Theoretical and Empirical Perspectives in Ecology and Evolution: A Survey

BENJAMIN C. HALLER

Scientific research is often conceptually divided into empirical and theoretical approaches, and researchers often specialize as empiricists or theorists. Both approaches are essential to scientific progress, but interactions between the two groups have at times seemed problematic. I present results from a recent survey of 614 scientists (predominantly ecologists and evolutionary biologists) regarding interactions between theoretical and empirical work. Some overall themes emerged from these results. One theme is a widespread and mutual lack of trust, understanding, and interaction between empiricists and theorists. Another is a general desire, among almost all of the respondents, for greater understanding, more collaboration, and closer interactions between empirical and theoretical work. The final theme is that institutions, such as journals, funding agencies, and universities, are often seen as hindering such interactions. These results provide a clear mandate for institutional changes to improve interactions between theorists and empiricists in ecology and evolutionary biology.

Keywords: theory, data, modeling, experiments, methodology

cientific investigation comprises many different sorts of activities, and these activities are often roughly classified as either *empirical* or *theoretical*. Empirical work might be defined as the gathering and analysis of data from phenomena observed in the real world; it spans a range from purely observational field studies to hypothesis-driven experimentation in the laboratory. Theoretical work can be inspired by real-world phenomena, but it does not involve the gathering or analysis of data from those phenomena; rather, it might be defined as an exploration of what could be, rather than what is, using tools ranging from analytical models to individual-based simulations. Like most dichotomies, this classification is an oversimplification, and some types of scientific inquiry are not easily categorized, such as biostatistics and meta-analysis. Nevertheless, the distinction between empirical and theoretical work is widely accepted, many types of scientific research do clearly fall into one category or the other, and many researchers consider themselves to work primarily in one area or the other.

One could debate these definitions of empirical and theoretical work, discuss the proper role of each type of work in the scientific process, give further examples of each, and consider in detail the types of interactions that can exist between them (Watt 1962, Hall 1991, Odenbaugh 2005, Bailer-Jones 2009, Pickett et al. 2010, Colyvan 2011, Gorelick 2011, 2012, Choate et al. 2012, Griesemer 2012, Scheiner

2012, 2013, Callebaut 2013, Pigliucci 2013). As worthwhile as it might be, however, such philosophical discussion is not the aim of this article. Instead, I will investigate a more empirical aspect of this dichotomy: how theoretical researchers (theorists) and empirical researchers (empiricists) interact in their practice of science and how they view that interaction. For this reason, I will assume that the categories of theoretical and empirical research are generally understood, even if they are also somewhat vague and subject to debate. The interaction between theoretical and empirical work in ecology and evolution has been the subject of much discussion (Kareiva 1989, Grimm 1994, Noss 1996, Lawton 1999, Colyvan and Ginzburg 2003, Belovsky et al. 2004, Ellner 2006, Scheiner and Willig 2008, Roughgarden 2009, Gorelick 2011, Lindenmayer and Likens 2011, Cadotte et al. 2012, Fawcett and Higginson 2012, Lindenmayer et al. 2012, Scheiner 2013, Matzek et al. 2014). My goal is to both clarify and advance that discussion by providing empirical data on the interaction between theoretical and empirical approaches.

Here, I present results from a recent survey of 614 scientists. These scientists work predominantly in ecology, evolutionary biology, and related fields. They span a wide range of ages, career stages, nationalities, and positions along the theoretical–empirical continuum, and so constitute a broad sampling of perspectives. The survey explored their views on theoretical and empirical work, including questions

BioScience XX: 1–10. © The Author(s) 2014. Published by Oxford University Press on behalf of the American Institute of Biological Sciences. All rights reserved. For Permissions, please e-mail: journals.permissions@oup.com.

doi:10.1093/biosci/biu131

Advance Access publication XX XXXX XXXX

regarding their reading habits, collaboration, and coauthoring, and their opinions on ideal and actual patterns of interaction between theorists and empiricists. Several free-form, open-ended questions also allowed the respondents an opportunity to express their views. In my discussion of the results, I emphasize three themes: (1) Substantial mistrust and tension exists between theorists and empiricists, but despite this, (2) there is an almost universal desire among ecologists and evolutionary biologists for closer interactions between theoretical and empirical work; however, (3) institutions such as journals, funding agencies, and universities often hinder such increased interactions, which points to a need for institutional reforms.

Survey design and administration

The survey was designed and administered using Google Forms (www.google.com/google-d-s/createforms.html). The full text of the survey is provided as supplement S1. At the beginning of the survey, the following definitions were provided:

By "empiricists" we mean researchers that do empirical work: fieldwork, lab work, or any other gathering of data from phenomena observed in the real world. By "theorists" we mean researchers that do theoretical work: mathematical models, numerical simulations, and other such work.

At the time the survey was posted, I was not affiliated with or funded by any institution, so no institutional human subjects protocol applied. To minimize possible concerns in this area, however, no strongly identifying information, such as the respondent's name, e-mail address, institution, or IP (Internet Protocol) address, was collected. The responses were, therefore, anonymous, except where the respondents chose to identify themselves; this anonymity had the side effect of preventing any check for multiple responses from the same individual, but multiple responses are very difficult to prevent in any case, and no duplicate responses were observed. To further protect anonymity, the order of responses to the free-form questions was randomized.

The survey was open from 12 October 2013 to 3 November 2013. I requested that it be publicized by a wide range of forums associated with ecology and evolutionary biology (supplemental table S1). No attempt was made to monitor which forums actually posted the survey.

Survey analysis

An analysis of the response data was conducted in R (version 3.0.0; R Foundation for Statistical Computing, Vienna, Austria). The responses for country names, career points, and scientific fields were standardized (e.g., "Britain" to "U.K."). Quotes from free-form responses were lightly edited for clarity. Unedited responses, and the R script used for the analysis, have been made available in the Dryad data repository (doi:10.5061/dryad.jh421); details regarding grouping and standardization of responses are contained in that script.

Two-sample Wilcoxon rank sum tests (also called Mann-Whitney tests; using the function wilcox.test in R) were used to test for differences between groups in the location of the distribution of quantitative responses (Everitt and Hothorn 2010); these tests were two sided in all cases. Randomization tests to calculate an approximate Pearson's chi-squared value were used to test for significance in the differences between groups in their responses to multiple-choice questions (using the function chisq_test in the R package coin, 10⁶ replicates). These randomization tests were conditional on row and column marginal totals; there is debate as to the correct method, but this choice was conservative since unconditional tests would provide smaller *p*-values (Agresti 2002).

Respondent demographics

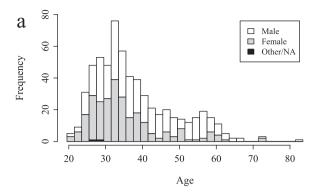
A total of 614 responses were obtained, spanning a broad demographic spectrum (figure 1). The respondents' ages ranged from 20 to 82 years; six of the respondents did not answer that question (mean = 37.6, median = 35.0, standard deviation = 10.7). The respondents designated their gender as "male" (350 respondents; 57%), "female" (260 respondents; 42%), or "other" (1 respondent); 3 respondents did not answer that question.

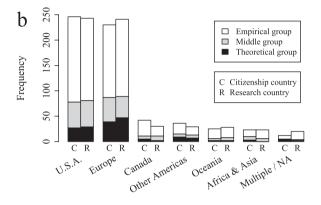
They were citizens of 45 countries (with 2 dual citizens and 10 blank responses): predominantly, the United States (247), Germany (49), Canada (43), the United Kingdom (28), and France (27); other countries were represented by fewer than 20 respondents. They reported performing research in 42 countries (with 5 dual-country researchers and 15 blank responses): predominantly, the United States (247), Germany (41), the United Kingdom (37), Canada (31), France (27), and Sweden (25); other countries were represented by fewer than 18 respondents. Of the respondents who specified countries of both citizenship and research, a majority (69.4%) conducted their research in their country of citizenship.

They were primarily students (5 undergraduate, 28 master's, 152 PhD), paid researchers (144 postdocs, 48 other types), and professors (87 untenured, 142 tenured, 2 emeritus); 6 did not fit into these categories. Overall, 206 (34%) worked in ecology, 161 (26%) in evolutionary biology, and 232 (38%) in both, with 11 (2%) in other areas of biology and 4 (1%) in nonbiology fields. The respondents also reported their specific subfields (not reported here).

Empirical work predominated, with 299 (49%) of the respondents doing "mostly empirical work" and 103 (17%) doing "exclusively empirical work"; these respondents are hereafter called the empirical group. By contrast, 50 (8%) "mostly" and 39 (6%) "exclusively" did theoretical work (the theoretical group). A total of 123 (20%) reported doing both roughly equally (the middle group).

Figure 1 illustrates these demographics and shows interactions between age and gender (figure 1a), between citizenship or research country and empirical or theoretical position (figure 1b), and between career position and overall field (figure 1c). Notably, the percentage of female respondents fell steadily with age, from 54% among those under





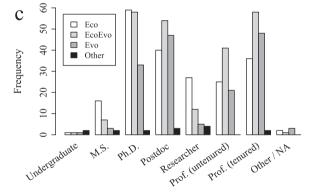


Figure 1. Respondent demographics. (a) Age distribution of the respondents. Note the decreasing representation of women with increasing age. (b) The country of citizenship and of research. The United States and Canada are grouped separately from the rest of the Americas because of the United States's size and Canada's obvious differences from Central and South America. Note the proportionately larger theoretical community in Europe, and the almost total absence of theorists in Canada, Oceania, Africa, and Asia. (c) Career stage. Note the greater focus on evolutionary ecology among postdocs and professors, and the greater focus on ecology among students and professional researchers. Abbreviations: Eco, researchers in ecology; EcoEvo, researchers in both ecology and evolutionary biology; Evo, researchers in evolutionary biology; NA, not applicable.

30, to 49% among those in their 30s, 27% of those in their 40s, and only 25% of those 50 and over—a pattern that has been attributed to a "leaky pipeline" in academia (Alper 1993, Blickenstaff 2005). Among the respondents, as a result, women accounted for 50% of the students and 53% of the postdoctoral researchers, but 40% of untenured professors and only 22% of tenured professors. Women were 43% of the respondents in both ecology and evolutionary biology but were not equally represented across research countries: 52% of the respondents in Africa and Asia, 50% in Oceania, 47% in Canada, 43% in the United States, 40% in Europe, and only 28% in Central and South America were female (and the results were similar for the citizenship country). Women were also unequally represented across the theoreticalempirical continuum: 29% of the theoretical group and 30% of the middle group were female, as compared with 49% of the empirical group.

Reading, collaboration, and coauthoring

Figure 2a shows the paper-reading habits of the respondents, for papers classified by the respondent as "primarily theoretical," "primarily empirical," and "roughly equal parts theoretical and empirical." Both the theoretical group and the empirical group reported reading more papers per week from their own group than from the other group, but this tendency was significantly more pronounced in the empirical group (Wilcoxon rank sum test on the differences between within-group and opposite-group papers read; empirical group, median = 2.9, n = 402; theoretical group, median = 0.5, n = 89; W = 28,650, p < .001). This does not necessarily represent greater bias on the part of empiricists, because there are probably fewer theoretical papers than empirical papers published each year (Scheiner 2013).

Figure 2b shows patterns of collaboration. The theoretical and empirical groups both reported having collaborated within their group more often than outside their group, but this tendency was significantly more pronounced in the empirical group, with 93% of theorists having collaborated with empiricists but only 60% of empiricists having collaborated with theorists (Wilcoxon rank sum test on the differences between within-group collaboration and oppositegroup collaboration; empirical group, median = 0, n = 402; theoretical group, median = 0, n = 89; W = 23,797, p < .001). Again, this does not necessarily represent greater bias among empiricists, because there are apparently fewer theorists than empiricists in ecology and evolutionary biology (figure 1b).

Figure 2c shows patterns of coauthorship. The theoretical and empirical groups both reported having coauthored papers with others within their group more often than with those outside their group, but again, this tendency was significantly more pronounced in the empirical group, with 78% of the theorists having coauthored with empiricists but only 42% of the empiricists having coauthored with theorists (Wilcoxon rank sum test on differences between within-group coauthorship and opposite-group coauthorship; empirical group, median = 1, n = 402; theoretical group, median = 0, n = 89; W = 24,493, p < .001). As before, this does not necessarily indicate greater bias among empiricists, given the relative scarcity of theorists.

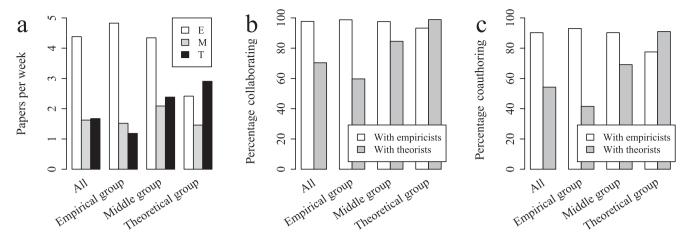


Figure 2. Reading, collaboration, and coauthorship. (a) The number of papers read per week of each of three types: primarily empirical (E), roughly equal parts theoretical and empirical (M), and primarily theoretical (T). (b) The percentage of the respondents reporting having collaborated with empiricists and with theorists. (c) The percentage reporting having coauthored at least one paper with an empiricist and with a theorist. The responses of the empirical and theoretical groups are significantly different in all panels (see the text).

Views on the interaction of theoretical and empirical work

A pair of questions explored two related concepts: how respondents believe that theoretical work and empirical work should interact, and how they actually do interact (figure 3). There was remarkable consensus regarding how they should interact, with a large majority of the empirical, middle, and theoretical groups all believing that, ideally, "theoretical work and empirical work would coexist tightly, driving each other in a continuing feedback loop" (figure 3a). The theoretical group was closer to unanimity, however, with 91% supporting this idea; no other choice received more than 4% of their vote. The empirical group showed 80% support for this idea; much of the rest (13%) believed that, ideally, "work would primarily be data-driven; theory would be developed in response to questions raised by empirical findings." The two groups were significantly different (randomization test, $\chi^2 = 11.16$, p = .027).

Much less consensus existed regarding how theoretical and empirical work actually interact in today's world, but the responses of the empirical group and the theoretical group were nevertheless remarkably similar (figure 3b). Across all respondents, a large plurality (47%) believed that theoretical and empirical work "coexist, but do not interact much," a somewhat smaller subset (26%) believed that empirical findings drive theoretical work, a smaller subset (18%) believed that the two "coexist tightly" in a "feedback loop," and still fewer (7%) believed that theoretical findings drive empirical work; no other choice received more than 1%. One striking difference did exist: A minority of the empirical group (8%) claimed a belief in the idea that theoretical findings presently drive empirical work, whereas not a single theorist shared that belief. The two groups were significantly different (randomization test, $\chi^2 = 14.11$, p = .034).

In summary, then, many believed that, in today's world, empirical and theoretical work coexist in separate, non-interacting realms or that empirical work largely drives the scientific process, but most respondents believed that in an ideal world theoretical and empirical work would be tightly bound in a continuing feedback loop. Small but significant minorities of the empiricists believed that empirical work ought to drive the process and that theorists presently drive the process; almost no theorists shared those beliefs.

Perceptions of attention, collaboration, and intimidation

A set of questions asked respondents for their opinions regarding whether theorists and empiricists pay attention to each other's findings, whether they would like to collaborate more but have difficulty doing so, whether each finds the other intimidating, and whether each skips over the technical sections of papers written by the other. All of these questions asked the respondents to rate given statements from "strongly agree" to "strongly disagree" (or "don't know"). These responses are shown in figure 4, including indications of statistical significance; some highlights are summarized here.

The divergence of worldviews between the empirical and theoretical groups was often striking. For example, a majority of the theorists agreed or strongly agreed that theorists generally "pay a lot of attention to empirical findings," but a substantial plurality of the empiricists disagreed or strongly disagreed that theorists do so. Conversely, the empiricists were split as to whether empiricists generally "pay a lot of attention to theoretical findings," but a majority of the theorists disagreed or strongly disagreed that empiricists do so. However, when they were asked about their own habits, a substantial majority of both groups agreed or strongly

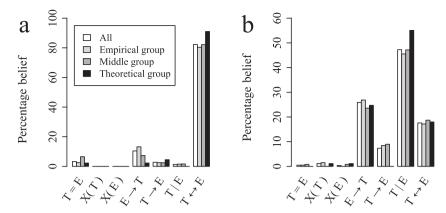


Figure 3. Views on the ideal and actual patterns of interaction between theoretical (T) and empirical (E) work, for all respondents and for the empirical, middle, and theoretical groups. (a) The percentage of respondents who agreed with each of seven statements regarding the ideal interaction pattern. Abbreviations: $E \rightarrow T$, theoretical work should be driven by empirical findings; T = E, the distinction between the two should not exist; $T \rightarrow E$, empirical work should be driven by theoretical predictions; $T \mid E$, the two should coexist without much interaction; $T \leftrightarrow E$, the two should coexist in a tight feedback loop; X(E), empirical work should not exist; X(T), theoretical work should not exist. (b) The percentage of respondents who agreed with each of seven statements regarding the actual interaction pattern. Abbreviations: $E \rightarrow T$, theoretical work is driven by empirical findings; T = E, the distinction between the two is meaningless: $T \rightarrow E$, empirical work is driven by theoretical predictions: $T \mid E$, the two coexist without much interaction; $T \leftrightarrow E$, the two coexist in a tight feedback loop; X(E), empirical work is worthless/pointless; X(T), theoretical work is worthless/pointless. The exact wording of all statements is given in the full survey text (see supplement S1, questions 18 and 19). The responses of the empirical and theoretical groups were significantly different in both panels (see the text).

agreed that they themselves pay a lot of attention to both empirical and theoretical findings.

Close to or more than a majority of the respondents in each group agreed or strongly agreed that many empiricists would like to collaborate with theorists but have trouble making that connection, and a plurality of empiricists agreed that this is the case for them personally. A majority of the theorists also agreed or strongly agreed that many theorists would like to collaborate with empiricists but are unable to connect (although few felt this way about their own collaborations); few of the empiricists agreed or strongly agreed with this, however, and a plurality stated that they did not know

Few respondents, among both the theorists and the empiricists, agreed or strongly agreed that theorists find empirical methods "intimidating and/or obscure," but a large majority of both groups agreed or strongly agreed that empiricists find theoretical methods to be so. The idea that empiricists often find theoretical methods difficult was supported by the respondents' own feelings about empirical and theoretical methods.

When the empiricists read empirical papers and when the theorists read theoretical papers, a large majority of both groups disagreed or strongly disagreed that they skip over technical sections (materials and methods in empirical papers, formulas and model descriptions in theoretical papers). However, close to half of both groups agreed or strongly agreed that they skip technical sections in papers from the other group. The respondents from both groups knew that empiricists often skip theoretical technical sections, but many of the empiricists seemed not to know that theorists often skip empirical technical sections.

Good interactions between theoretical and empirical work

A free-form question regarding examples of good interactions between theoretical and empirical work received 157 responses. Many of these responses included citations of papers (100 papers in all); those citations are provided in the online data (doi:10.5061/dryad.jh421) in several citation file formats. Many responses also named specific researchers who the respondent felt had done a good job of integrating theoretical and empirical approaches through a substantial portion of their career (box 1). All of the responses are available in the online Dryad data; here are a few selected quotes regarding good interactions:

In my opinion good interactions are more likely if the project integrates theory and empirical work from an early stage.

No theoretician should be satisfied with an untested model, and no empiricist should be satisfied with a pattern without an underlying model to explain the pattern.

The thing that connects the best examples is that the researchers are thoughtful, and prioritize really *wanting to know* over politics or preconceptions.

Bad interactions between theoretical and empirical work

Another free-form question, regarding examples of bad interactions between theoretical and empirical work, received 102 responses. Here are a few selected responses regarding bad interactions:

I don't like when empiricists wrap up their work in an existing theory/big theoretical question to make it look sexier, even though their work is actually poorly related to this theory, or the links between theory and experiment are not convincingly drawn.

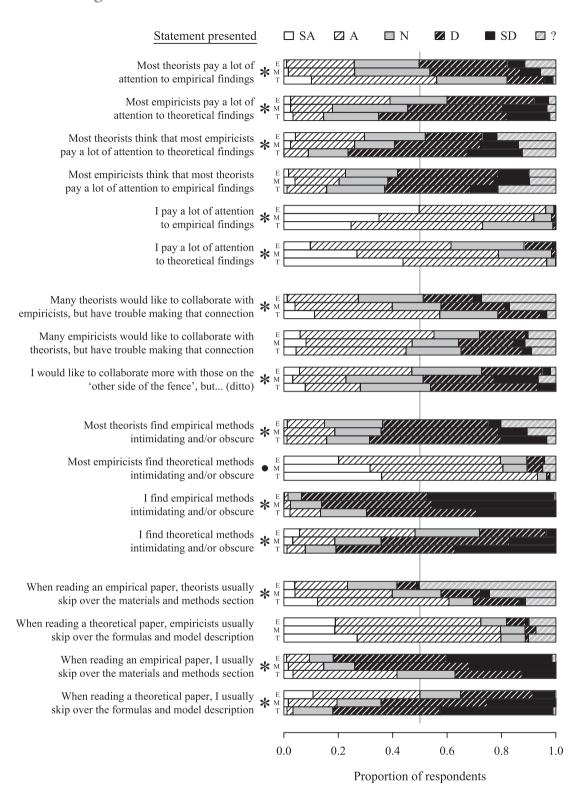


Figure 4. Degrees of agreement or disagreement with statements about attention, collaboration, and intimidation. For each statement, three stacked bars are shown, representing, from top to bottom, responses from the empirical (E), middle (M), and theoretical (T) groups. Each stacked bar shows the proportion of respondents in the depicted group that expressed a given reaction to the statement: "strongly agree" (SA), "agree" (A), "neutral" (N), "disagree" (D), "strongly disagree" (SD), or "don't know" (?); all segments in each stacked bar therefore add up to 1.0. The center line is drawn at 0.5, as an easy way to see whether a majority of the respondents agreed with each statement. The statistical significance of the difference between the empirical and theoretical groups (excluding the middle group from the tests) was determined using randomization tests (see the "Survey analysis" section). *p < .001. •p = .0091. All others, p > 0.05. The Bonferroni-corrected significance threshold across these tests was 0.00294.

Box 1. Individual researchers named by respondents as exemplifying a good interaction between theoretical and empirical work through a substantial portion of their career.

Nick Barton	Hanna Kokko	Mike Fowler	André de Roos
Pitr Bijma	Richard Lenski	Andrew Gonzalez	Russell Lande
Ottar Bjørnstad	Elena Litchman	Charles Goodnight	Dolph Schluter
Butch Brodie	Curtis Lively	Jeff Gore	Maria Servedio
Joel Brown	Michael Lynch	Bryan Grenfell	Dan Simberloff
Bryan Carsten	Robert MacArthur	Nelson Hairston	Elliott Sober
Robert Costantino	Ed McCauley	Bill Hamilton	David Tilman
Jean-Louis Deneubourg	Joel McGlothlin	Ilkka Hanski	Peter Turchin
Michael Desai	Belinda Medlyn	Jef Huisman	Michael Turelli
Robert Desharnais	Allen Moore	G. E. Hutchinson	David Vasseur
Theodosius Dobzhansky	William Muir	Tony Ives	Michael Wade
Greg Dwyer	William Murdoch	Dan Janzen	David Wilson
Steve Ellner	Scott O'Neill	Bruce Kendall	Edward O. Wilson
Laurent Excoffier	William Nelson	Matt Keeling	Jason Wolf
Joe Felsenstein	Allen Orr	Aaron King	Simon Wood
Matt Ferrari	Sally Otto	Mark Kirkpatrick	Sewall Wright
Ben Fitzpatrick	Lennart Persson	Chris Klausmeier	
Richard Forman	Owen Petchey	Andrew Read	

I have often read theoretical papers that are so arcane as to leave them entirely useless for empiricists. By arcane, I do not mean that the models are too complicated to be understood, but rather that they are so far removed from reality as to leave them largely untestable.

Theorists are not just consultants to help empiricists with the fiddly details of models to mathematically show what the empiricist already knows.

Theoreticians thinking they have the answer to all biological problems and that empiricists are just servants that produce data for them.

Other thoughts

A third free-form question, regarding other thoughts that the respondents might have about how theoretical and empirical work can, should, or do interact, received 113 responses. The responses to this open-ended question were particularly difficult to distill. A few thought-provoking responses are reproduced below:

Theoreticians sometimes struggle if they have limited biology in their background.

I feel like a big part of the divide comes from empirical ecologists who don't take time out to consider models

or theoretical work . . . Training courses or workshops where theorists could explain their models to empiricists and talk about crossover would help I think.

Many interactions between theorists and empiricists are hampered because they do not understand the purpose of each other.

It would be great if theorists had on-call empiricists, and vice-versa.

Institutional effects

In the free-form responses to the previous three questions, the respondents also raised issues regarding the role that institutions play in the interaction between theoretical and empirical work. Several of the respondents discussed the role of journals:

I think [papers at the interface of theory and empirical work] are more difficult to get through peer review because of the higher frequency of mostly empirical researchers and because such papers have to please a wider audience of peer reviewers.

It would be nice if editors were more awed by work that actually connects models and empirical work.

Papers published in journals totally oriented towards theory in reality are not followed by people conducting

empirical research; it could be important to change the philosophy of these journals.

Similarly, several respondents cited issues with obtaining funding for cross-boundary work:

Especially in ecology & evolution, where everything varies all the time, theory needs to be tested in multiple systems, in multiple contexts. However, the U.S. funding system and the global publication system does not reward this.

I think that most funding is awarded to strictly empirical projects which emphasize study system and organism. Theoretical funding is really hard to get unless you are at the very top of your field. Requests for funding for work at the interface of theory and empirical data collection, like papers, has to please a very broad audience and is hard to get.

Funding agencies should give extra points for explicit collaborations and explicit inclusion of both approaches in a grant.

The respondents also called attention to problems caused by universities-particularly, inadequate teaching and polarized faculties:

More professors from the 'two sides' . . . should join together to co-teach graduate classes.

It would be extremely nice to have somebody in the department who knew theory and could combine it with empirical work.

Both need training to appreciate each others work. Ecology/evolution programs need better quantitative training. Theorists need experiences with empiricists to understand difficulties/limitations of data collection. This has been paid lip service for a long time, but it really needs to happen.

The respondents mentioned a few institutions (the National Center for Ecological Analysis and Synthesis, the National Evolutionary Synthesis Center, and the Bering Sea Integrated Ecosystem Research Program) and a few journals (Ecology, Trends in Ecology and Evolution, and The American Naturalist) that promote good interactions between theorists and empiricists.

Survey problems

The final free-form question, regarding difficulties with the survey itself, received 155 responses, many of which (approximately 66) expressed a positive view of the survey and its accuracy in capturing the respondent's opinions, but many of which did not. The responses often questioned the definitions of "theoretical" and "empirical" used (or the assumption that such a dichotomy exists), objected to being asked what a particular group thinks or feels, objected to

the stark alternatives provided in multiple-choice questions, or stated that the survey was biased. In particular, many respondents felt that question 21, regarding difficulties in establishing collaborations, was worded ambiguously; it might therefore be best to discount those results.

Interactions with age, gender, career stage, and overall field

The interactions between the results presented and the demographic variables of age, gender, career stage, and overall field (ecology, evolutionary biology, or both) were generally small. In particular, gender, age, and career stage had little effect; the conclusions inferred here are, therefore, robust across demographic subsets. The conclusions inferred here are also robust for ecologists and for evolutionary biologists, analyzed individually; however, small differences did exist between these two groups (see the "Related work" section below).

Implications and discussion

Three main themes emerged from the results of this survey. First, the worldviews of the theorists and the empiricists had areas of strong divergence. Both groups tended toward insularity in their reading habits and their collaborations, and the empiricists seemed particularly isolated from theoretical work. A plurality of each group believed that the other group ignored their work. Some of the theorists felt that empiricists perceived them as "consultants" to "help empiricists with the fiddly details," whereas some of the empiricists felt that theorists perceived them as "servants to produce data for them." These results do not indicate a healthy relationship.

Second, despite these areas of divergence, there are areas of overlap and agreement that provide cause for optimism. One thing I found particularly heartening, in conducting this survey, was that many respondents named colleagues who exemplified a good balance between theoretical and empirical approaches, even though the survey did not explicitly ask them to do so. Another encouraging fact is that 82% of the respondents felt that theoretical and empirical work should "coexist tightly", even though only 18% felt that they "coexist tightly" in today's world.

Third, many of the respondents stated that institutions in ecology and evolutionary biology-journals, funding agencies, and universities—do not help empirical and theoretical researchers to interact productively; indeed, these institutions often hinder such interactions. Journals are often focused exclusively on either theoretical or empirical work, which encourages isolationism, and research that bridges the gap is harder to get through peer review because it has to satisfy both audiences. This criticism also seems to apply to conferences, where separate theoretical and empirical sessions encourage theorists and empiricists to avoid interactions even when working on the same scientific questions. Funding agencies also discourage work at the interface; programs specifically aimed at promoting such research do not exist, and such research has to please reviewers in both groups. Universities do not encourage coteaching by empiricists and theorists and often neglect training in theory for empiricists entirely, whereas theorists often come from physics or mathematics and receive little or no empirical training. University faculties often do not have a balanced mix of empiricists and theorists, which deprives students (and themselves) of opportunities for interaction.

Related work

A number of previous papers have raised related issues regarding the interaction of theoretical and empirical approaches. A comparison of the results presented here with that previous work is fruitful; I will briefly discuss three particularly relevant examples here.

Kareiva (1989) provides the earliest paper I have found in which these issues are discussed at length. Twenty-five years have passed since its publication, and so it is striking that Kareiva's (1989) statement that "experimental ecology and theoretical ecology are developing as almost separate fields and both pursuits suffer as a result" (p. 68) seems to ring true for so many—even today (figure 3). Many of the specific issues raised by Kareiva (1989)—a lack of constructive dialogue, PhD training that neglects the theoretical-empirical interface, theoretical models that are too removed from reality to be useful, empirical studies that ignore relevant theory—were also raised by many of the respondents to this survey. For a more in-depth discussion of the problems raised here, Kareiva's paper is an excellent resource, because (unfortunately) little seems to have changed during the intervening years.

Fawcett and Higginson (2012) explored a specific aspect of the theoretical-empirical interaction: the effect of mathematical equations in a paper on the paper's tendency to be cited. They found that papers with many equations tended to be cited somewhat more frequently in theoretical papers but much less frequently in empirical papers; there was thus an overall decrease of 28% in the citation count for each additional equation per page in the main text of a paper. This provides quantitative evidence in support of the present survey's results: Empiricists read relatively few theoretical papers (figure 2a), find theoretical methods intimidating and/or obscure (figure 4), and often skip over formulas and model details when they read theoretical papers (figure 4). As Fawcett and Higginson (2012) discussed, there are ways in which theorists might make their work more accessible but because theory is fundamentally mathematical in nature, there is also a need for better training in quantitative methods for empiricists, as many of the survey respondents observed.

Finally, Scheiner (2013) conducted a quantitative investigation of the theoretical underpinnings of articles published in three prominent journals, and found that theoretical and empirical approaches are less integrated in ecology than in evolutionary biology. Survey results analyzed separately for ecologists and for evolutionary biologists (not presented here) indicated that empiricists in ecology collaborate and coauthor with theorists less frequently than do empiricists in evolutionary biology. Ecologists also more

frequently believe that empirical work should drive research or that theoretical and empirical work ought to be separate, whereas evolutionary biologists more frequently believe that theoretical and empirical work should interact tightly or that the two should be considered the same. Similar differences were observed in the responses to many other questions. These differences were small; nevertheless, these results both support the findings of Scheiner (2013) and suggest some underlying causal mechanisms driving the difference that he observed.

Conclusions

Overall, these results convey a very clear message: Theorists and empiricists often interact poorly (if at all), and yet, there is overwhelming agreement that theorists and empiricists should interact closely. Notably, many of the respondents felt that this problem was exacerbated by institutions such as journals, funding agencies, and universities, which often specifically discourage interaction. In addition to suggesting that individuals might work toward improved interactions, then, these results also provide a clear mandate for institutional changes to promote increased interaction between theorists and empiricists.

I have seen little discussion of this institutional aspect of the problem, and yet, such institutional changes seem relatively tractable. Journal editorial policies, conference schedules, funding decisions, university hires, and other institutional decisions are often controlled by just a handful of individuals—individuals who probably, like almost all of the respondents to this survey, would like to see a closer interaction between theoretical and empirical approaches. Changes to institutional practices seem more likely to bear fruit than expecting individual scientists to altruistically change their behavior in the face of institutional incentives that often specifically discourage stronger interactions. Once institutional changes have been made that provide better incentives for interaction, a shift in individual behavior should follow.

By raising such issues and ideas, I hope that this article initiates a constructive discussion about achieving better interactions and, ultimately, better science.

Acknowledgments

Thanks to Daniel I. Bolnick, Kiyoko M. Gotanda, Lisa Jacquin, and Felipe Pérez-Jvostov for comments on the survey design. Thanks to Andrew P. Hendry, Maria R. Servedio, Tadeas Priklopil, Philip N. Cohen, and three anonymous reviewers for comments on a previous version of this manuscript. Thanks also to all of the institutions and groups that posted the survey, and to the many individuals who took the time to respond to it.

Supplemental material

The supplemental material is available online at http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biu131/-/DC1.

References cited

- Agresti A. 2002. Categorical Data Analysis, 2nd ed. Wiley.
- Alper J. 1993. The pipeline is leaking women all the way along. Science 260:
- Bailer-Jones D. 2009. Scientific Models in Philosophy of Science. University of Pittsburgh Press.
- Belovsky GE, et al. 2004. Ten suggestions to strengthen the science of ecology. BioScience 54: 345-351.
- Blickenstaff JC. 2005. Women and science careers: Leaky pipeline or gender filter? Gender and Education 17: 369-386.
- Cadotte MW, Mehrkens LR, Menge DNL. 2012. Gauging the impact of meta-analysis on ecology. Evolutionary Ecology 26: 1153-1167.
- Callebaut W. 2013. Naturalizing theorizing: Beyond a theory of biological theories. Biological Theory 7: 413-429.
- Choate DM, Prather CM, Michel MJ, Baldridge AK, Barnes MA, Hoekman D, Patrick CJ, Rüegg J, Crowl TA. 2012. Integrating theoretical components: A graphical model for graduate students and researchers. BioScience 62: 594-602.
- Colyvan M. 2011. A philosopher's view of theory: A response to Gorelick. Ideas in Ecology and Evolution 4: 11-13.
- Colyvan M, Ginzburg LR. 2003. Laws of nature and laws of ecology. Oikos 101: 649-653.
- Ellner S. 2006. How to write a theoretical ecology paper that people will cite. Cornell University. (10 June 2014; www.eeb.cornell.edu/Ellner/ CitedPapers.pdf)
- Everitt BS, Hothorn T. 2010. A Handbook of Statistical Analyses Using R. CRC Press.
- Fawcett TW, Higginson AD. 2012. Heavy use of equations impedes communication among biologists. Proceedings of the National Academy of Sciences of the United States of America 109: 11735–11739.
- Gorelick R. 2011. What is theory? Ideas in Ecology and Evolution 4:
- -. 2012. Theory may not be definable and its development is not efficient. Ideas in Ecology and Evolution 5: 25-26.
- Griesemer J. 2012. Formalization and the meaning of "theory" in the inexact biological sciences. Biological Theory 7: 298–310.
- Grimm V. 1994. Mathematical models and understanding in ecology. Ecological Modelling 75-76: 641-651.

- Hall CAS. 1991. An idiosyncratic assessment of the role of mathematical models in environmental sciences. Environment International 17: 507-517.
- Kareiva P. 1989. Renewing the dialogue between theory and experiments in population ecology. Pages 68-88 in Roughgarden J, May RM, Levin SA, eds. Perspectives in Ecological Theory. Princeton University Press.
- Lawton JH. 1999. Are there general laws in ecology? Oikos 84: 177-192.
- Lindenmayer DB, Likens GE. 2011. Losing the culture of ecology. Bulletin of the Ecological Society of America 92: 245.
- Lindenmayer DB, et al. 2012. Value of long-term ecological studies. Austral Ecology 37: 745-757.
- Matzek V, Covino J, Funk J, Saunders M. 2014. Closing the knowing-doing gap in invasive plant management: Accessibility and interdisciplinarity of scientific research. Conservation Letters 7: 208-215.
- Noss RF. 1996. The naturalists are dying off. Conservation Biology 10: 1-3.
- Odenbaugh J. 2005. Idealized, inaccurate but successful: A pragmatic approach to evaluating models in theoretical ecology. Biology and Philosophy 20: 231-255.
- Pickett STA, Kolasa J, Jones CG. 2010. Ecological Understanding: The Nature of Theory and the Theory of Nature. Academic Press.
- Pigliucci M. 2013. On the different ways of "doing theory" in biology. Biological Theory 7: 287-297.
- Roughgarden J. 2009. Is there a general theory of community ecology? Biology and Philosophy 24: 521-529.
- Scheiner SM. 2012. The multiple roles of theory: A reply to Gorelick. Ideas in Ecology and Evolution 5: 22-24.
- 2013. The ecological literature, an idea-free distribution. Ecology Letters 16: 1421-1423.
- Scheiner SM, Willig MR. 2008. A general theory of ecology. Theoretical Ecology 1: 21-28.
- Watt KEF. 1962. Use of mathematics in population ecology. Annual Review of Entomology 7: 243-260.

Benjamin C. Haller (benhaller@benhaller.com) was affiliated with McGill University, in Montreal, Québec, Canada, during some of the work on the present article