variables are involved in these relationships, and consider testing the improved conceptual frameworks that have been developed to help us better understand these relationships.

## LITERATURE CITED

- Abrams, P. A. 1995. Monotonic or unimodal diversity–productivity gradients: What does competition theory predict? *Ecology* 76:2019–2027.
- Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9:1146–1156.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodal inference*. Second edition. Springer, New York, New York, USA.
- Cardinale, B. J., H. Hillebrand, W. S. Harpole, K. Gross, and R. Ptacnik. 2009. Separating the influence of resource “availability” from resource “imbalance” on productivity–diversity relationships. *Ecology Letters* 12:475–487.
- Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443:989–992.
- Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau, and J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time due to complementary resource use: a meta-analysis. *Proceedings of the National Academy of Sciences USA* 104:18123–18128.
- Chase, J. M., and M. A. Leibold. 2002. Spatial scale dictates the productivity–biodiversity relationship. *Nature* 416:427–430.
- Declerck, S., M. Vanderstukken, A. Pals, K. Muylaert, and L. de Meester. 2007. Plankton biodiversity along a gradient of productivity and its mediation by macrophytes. *Ecology* 88:2199–2210.
- Ellison, A. M. 2010. Repeatability and transparency in ecological research. *Ecology* 91:2536–2539.
- Englund, G., O. Sarnelle, and S. D. Cooper. 1999. The importance of data-selection criteria: meta-analyses of stream predation experiments. *Ecology* 80:1132–1141.
- Foster, M. S., M. S. Edwards, D. C. Reed, D. R. Schiel, R. C. Zimmerman, M. A. Steele, S. C. Schroeter, R. C. Carpenter, D. J. Kushner, B. S. Halpern, K. Cottenie, and B. R. Broitman. 2006. Top-down vs. bottom-up effects in kelp forests. *Science* 313:1737–1739.
- Gross, K., and B. J. Cardinale. 2007. Does species richness drive community production or vice versa? Reconciling historical and contemporary paradigms in competitive communities. *American Naturalist* 170:207–220.
- Gurevitch, J., and L. V. Hedges. 1999. Statistical issues in ecological meta-analyses. *Ecology* 80:1142–1149.
- Gurevitch, J., and L. V. Hedges. 2001. Meta-analysis: combining the results of independent experiments. Pages 347–369 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Chapman and Hall, New York, New York, USA.
- Gurevitch, J., and K. Mengersen. 2010. A statistical view of synthesizing patterns of species richness along productivity gradients: devils, forests, and trees. *Ecology* 91:2553–2560.
- Gurevitch, J., L. L. Morrow, W. Alison, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. *American Naturalist* 140:539–572.
- Halpern, B. S., K. Cottenie, and B. R. Broitman. 2006. Strong top-down control in southern California kelp forest ecosystems. *Science* 312:1230–1232.
- Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–1156.
- Hillebrand, H., D. S. Gruner, E. T. Borer, M. E. S. Bracken, E. E. Cleland, J. J. Elser, W. S. Harpole, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences USA* 104:10904–10909.
- Holker, F., D. Beare, H. Dorner, A. di Natale, H.-J. Ratz, A. Temming, and J. Casey. 2007. Comment on “Impacts of Biodiversity Loss on Ocean Ecosystem Services.” *Science* 316:1285.
- Ives, A. R., and S. R. Carpenter. 2008. Stability and diversity of ecosystems. *Science* 317:58–62.
- Jaenike, J. 2007. Comment on “Impacts of Biodiversity Loss on Ocean Ecosystem Services.” *Science* 316:1285.
- LaJeunesse, M. J., and M. R. Forbes. 2003. Variable reporting and quantitative reviews: a comparison of three meta-analytical techniques. *Ecology Letters* 6:448–454.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84:177–192.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808.
- Mitchell-Olds, T., and R. G. Shaw. 1987. Regression analysis of natural selection: statistical influence and biological interpretation. *Evolution* 41:1149–1161.
- Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82:2381–2396.
- Osenberg, C. W., O. Sarnelle, and S. D. Cooper. 1997. Effect size in ecological experiments: the application of biological models in meta-analysis. *American Naturalist* 150:798–812.
- Rosenberg, M. S. 2005. The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution* 59:464–468.
- Rosenzweig, M. L., and Z. Abramsky. 1993. How are diversity and productivity related? Pages 52–65 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Schmid, B. 2002. The species richness–productivity controversy. *Trends in Ecology and Evolution* 17:113–114.
- Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. *American Naturalist* 152:510–529.
- Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* 58:338–348.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey, USA.
- Whittaker, R. J. 2010. Meta-analyses and mega-mistakes: calling time on meta-analysis of the species richness–productivity relationship. *Ecology* 91:2522–2533.
- Wilberg, M. J., and T. J. Miller. 2007. Comment on “Impacts of Biodiversity Loss on Ocean Ecosystem Services.” *Science* 316:1285.
- Worm, B., et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787–790.
- Wright, D. H. 1983. Species–energy theory: an extension of species–area theory. *Oikos* 41:496–506.