Theory Meets Empiry: A Citation Network Analysis

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According to a recent survey, ecologists and evolutionary biologists feel that theoretical and empirical research should coexist in a tight feedback loop but believe that the two domains actually interact very little. We evaluate this perception using a citation network analysis for two data sets, representing the literature on sexual selection and speciation. Overall, 54%–60% of citations come from a paper's own category, whereas 17%–23% are citations across categories. These cross-citations tend to focus on highly cited papers, and we observe a positive correlation between the numbers of citations a study receives within and across categories. We find evidence that reviews can function as integrators between the two literatures, argue that theoretical models are analogous to specific empirical study systems, and complement our analyses by studying a cocitation network. We conclude that theoretical and empirical research are more tightly connected than generally thought but that avenues exist to further increase this integration.

Keywords: science of science, sexual selection, speciation, citation network, theory

The ideal: A union between "theory" and "empiry"

Lasting advances in evolutionary biology and ecology often emerge from the complementarity of theoretical and empirical perspectives. Theoretical models use mathematics as a tool to formalize hypotheses, thereby distilling biological complexity down to the components that are thought to be most significant. Models can also increase our understanding of processes that are obscured because they happened in deep time or because they span many human generations, and can unify observations across diverse groups of organisms.

Of course, theoretical biology is only meaningful in so far as it relates—even if only as an abstraction—to real, observable phenomena. Empirical observations and experiments are essential to provide a foundation of realistic assumptions that can form the basis of theoretical studies. Likewise, controlled empirical experiments (analogous to the formal precision of theoretical research) tease signal from noise to identify the real drivers of biological processes. That is, the theoretical and the empirical approach each yields unique insights, and the integration of both is required for a full understanding of any biological phenomenon.

Because the word "theory" is used in a variety of ways across disciplines—and even within disciplines—it is worth specifying our usage of the word. We are using the word theory in what has become its contemporary meaning within the fields of ecology and evolutionary biology. That is, we focus on the type of research that uses mathematics or computer simulations to represent and investigate biological processes.

Indeed, the synergy between theoretical and empirical approaches ("theory" and "empiry"; we coopt the latter word from German) has a long history in ecology and evolutionary biology, which runs the gamut from productive and agreeable cooperation to an uneasy marriage fraught with rivalry and conflict. For example, Darwin's empirical observations and verbal models gave way to mathematical formulations by Fisher (1930), Haldane (1932), and Wright (1932), which, in turn, have inspired decades of empirical research. In the study of sexual selection, the classical empirical and theoretical literature made equally important contributions to a concrete understanding of how competition for mates shapes extravagant phenotypes (see Bennet 2000 for communication between them that is both productive and contentious). Thus, both theory and empiry are involved in the testing of hypotheses (Servedio et al. 2014). Theory's role is to make sure that hypotheses, especially complex ones, are logically consistent (i.e., what follows logically from a set of assumptions), whereas empiry tests whether they adequately explain nature.

A recent survey confirms that ecologists and evolutionary biologists share the view that integration should exist between theoretical and empirical research (Haller 2014). An overwhelming majority of both self-identified

BioScience 68: 805–812.
doi:10.1093/biosci/biy083 Advance Access publication 22 August 2018

theoreticians and self-identified empiricists reported that they believe theoretical and empirical work should "coexist in a tight feedback loop" (Haller 2014), with each one informing the other. However, results from this same study suggest that the community perceives a collective failure to achieve its reported ideal. Although a small minority believe theory and empiry already coexist in a feedback loop, most reported that they believe the two approaches interact very little. This disconnect between the shared ideal (theory and empiry should be integrated) and the shared perception of reality (an absence of that integration) invites further investigation.

Reality check: A citation network analysis

A quantifiable—though obviously incomplete—metric of communication among scientists is provided by citations between published articles. Here, we quantify the connections between theoretical and empirical research by means of a citation network analysis. By way of example, we focus on a specific area of research that has an established history of drawing from both theoretical and empirical approaches: the literature on sexual selection and its relationship to speciation. We started out by generating two data sets: one that represents a sample of the general sexual-selection literature since the 1970s (SS), and a second one, more narrowly defined and more complete, that reflects the increasing interest in sexual selection and speciation over the past 20 years (SS and S). A detailed description of our sampling approach and other methods is provided in supplemental appendix S1. We then assigned all papers in the two data sets to one of four categories: empirical (E), theoretical (T), mixed (M), and reviews and ideas (R); for detailed definitions, see supplemental appendix S1. Finally, we constructed citation networks, in which nodes stand for published papers and directed links represent citations going from a cited paper (the "source") to the citing paper (the "target"; again, see supplemental appendix S1).

Basic results

In both data sets, the number of citations received by individual papers—both locally (i.e., within the coded network) and globally (numbers taken directly from Web of Science; see supplemental appendix 2 for some results from the global network)—is heavily biased toward a relatively small number of highly cited papers (supplemental figures S2 and S3). Although R papers tend to get more citations than both E and T papers, overall median citation numbers do not differ strongly between the three types. In particular, T papers receive at least as many citations as E papers (and, as we shall see below, a large proportion of their citations comes from empirical studies). These results do not change qualitatively when citation numbers are calculated on a per-year basis (results not shown). Basic citation patterns within and between categories are visualized in figure 1 and summarized by the following dyadic citation frequencies (see supplemental appendix S1 for details of the calculation).

Empiry. Of all citations in the coded Sexual Selection (SS) network made by E articles, the majority (54%) were of other E articles, whereas 22% were of R articles, and 20% were of T articles. Citations in the Sexual Selection and Speciation (SS and S) network by empirical research were distributed similarly: 59% were of other E articles, 23% were of R articles, and 17% were of T articles.

Review. Citation frequencies by R papers were more evenly distributed across article types as compared with citation frequencies by E and T papers. Of all citations in the SS network made by R papers, 40% were of E articles, 33% were of other R papers and 24% were of T articles. A similar pattern was found in the SS and S data set; of the citations made by R papers, 48% were of E articles, 23% were of other R papers, and 28% were of T articles (see supplemental table S1 and figure 1 for full summary of dyadic citation frequencies).

Theory. Of all citations in the SS network made by T papers, the majority (56%) were of other T articles, whereas 21% were of R articles and 19% were of E articles. A similar pattern was found in the SS and S data set; of the citations made by T papers, 59% were of other T papers, 17% were of R papers, and 23% were of E articles.

Mixed. Of all citations in the SS network made by M papers, 33% were of E articles, whereas 24% were of R articles and 32% were of T articles. In the SS and S data set 42% of the citations made by M papers were of E papers, whereas 28% of the citations were allocated both to T and R papers.

The above frequencies differ somewhat from year to year, but we found no clear trends over time (supplemental figure S4), the only exception being E to E citations that increase over time, reflecting the overall increase in the number of published empirical studies (see supplemental figure S1).

Seven hypotheses about citation patterns

Citations within and between theoretical and empirical studies might be influenced by a number of causal factors, which might, in turn, generate a number of patterns. In the following, we discuss these as a set of nonmutually exclusive hypotheses and put them forward as potential explanations, although not necessarily as an exhaustive list (see table 1).

The lack-of-integration hypothesis. The first hypothesis states that researchers cite primarily within their own category, such that empiry cites mostly empiry and theory cites mostly theory. This is the hypothesis that most closely reflects the perception reported by Haller (2014). Indeed, our results are consistent with this prediction (figure 1). However, this pattern is perhaps not surprising; some degree of increased citation frequency within-category should be expected, pointing to a question that, although at the heart of our study, is subjective and therefore empirically unanswerable. That is, what level of citation between categories reflects an ideal integration? We do not propose to have an answer to that

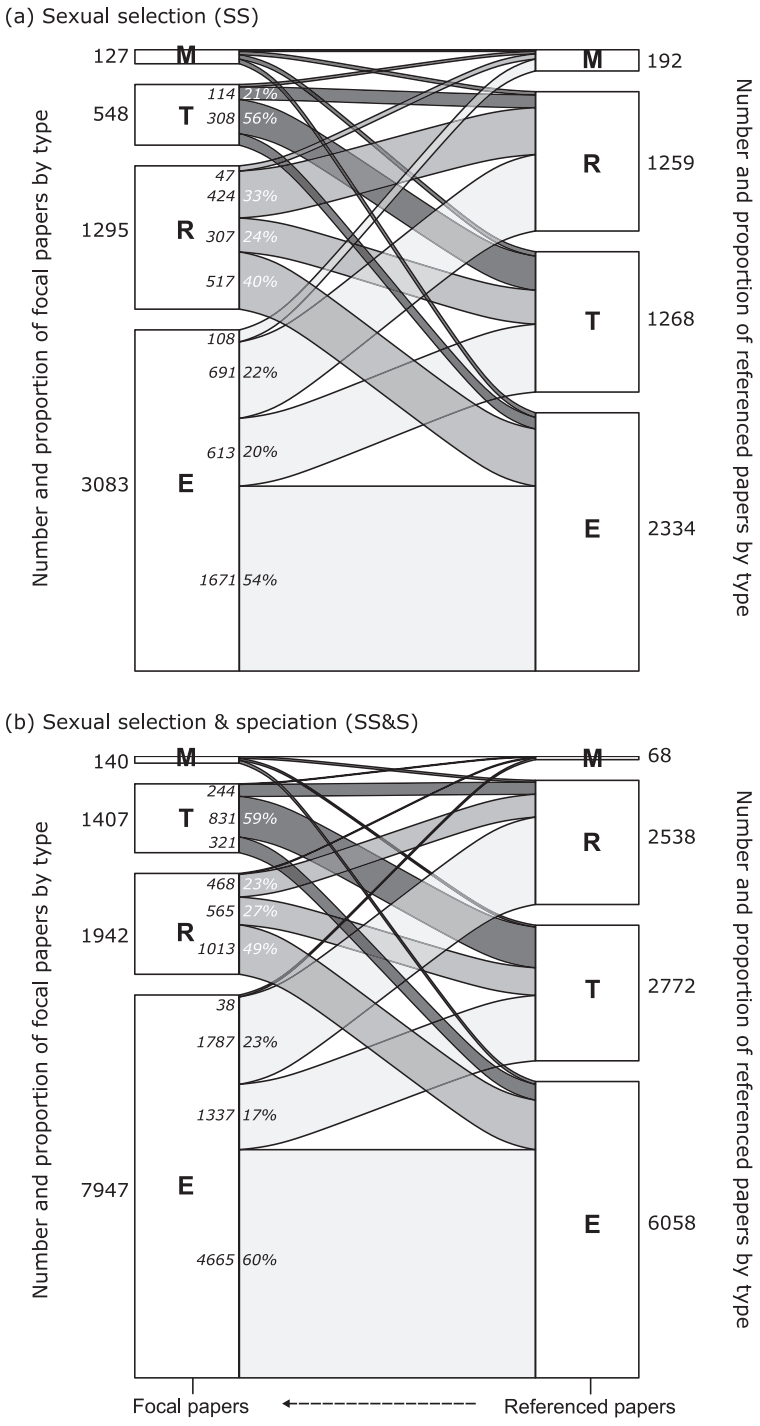

Figure 1. Citation patterns for the different types of papers (E, empirical; R, review; T, theory; M, mixed), for the (a) sexual selection (SS) and (b) sexual selection and speciation (SS and S) data sets. The figure shows the answers to the question, "Which types of papers are papers of each category citing?" The vertical white boxes are scaled by the proportion of papers by type for the papers that cite (targets) and the papers that are cited (source) in the coded network. The size of the ties that flow between these categories are proportional to the total number of citations made by a given type of paper (i.e., the four ties that flow from each white box sum to 100% of the citations made by that category type, and all 16 ties in the whole plot show 100% of total citations made in our coded network). The numbers in the margins indicate the total number of citations made by category, the italicized numbers within the target paper boxes indicate the number of citations made by papers of each type cited in each type of paper, and the major links are labeled with the percentage of total citations for each paper type. For example, in the SS data (a), there were 3083 citations made by empirical papers, and of these citations, 1671, or 54%, referenced other empirical papers. Note that not all the links are labeled; see table S1 for all values.

Table 1. Possible patterns of citation behavior. All scenarios hypothesize citation patterns within and between theory and empiry except for scenario v, which posits a role for review articles.

i	Researchers cite primarily within their own category (Haller 2014).
ii	Researchers cite each category (theory versus empiry) in proportion to its frequency in the literature (null hypothesis).
iii	Citation frequency is driven by the size of research community (size-of-community hypothesis).
iv	Theory functions analogously to a specific taxonomic study system in its citation patterns (theory-as-system hypothesis).
v	Reviews are cited in lieu of primary literature across categories (reviews-as-proxies hypothesis).
vi	Citations between categories are concentrated among a small number of publications (concentrated-cross-citation hypothesis).
vii	Influential papers in one category are likely to transcend category and be highly influential in the other (transcendence-of-influence hypothesis).

question and instead will discuss our results in the context of additional factors (hypotheses ii–vii) that have the potential to influence observed citation patterns. Subsequently, we add some insights gleaned from a cocitation network analysis, and close by highlighting both the ways that theory and empiry "talk" to each other as well as the ways in which that communication might be enhanced.

The null expectation hypothesis. Researchers might cite in proportion to the frequency of papers from each category in the literature. This represents something of a null hypothesis and predicts, for instance, that if 70% of published papers are empirical (as in the SS data set), then 70% of citations from both theory and empiry would be of empirical research. However, this is not what we found in our data sets. Although there is no a priori reason to view the null hypothesis as a reasonable expectation, one especially marked deviation merits discussion: the citations made by the theoretical literature. That is, theory cited theory at a substantially higher rate than it appeared in the literature and empiry at a lower rate than it appeared in the literature. Although this is, of course, consistent with hypothesis i, two other potential explanations are given by the size-of-the-community and the theory-as-system hypotheses, which we discuss next.

The size-of-the-community hypothesis. Citation patterns might be influenced by the size of the research community. In particular, smaller communities might be more able to cite their own type exhaustively, because the number of papers is not overwhelming. In this scenario, citing exhaustively within a smaller community is feasible, and omitted citations are more noticeable. Because theoretical biology is a smaller community than empirical biology (as reflected by the difference between the number of theoretical and empirical papers in our data set), this hypothesis predicts that theory would cite theory at higher rates than it is represented in the literature. Indeed, this pattern is what we found.

Moreover, the theory-biased citation pattern within theoretical research might result not only from the effect of working within a smaller community but also from an interaction between disparity in abundance (empiry is represented more heavily than theory) and familiarity (theoreticians are more familiar with theory and empiricists with empiry). In this scenario, theoretical biologists are presented with a double obstacle: Not only do they, like empiricists, face the challenge of learning material that is outside their area of expertise, but also the unfamiliar body of literature (empiry) for theoreticians is many times larger than the unfamiliar body of literature (theory) for empiricists. This might effectively create a higher threshold for theoretical biologists than empiricists when it comes to learning enough about the other approach to reference it comprehensively. Here, there would seem to be a great opportunity for reviews of the empirical literature in an effort to invite theoretical treatment of contemporary empirical patterns or puzzles (see below for further discussion of how reviews might facilitate integration).

The theory-as-system hypothesis. Another potential explanation for the theory-biased citations by theory might be that theoretical approaches to a given research question are similar to work on that question in a specific empirical system. From this perspective, theory is analogous to research within a unique study system such as *Drosophila* or sticklebacks. Although these research communities employ specific biological systems to examine a range of broader research questions, a given study will necessarily cite other research from that same system at a disproportionate rate in order to provide appropriate background and context for the specific work being presented. Extending this analogy, theoretical papers may cite other theoretical papers disproportionately.

Indeed, of all the citations made by cichlid papers in the coded SS and S network, 68% were of other cichlid papers (1808 out of 2650). For the three other most frequently studied systems in that data set, approximately 40% of the citations were from the same system (*Drosophila*, 228 of 538 citations; sticklebacks, 217 of 516 citations; *Heliconius*, 48 of 121 citations; see supplemental appendix S1 for details). These percentages are similar to the 56% (SS) and 59% (SS and S) at which T papers cited other T papers in our data sets and are consistent with the idea that the specialization of a paper, whether on study system or methodology, means that a disproportionate number of the citations (around 50%) will be of papers with the same specialization.

The reviews-as-proxies hypothesis. Researchers from each of the two main categories (empiry and theory) might use reviews as proxies for the primary literature from the other one. In other words, empiry might cite reviews of theory *in lieu* of theory itself and vice versa. To investigate this hypothesis, we analyzed "indirect citation networks" in which papers are linked when one is cited by a review that is cited by the other paper (see supplemental appendix S1). We found that reviews cited by E papers cite a higher proportion of T papers than E papers cite themselves, and R papers cited by T papers likewise cite a higher proportion of E papers than T papers cite themselves. As a consequence, patterns of indirect citations (citations by R papers that are cited either by E or T papers) differ less between types of target papers than do patterns of direct citations. Furthermore, T papers are overrepresented in indirect citations relative to their frequency in both data sets (see supplemental figure S5 for full comparisons).

The above analysis provides some support for the idea that both empirical and theoretical studies cite reviews in lieu of original articles. Indeed, the purpose of a review is to consolidate information. Theory, in particular, might be more likely to cite reviews than the original empirical articles for the reasons outlined above (see the size-of-the-community and the theory-as-systems hypotheses), but also because they highlight broad patterns that emerge from many individual studies. If the primary goal of theoretical studies is to investigate the processes that give rise to general patterns, review articles may provide better context than individual empirical studies because effective reviews summarize the broad patterns that are collectively demonstrated by empirical studies. Indeed, indirect citations of empirical work by theoretical studies were closer to the distribution expected under hypothesis ii (i.e., the representation in the literature), and the disparity between theoretical citations of theory and empiry was reduced. This analysis is consistent with the idea that reviews may function to integrate the theoretical and empirical domains by grouping relevant pieces of research together, which may, in turn, convert an unmanageable task (learning a large body of unfamiliar literature by reading each incremental contribution) into a manageable one. This hypothesis is further supported by our finding that, of all the categories of papers, reviews are globally cited most frequently (see the top panels of supplemental figures S2 and S3). Finally, the results from the co-citation network analysis presented below suggest that, especially in the SS data set, reviews often bridge otherwise disconnected groups of literature together, as would be the case if researchers were relying on reviews as representatives of collections of original research articles. Thus, review articles may play an important role in integrating across approaches.

The concentrated-cross-citation hypothesis. This hypothesis states that cross-citations between empiry and theory might be concentrated on a small number of high-impact source papers, whereas the majority of papers from each category remains uncited by the other category. To investigate this hypothesis, we first calculated the number of papers from the E, R, and T categories that are cited by at least one paper from each of these categories (see the Venn diagrams in supplemental figure S6). The results show, in particular, that a large proportion of theoretical papers receive citations from empirical papers: In the SS data set, 65 out of 94 theory papers (69%) are cited by E papers from the coded network; similarly, in the SS and S data set, 90 out of 162 T papers (58%) receive citations from E. In contrast, only 10% of E papers in SS (72 out of 713) and 14% in SS and S (138 out of 998) are cited by T papers. This asymmetry reflects, at least in part, the much greater number of E papers in the networks but likely also the fact that many specialized E studies have low chances of getting read by theoreticians. Note that no such asymmetry exists for target papers: As we show in supplemental figure S7, about 50% of both E and T papers cite studies from the other category (SS: 297 of 713, or 42% of, E papers cite at least one T paper from the coded network, and 50 of 94, or 53% of, T papers cite at least one E paper; in the SS and S data set, the corresponding figures are 540 of 998, or 54%, for E citing T and 90 of 162, or 56%, for T citing E).

The preceding analysis (supplemental figures S6 and S7) only counted the number of papers that are part of at least one cross-citation within the coded network. This does not rule out the possibility that most cross-citations have the same source papers. To further quantify the distribution of cross-citations, we calculated Gini (1936) coefficients to compare the unevenness of the number of across- versus within-category citations received by both E and T papers (see supplemental appendices S1 and S3). This analysis shows that after correcting for differences in sample size, citations between categories have somewhat higher Gini (1936) coefficients than within-category citations (see supplemental appendix S3 for detailed presentation of results). Thus, cross-citations are indeed biased toward highly cited source papers, but not to the point of involving only a small number of citation classics. Interestingly, the difference between the Gini (1936) coefficients for within- and between-category citations seems to be higher for E than T source papers (compare the left and right columns of supplemental figure S3). This again suggests that empiricists access a larger proportion of the theoretical literature than vice versa.

In summary, the idea that only a small number of source papers from each category are responsible for the lion's share of communication between theory and empiry is only partially supported by our analysis. In particular, a large proportion of theoretical papers receive citations from empirical studies in the network (supplemental figure S6). Nevertheless, the distribution of citations across categories is more uneven then within categories, indicating that many cross-citations are, indeed, directed toward highly cited source papers (especially for empirical sources).

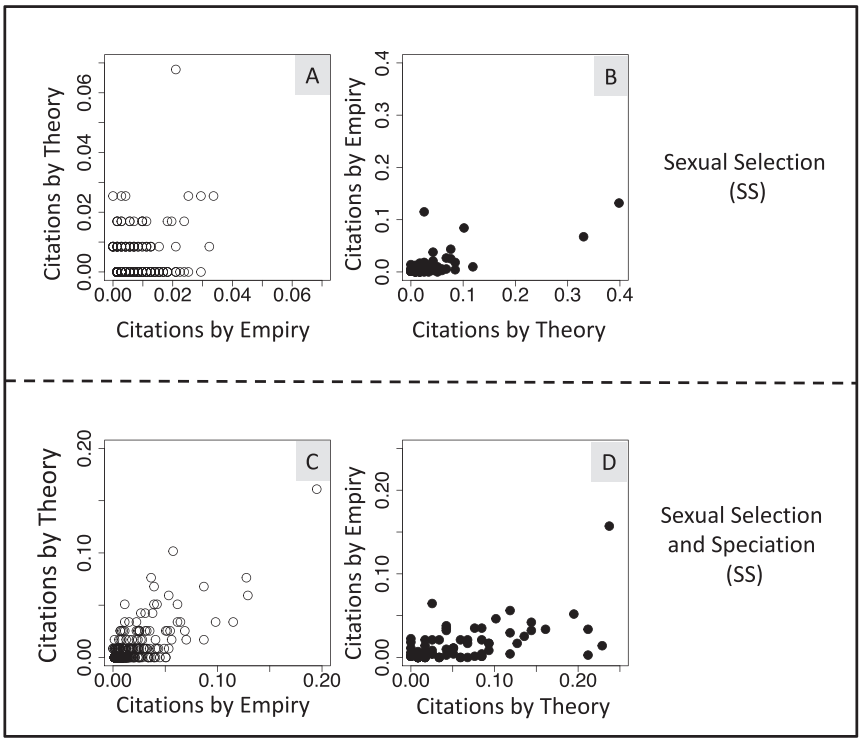

Figure 2. The relationship between same-category (e.g., theory citing theory) and other-category (e.g., empiry citing theory) influence for empirical (E) and theoretical (T) papers. Each data point represents one paper (the "focal" paper). The position of each data point describes the proportion of all same-category papers in the coded network that cite the focal paper (x-axis) and the proportion of all other-category papers in the coded network that cite the focal paper (y-axis) for (a) empirical papers (Spearman's rank correlation, ρ = .10) and (b) theoretical papers (Spearman's rank correlation, ρ = .49) in the sexual selection (SS) data set and for (c) empirical papers (Spearman's rank correlation, ρ = .49) and (d) theoretical papers (Spearman's rank correlation, ρ = .57) in the sexual selection and speciation (SS and S) data set.

The transcendence-of-influence hypothesis. Our final hypothesis states that papers that are highly influential within their field tend to transcend their own category, exerting influence in other categories as well. The hypothesis thus predicts a positive correlation between the citation frequency for a given paper within its own category (e.g., theoretical papers cited by other theoretical papers) and the citation frequency for that same paper outside of its own category (e.g., theoretical papers cited by empirical research). Indeed, in three of the four cases we examined (see supplemental appendix S1), we found evidence of this correlation (the only exception being empirical studies in the sexual selection data set; see figure 2 and supplemental figure S8). In particular, theoretical studies that are highly cited by other theoretical papers also tend to be highly cited by empirical papers. A positive correlation between theoretical and empirical citations exists also for highly cited first authors, be they theoreticians or empiricists (see supplemental appendix S2). This lends support to the idea that high-impact papers and authors tend to not only influence their own research community but also transcend those boundaries to influence thinking more generally. This finding is good news in light of the shared goal of integration between theoretical and empirical research approaches, because it provides evidence that high-impact research from each approach does have an impact on the other.

Additional insights from a cocitation network

In addition to the directed citation networks, we also studied undirected cocitation networks, which link source papers that are cited by the same target paper (for details, see supplemental appendices S1 and S4). Consequently, cocitations reflect decisions in the community about which citations "belong together" and illustrate patterns of general consensus about connections within the literature.

We measured the extent to which papers from the different categories contribute to the structure of the cocitation network, using three common measures of network centrality: degree strength, eigenvector centrality, and betweenness (see supplemental appendix S1). The highest score for all three metrics was obtained by theory papers, followed by reviews. First, theory papers had the highest median degree strength, indicating that they are cited together with many other papers in our data set. Similarly, theory papers had the highest eigenvector centrality scores, indicating not only that they are often cited with other papers but also that they tend be co-cited with other heavily co-cited papers. Finally, theory and reviews had the highest median betweenness, although the differences in this metric between categories were not as pronounced as in the other two metrics. Nonetheless, the high median betweenness values for theory and reviews indicate that they often bridge between groups of cocited papers that are otherwise more isolated (see supplemental figure S9 for full results). Specifically, the highest betweenness value was for a review paper (Emlen and Oring 1977) in the SS data set and a theoretical paper (Lande 1981) in the SS and S data set. Indeed, the high betweenness score for these papers is apparent when visualizing the networks (see supplemental figure S10 for a full visualization of the co-citation networks).

Thus, our analysis of the co-citation networks provides some support for the idea that some paper types more often play critical roles in bridging gaps between otherwise less-connected factions within the literature. Specifically, in the

SS data set, theory and mixed papers were more likely to fill this role than other paper types. In the SS and S data set, however, this role was filled mainly by review and theory papers. This bridging role was not filled by empirical papers in the SS data set, in which none of the empirical papers had high betweenness scores. In contrast, a few empirical papers in the SS and S data set had higher betweenness scores, which suggests that in that subset of literature, particular empirical papers may contribute to connecting the body of literature together, although to a lesser extent than review and theory papers.

More integration exists between theory and empiry than anticipated, and it can still be improved

In conclusion, using a citation network analysis to quantify citations across methodological approaches, we find reason to challenge the intuition that theory and empiry are poorly integrated in evolutionary biology (Haller 2014).

Indeed, the main message of our study is twofold: (1) Despite our finding that empirical and theoretical research more often cite within category than not, theoretical and empirical biology might inform each other more than the community thinks. (2) Nonetheless, opportunities exist to enhance communication and integration between theoretical and empirical research.

We found that neither theory nor empiry self-cited more than 60% of the time, meaning that—assuming citations are a reasonable proxy for integration—at least 40% of citations represented a form of integration (either direct or indirect via reviews). In addition, we found that both highly cited papers and highly cited authors from one domain tend to be well received by the other domain, too. Thus, the observed citation patterns indicate that, at least at some level, practitioners of each approach are following and valuing advances in the other approach.

Why, then, do many researchers report a disconnect between theory and empiry? There are at least two potential explanations. First, the perceived disconnect between theoretical and empirical approaches may reflect unrealistic expectations. Among the coauthors of this article, we have had extensive and productive conversations about the goals of theory and empiry, centering around how closely theory and empiry match when they do inform each other. Many empiricists envision theoretical models that match empirical systems at the level of specific parameter values, whereas theorists often work at a higher level of abstraction, seeking to test the validity of concepts rather than arriving at specific numerical predictions (Servedio et al. 2014). Second, citation patterns may overestimate integration of theory and empiry, because cross-citations are mostly used to provide background and context to a paper rather than being a direct inspiration for a framework of research. Although measuring the importance of this effect is beyond the scope of this study, in the following, we detail three general modes by which theory and empiry are, indeed, integrated or connected and, in each case, we advocate for explicit attempts by researchers to engage with each other more often.

First, integration between theory and empiry can happen sequentially, in which one approach inspires the other. Formal theory is often motivated by long-standing empirical observations that may be especially difficult to explain. For example, the observation that females of many species prefer males with elaborate and exaggerated traits motivated the now sizeable theoretical literature about sexual selection and, even more specifically, the somewhat technical studies investigating the relative strengths of direct and indirect selection (e.g., Weatherhead and Robertson 1979, Kirkpatrick 1985, Kirkpatrick and Barton 1997). In turn, new empirical areas of study are sometimes preceded by and born out of theoretical formulations. For example, the mathematical models that examine how the relative strengths of direct and indirect selection interact and how they can lead to reinforcement (Servedio 2001) directly motivated a subsequent empirical study (Albert and Schluter 2010).

Second, as we outlined above, review papers provide powerful opportunities for researchers to contribute to integration, and our results show both that their citations are more evenly distributed across domains than those of papers reporting original studies and that they often function as bridges between disparate groups of cited literature. Indeed, the job of condensing a large body of literature may become ever more important as publication rate increases and as computational and molecular technologies grow, making unfamiliar domains of science even more difficult to master. Although reviews are sometimes regarded with skepticism and viewed as a mechanism by which researchers can increase their citations (because reviews are cited more frequently than original studies), we do not endorse this cynical view. Instead, we encourage theoreticians and empiricists alike to continue the practice of, first, identifying places in the literature with an abundance of current research articles and, next, synthesizing the results for a broader audience. Furthermore, we advocate explicit collaborations between empiricists and theoreticians in writing reviews that summarize contemporary empirical and theoretical research on a given topic in one paper (e.g., Kopp et al. 2017).

Finally, explicit integration of theory and empiry occasionally happens *within one research paper* (i.e., our mixed (M) category). These papers were rare in our data sets, probably reflecting the fact that models of both sexual selection and speciation are situated at a rather abstract level and that it is often therefore challenging to draw direct analogies with empirical data from a specific study system. Furthermore, we know from our own experience as coauthors that collaborations across specialization can be difficult. Nonetheless, we contend that the relative dearth of these mixed papers represents an underused opportunity for increased collaboration and integration. It is interesting in this context that citation patterns of mixed papers are closest to the null expectation given by the distribution of studies in the literature.

We hope that our analysis will be of use to researchers that feel there is a lack of integration between theory and empiry. If you have the impression that the question of interest to you is not being addressed by authors who use the other approach, writing a review or a mixed paper might be an effective way to draw attention to it.

Acknowledgments

This work was supported by the National Evolutionary Synthesis Center (NESCent), NSF no. EF-0905606. MRS was supported by NSF grant no. DEB1255777. We thank NESCent staff for their support and Angela Zoss of Duke University Libraries for assistance with the Sci2 tool. We thank resident NESCent colleagues and additional members of the working group "Toward a Unified Evolutionary Theory of Decision Making in Animals" for helpful discussion and the Santa Fe Institute for funding a collaboration visit (CLF to work with EAH). During the final stages of revision and writing, CLF was supported by NIH award no. 5T32HD049336-12.

Supplemental material

Supplementary data are available at *BIOSCI* online.

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