Widespread Biases in Ecological and Evolutionary Studies

ZACHARY W. CULUMBER, JAIME M. ANAYA-ROJAS, WILLIAM W. BOOKER, ALEXANDRA P. HOOKS, ELIZABETH C. LANGE, BENJAMIN PLUER, NATALI RAMÍREZ-BULLÓN, AND JOSEPH TRAVIS

There has been widespread discussion of biases in the sciences. The extent of most forms of bias has scarcely been confronted with rigorous data. In the present article, we evaluated the potential for geographic, taxonomic, and citation biases in publications between temperate and tropical systems for nine broad topics in ecology and evolutionary biology. Across 1,800 papers sampled from 60,000 peer-reviewed, empirical studies, we found consistent patterns of bias in the form of increased numbers of studies in temperate systems. Tropical studies were nearly absent from some topics. Furthermore, there were strong taxonomic biases across topics and geographic regions, as well as evidence for citation biases in many topics. Our results indicate a strong geographic imbalance in publishing patterns and among different taxonomic groups across a wide range of topics. The task ahead is to address what these biases mean and how they influence the state of our knowledge in ecology and evolution.

Keywords: tropical biology, biodiversity, conservation, geographic bias

The scientific community has increasingly recognized that the gap between the ideal world and the world of real scientific practice may be wider than desirable (Baker 2016). Although much of the discussion has been dominated by concerns over reproducibility (Open Science Consortium 2015, Parker et al. 2016, Ives 2018), the broader conversation has shed new light on the need to recognize and reduce diverse forms of bias that may negatively affect scientific progress. For example, broader implementation of double-blind peer review aims to limit conscious and unconscious bias on the part of peer reviewers (Cuthill 2001, Budden et al. 2008). Despite growing attention to the issue of bias in the sciences, we still have only a tenuous grasp on the extent of bias within major disciplines. More importantly, although some forms of bias may be relatively easily controlled (e.g., implementing changes to the peer-review process), bias in the balance of our scientific content may be less obvious and difficult to circumvent.

For example, in ecology and evolutionary biology, some topics inevitably receive more attention than others, if for no other reason than the geographic distribution of researchers (Zuk 2016, Peirson et al. 2017a, Cayuela et al. 2018) or the availability of funding to work on certain organisms (Jenner and Wills 2007, Peirson et al. 2017b). This is problematic because the development of general principles in these disciplines relies on studying many species in many places. More subtly, identifying patterns that emerge only in certain circumstances, such as in certain taxa or geographic locations, depends on an even wider range of studies that can bring context-dependent patterns into focus and prevent them from being misdiagnosed as general patterns. This is not merely speculation; recent work has shown that using data from only a single sex can generate misleading interpretations of macroevolutionary patterns arising from sexual selection (Culumber and Tobler 2017), but sex biases are common in experimental studies (e.g., gene-expression data, Zucker and Beery 2010; ecophysiology, Caro 2012). Given the need for balanced content in order to develop robust basic principles, biases in ecological and evolutionary studies may be a particularly vexing problem but have not received rigorous consideration.

Taxonomic biases may also be widespread in the life sciences. How our choice of study organism matters has been a topic of interest for more than two decades (Burian 1993). Since that time, studies have offered perspectives on how our choice of study organisms may influence the inferences we draw from empirical studies (Travis 2006) and how funding opportunities shape our taxonomic choice of study organisms (Peirson et al. 2017a). Although empirical studies of taxonomic bias in any given discipline remain scarce, evidence of a variety of forms of geographic biases—across latitude, countries, biomes, and biogeographic regions—has been reported in some disciplines (e.g., biogeography, Schiesari et al. 2007; conservation, Archer et al. 2014; history of biology, Peirson et al. 2017b; invasion biology, Pyšek et al. 2008). There is also evidence for biases across biological disciplines, albeit with limited geographic scope (e.g., European university research programs, Cayuela et al. 2018).

BioScience XX: 1–10.
doi:10.1093/biosci/biz063

In ecology and evolution, there have been particularly strident claims of temperate bias (Stroud and Feely 2017), despite limited empirical support (Clarke et al. 2017). The concern over this potential bias has several facets; they include issues such as where tropical research is conducted (Cayuela et al. 2018), from which countries tropical researchers are drawn (Stocks et al. 2008), whether there is insularity in citations of work from tropical and developing regions (Ladle et al. 2012), and whether empirical trends differ between temperate and tropical regions (Macedo et al. 2008). Despite considerable discussion and some particularly strong claims, the scope of potential geographic and taxonomic biases across ecology and evolution has not been tested rigorously.

In the present article, we addressed questions of geographic, taxonomic, and citation bias directly with a literature search of nine broad topics. If the tropics are broadly underrepresented in ecological and evolutionary studies, then temperate studies should be numerically dominant or cited at higher rates across topics. We further examined whether certain taxa dominate our regional or topical understanding of ecology and evolution.

Reviewing the literature

We searched the primary literature using the ISI Web of Science, a database consisting primarily of English language journals, spanning the years 1991–2017. We used the following keyword searches to return papers for nine topics covering broad ecological and evolutionary research: *climate tolerance*, *density dependence*, *interspecific competition*, *local adaptation*, *mimicry*, *parental care*, *predator–prey interactions*, *sexual selection*, and *speciation* (supplemental table S1). These topics were selected arbitrarily on the basis of authors' own research interests and of their broad relevance to both temperate and tropical systems. For additional details on the literature search, see the supplemental material. We chose only primary empirical research, excluding review articles, papers developing theoretical models, and papers describing new methods. We further excluded model systems as defined by the National Institutes of Health and invasive species that were studied outside of their native range. When a paper met one of the criteria for exclusion, we randomly chose one paper above or below the excluded paper in our Web of Science search results until a suitable alternative was found. For each of the 200 papers within the nine topics, we recorded the region of study (temperate or tropical), the taxon that was the principal focus of each paper, and the number of citations the paper had received as of December 2017. To be consistent with the classical definition and that used by Stroud and Feeley (2017), studies were classified as being conducted in the tropics if they occurred between 23.5 degrees north (°N) and 23.5 degrees south (°S) latitude. The temperate zones were defined as outside of 23.5°N and 23.5°S latitude. The Arctic and Antarctic Circles were excluded because of a lack of study representation across topics (data not shown). The focal taxon of each study was categorized on the basis of a taxonomic classification broadly similar to that used by the US Fish and Wildlife Service: amphibian, arachnid, bird, crustacean, fish, insect, mammal, mollusk, plant, reptile, and other. A full list of citations is provided in supplemental table S2, and all raw data are provided as a separate supplemental file.

Statistical analyses. To assess whether tropical studies are broadly underrepresented, we tested whether the proportion of tropical papers varied among topics. To test whether certain taxa dominate our regional or topical knowledge, we tested whether the proportion of tropical papers varied among taxa and whether the proportions of papers focused on specific taxa varied across topics.

We tested these hypotheses in two steps. First, we did standard two-way contingency tests with a $2 \times k$ design (2 regions and k subjects) on the number of papers classified by region and topic, region and taxon, and topic and taxon using log-linear models. In these tests, all cells had expected values of 5 or greater. Second, we performed a Bayesian analysis of the number of papers in all of the combinations of region, topic, and taxon to adjust the two-factor comparisons for the presence of the third factor (see the supplemental material). We used a generalized linear mixed model to analyze data on the number of papers. The model included a Poisson error structure, with region and topic as fixed effects and taxon and all interactions including taxon as random effects, using the probabilistic programming language Stan (Carpenter et al. 2017). We used this approach to estimate the posterior probability densities for the number of papers focused on temperate and tropical regions for each topic, allowing for differential taxonomic representation across regions and topics (supplemental table S3a). To estimate these probability densities from the original model, we used the R package Rethinking (McElreath 2016) for Hamiltonian Monte Carlo (HMC) analyses using four HMC chains and 5000 iterations. We used nonadaptive, weakly informative priors with Gaussian (mu, sigma) distribution and parameters (0,10) for all intercepts and slopes and a half-Cauchy (x0, gamma) distribution with parameters (0,2). We verified that the HMC chains were stationary and well mixed. To compare models and choose among them, we used the widely applicable information criterion, which is a generalized Bayesian version of the Akaike information criterion (Watanabe 2010). In all analyses that included taxon as a factor, we deleted predator–prey papers, because they often involved multiple taxa, which introduces the potential for pseudoreplication. We tested whether the proportion of tropical papers focused on predator–prey interactions differed from the overall proportion in all other topics with a simple chi-square test.

We used the same type of Bayesian model to analyze citation data for the combinations of region, topic (without predator–prey studies), period, and taxon (supplemental table S3b). In the present article, *period* represented the temporal strata of our stratified sampling plan. In this case, we estimated the posterior probability densities for average citation rates of tropical and temperate papers in each topic, allowing for differential representation of taxa into our categories of region and topic. We tested whether the citation rates for predator–prey studies differed between regions via analysis of variance using time period and region as fixed factors.

Have the tropics been neglected? We conducted standardized sampling within approximately 60,000 peer-reviewed studies spanning the nine topics (mean = 6770 papers per topic, range = 2233–19,106; table S1). Among all of the topics, .24 of the papers were focused on tropical zone studies. However, there was considerable variation among topics in this proportion (figure 1a), from a low of .08 in local adaptation to a high of .49 in mimicry ($\chi2(9) = 94.35$, $p < .0001$; supplemental table S4). Although the numbers of publications for each topic increased steadily over the period of our survey, there was no evidence that the overall proportion of papers focused on tropical systems had changed over time ($\chi2(6) = 6.99$, $p = .32$). This was not true within some topics; for example, none of the 15 papers sampled on local adaptation before 2003 were conducted in the tropics.

Are there taxonomic biases between regions or among topics? There was substantial variation among taxa in their representation in studies between regions ($\chi2(9) = 94.35$, $p < .00001$; figure 2, supplemental table S5). Of 349 papers focused on plants across the nine topics, only .12 of these studies were done in the tropics. By contrast, although there were only 29 papers on arachnids, nearly half of them (.41) were on tropical systems. There was a high proportion of tropical papers devoted to amphibians (.41) and a low proportion devoted to birds (.18).

There were substantial differences in taxonomic representation in certain subjects (figure 3, supplemental table S6). For example, .47 of the sampled papers devoted to local adaptation were studies of plant populations. Fishes and insects were the subject of .15 and .11 of the papers, respectively, with no other group exceeding .06. A similar pattern appeared for climate tolerance: .41 of the literature was focused on plants, with .13 of the papers devoted to fish and .09 of the papers on insect systems.

Do taxonomic biases between regions or among topics generate the appearance of regional biases among topics? The answer, in short, is no. The posterior probability densities estimated from our Bayesian models (figure 1b, supplemental table S7) generally reflected the raw proportions of regional representation (figure 1a), indicating that, for most topics, taxonomic biases are not creating a misleading appearance of regional biases. The exception is interspecific competition, for which .79 of the papers were based on temperate studies but for which the posterior probability of a paper's being focused on the temperate zone had an average of .21. A look at the data revealed the source of this discrepancy. The papers on mammals and plants represented 85 of the 200 papers on interspecific competition (approximately .42), but 75 of those 85 papers were focused on temperate zone studies. This pattern makes temperate zone studies, when unadjusted for taxonomic distribution, appear overrepresented in studies of interspecific competition.

For two other topics, sexual selection and speciation, the Bayesian analyses indicated a higher posterior probability density of temperate papers than the raw proportions (compare figure 1a and 1b). This indicated a mild taxonomic bias. However, in these cases, the bias worked in the opposite direction. Accounting for this taxonomic bias, temperate papers were slightly underrepresented in the raw proportions. Papers focused on predator–prey interactions conformed to the general pattern, with 160 of 200 focused on temperate zone studies (.80). This was not significantly different from the overall proportion among all other topics ($\chi^2(1) = 2.08$, $p > 0.05$).

Are there regional or taxonomic biases in citation rates? The raw data suggested that the answer to this question is no: The average citation rates for tropical and temperate papers were similar (tropical average = 26.3, standard error [SE] = 1.87, $n = 430$; temperate average = 27.6, SE = 1.33, $n = 1370$). However, the citation rates varied widely among papers focused on different taxa. For example, the raw data show that papers devoted to mollusks were cited much more often, on average, than papers devoted to crustaceans (mollusks average = 29.7, SE = 6.4, $n = 73$; crustacean average = 16.3, SE = 2.3, $n = 42$). In the same vein, papers on plants were cited more often, on average, than papers on reptiles (plant average = 22.2, SE = 1.7, $n = 347$; reptile average = 15.5, SE = 2.2, $n = 55$). Given the disproportionate representation of some taxa between regions and topics, we turned to the Bayesian analysis to answer this question.

The Bayesian analysis indicated that the tropical papers were more likely to have higher citation rates in some topics but that the temperate papers were more likely to have higher citation rates in other topics (figure 4, supplemental table S8). For four topics—climate tolerance, density dependence, interspecific competition, and speciation—the posterior probability densities of citation rates were higher for tropical than temperate papers. Climate tolerance was especially notable in this regard, with tropical studies in this area playing an outsized role in citations compared with their representation in numbers of papers (compare figure 1b with figure 4). Papers on parental care and sexual selection had higher probability densities of citation rates for temperate studies. For predator–prey studies, citation rates were slightly higher for temperate zone papers (average = 72.4, SE = 6.2, $n = 160$) than for tropical papers (average = 63.2, SE = 11.8, $n = 40$).

Discussion

There is little debate that biases, whether conscious or unconscious, are at fundamental odds with the goal of science and

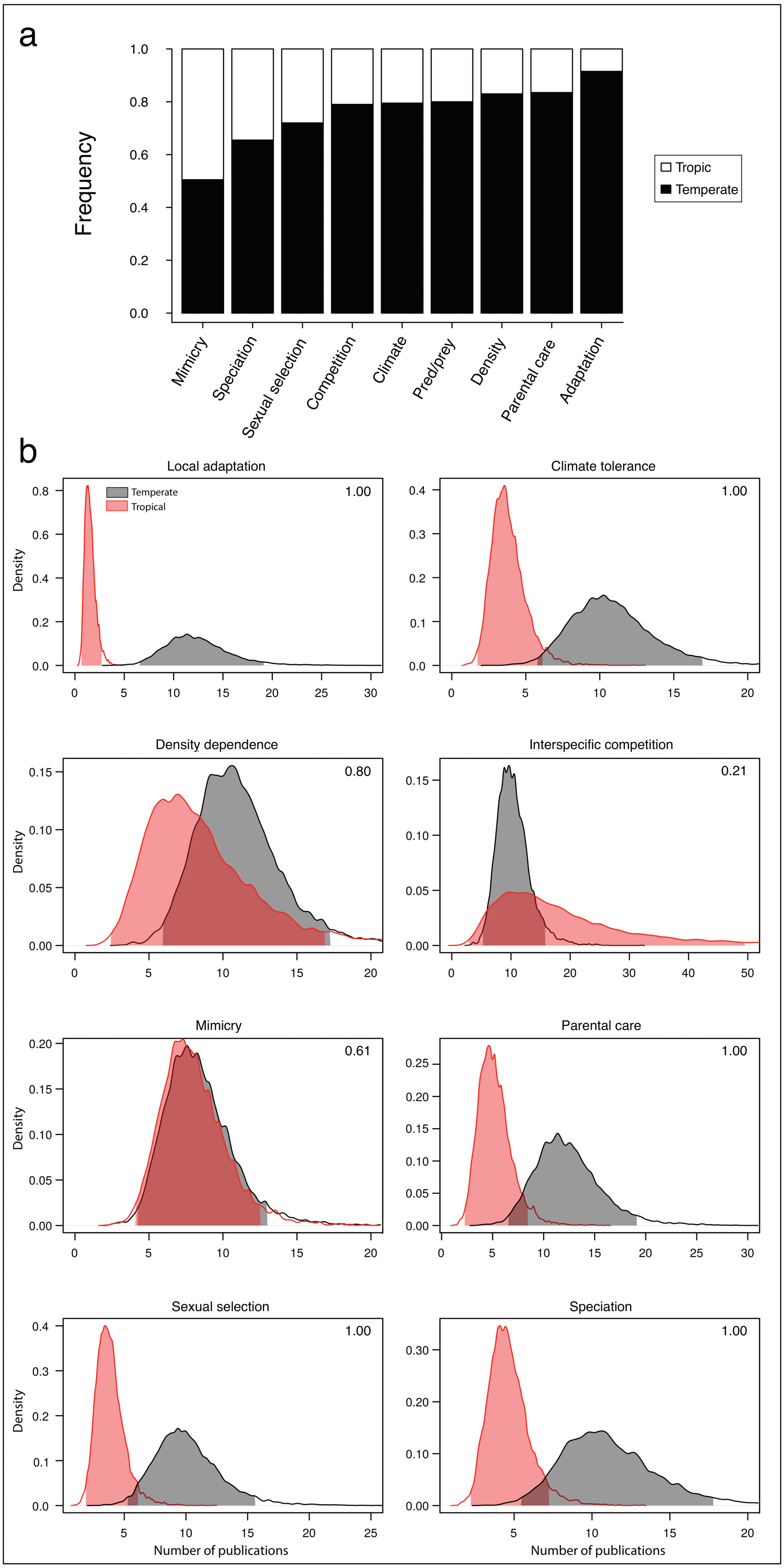

Figure 1. (a) Frequency of published empirical research sampled that were completed in temperate (black) and tropic (white) region by topic. The studies of local adaptation had the least tropical research, whereas the studies of mimicry had the most published tropical research. (b) Posterior probability densities from Bayesian models on regional representation by topic.

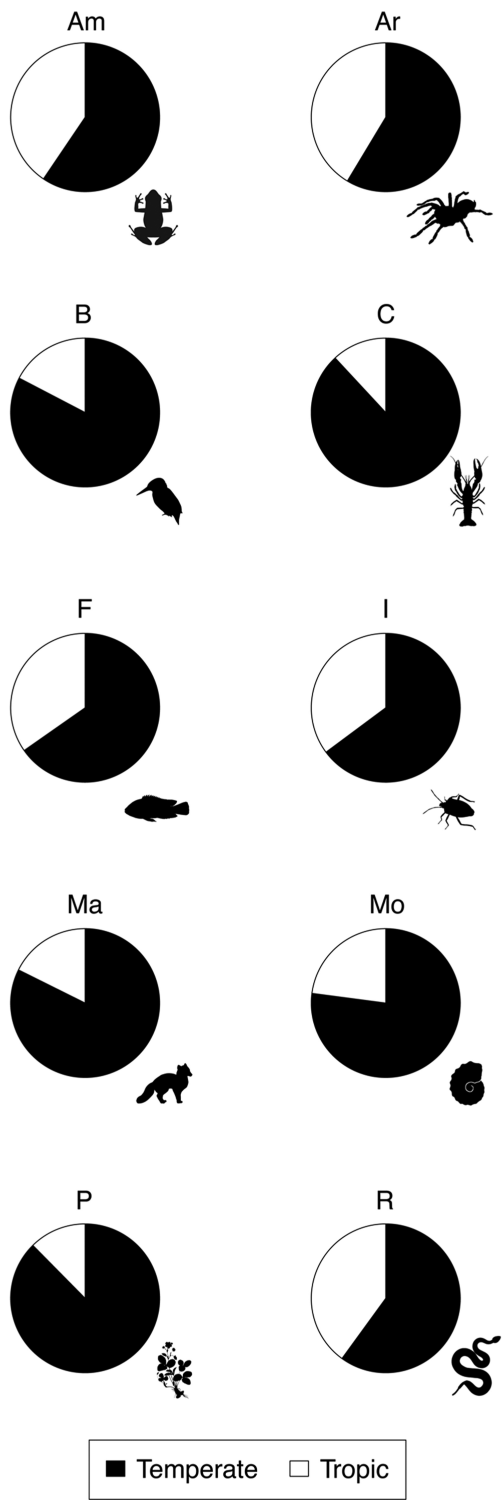

Figure 2. Proportion of published empirical research sampled per taxa that were completed in temperate (black) and tropic (white) region. Arachnids (Ar), amphibians (Am), and reptiles (R) had the most even distribution of temperate and tropical studies, whereas crustaceans (Cr) and plants (P) were the most unbalanced. Other taxon abbreviations were as follows: birds (B), fishes (F), insects (I), mammals (Ma), mollusks (Mo). The silhouettes for all figures were obtained from phylopic.org.

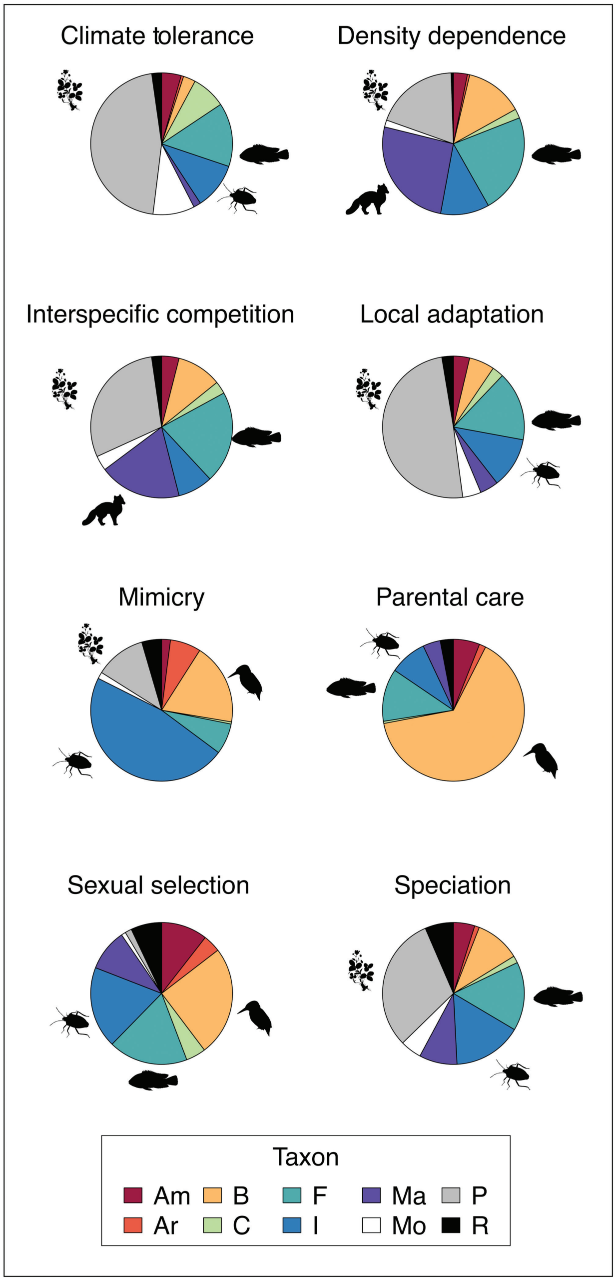

Figure 3. Taxonomic distributions within topics. Silhouettes indicate the three taxa with the highest proportion of studies within that topic. Taxonomic distribution differed among various topics. Predator–prey interactions were not included in this figure or associated analyses because of the difficulty in determining which species was the focal taxon. See figure 2 for abbreviations of taxa.

may negatively affect the development and dissemination of knowledge (Burian 1993, Travis 2006, Lee et al. 2013). Our literature search revealed a number of biases across diverse topics in ecology and evolution. First, tropical studies were underrepresented in seven of the nine topics examined, with the literature on some fundamental concepts exhibiting a strong bias toward temperate systems. Second, many topics

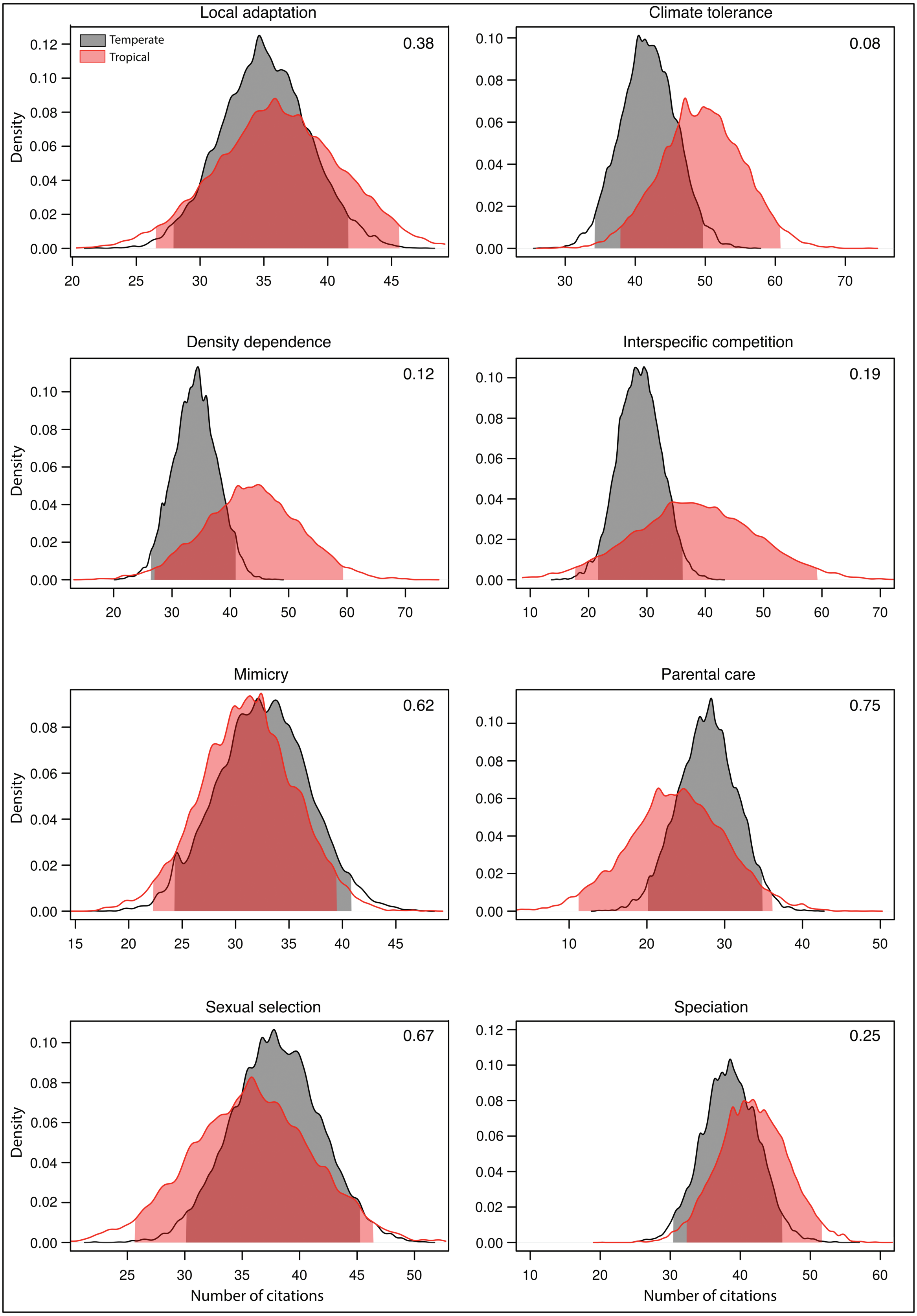

Figure 4. Posterior probability density estimates for the citation rates of tropical and temperate publications in major topics of ecology and evolution in the Web of Science. The probability of temperate bias in each topic is given at the top-right corner of each panel. The colored shades represent 95% credible intervals (see supplemental table S8 for more details).

also exhibited strong biases in taxonomic representation, with some of these biases driven by research in a specific geographic region. The taxonomic biases generated an artifactual evidence of a temperate bias for interspecific competition but not for the other topics. Finally, the citation rates varied among the taxonomic groups; when the rates were adjusted for this variation, the tropical papers actually had higher citation rates for some topics, whereas the temperate papers had higher citation rates for other topics.

Geographic bias. Across the nine broad topics, the tropics were underrepresented in the raw data (.08–.34) in all but one topic (mimicry: .49). Only for interspecific competition was this underrepresentation in the raw data misleading. This geographic bias in seven of nine topics indicates that the current state of knowledge and the way we think about important topics in ecology and evolution are dominated by our collective experience with temperate systems. Such geographic biases are especially critical in the present research climate of open data and big science. Meta-analyses in which functional, taxonomic, and genetic data are mined from databases and existing literature to make overarching inferences about putatively "global" patterns are frequently published, but the resources that are used for these studies are geographically biased. For example, the largest gaps in genetic data used for phylogenetic comparative methods are found in the tropics (Miraldo et al. 2016). Even if functional data exist for a tropical species, it may be excluded from meta-analyses because of a lack of genetic information. As such, the resulting studies may often have strong temperate biases (e.g., for a review, see Feeley et al. 2017). In a recent meta-analysis reporting on factors determining the strength of directional selection (Siepielski et al. 2017), only .10 of the studies were from the tropics. We should highlight that this does not mean that inferences from such meta-analyses are necessarily wrong, only that one should exercise caution in drawing broad generalizations about underrepresented regions. Furthermore, the results attributed to the tropics in meta-analyses may themselves be biased because of the potential for inflated effect sizes in small samples (Fanelli et al. 2017).

The degree of heterogeneity in temperate bias across topics was striking. For example, processes such as local adaptation, speciation, sexual selection, and parental care are very general, but publications in these topics were dominated by temperate studies. However, mimicry occurs in both tropical and temperate regions, and the literature on mimicry systems was almost perfectly balanced. The case of interspecific competition is an interesting one. There is a vast literature on latitudinal gradients in species diversity, much of which posits latitudinal variation in the incidence, strength, and complexity of biotic interactions (Pianka 1966, Schemske et al. 2009, Schemske and Mittelbach 2017). In that light, it would seem gratifying that tropical systems are well represented in studies of interspecific competition, after adjusting for the taxonomic biases. However, the strong taxonomic bias in this topic, which made the posterior probabilities of tropical publications look very different from the raw data, raises its own question about what we know about this subject. Are some taxa studied more often because we think, a priori, that they are more likely to experience interspecific competition? Or are they studied more often for practical reasons? In either case, it is apparent that our understanding of this process may be based on too narrow a subset of nature. A final consideration to make is that databases themselves may introduce some degree of bias. For example, a proportion of only .068 of journals in the Web of Science are published in tropical countries, whereas .67 of journals in the SciELO database (www.scielo.org) are published in tropical countries. Nonetheless, tropical papers can certainly be published in journals that are produced in temperate countries. Our literature review demonstrates that tropical papers are underrepresented in the mainstream journals with the widest circulation and significant citation rates.

Taxonomic bias. Taxonomic biases were common across the topics we examined. Within several topics, the literature was dominated by one or very few taxonomic groups. Some of these patterns may be expected on the basis of the topic. For example, parental care is found in most birds but relatively few invertebrates or fish. Other patterns of taxonomic bias suggest that our knowledge of some topics may be skewed by specific organisms. Again, parental care provides an example. Although care is common in mammals, mammals accounted for only .04 of the parental care studies, with none of those studies conducted in the tropics. Similarly, although all organisms are putatively capable of local adaptation, nearly half of the studies on local adaptation were based on plant systems. It may be the case that such biases arise because plant species are more numerous than vertebrates, for example, or that plants may be more capable of adaptation. However, it is also possible that local adaptation is understudied in taxa outside of plants that are less amenable to common garden and reciprocal transplant experiments. In contrast, given the well-documented latitudinal gradient in species diversity, plant studies were overwhelmingly underrepresented in the tropics (.12 of the plant studies). A similar trend was observed for other groups known to have striking levels of diversity in the tropics, including amphibians and reptiles, both of which showed subtle bias toward temperate systems. Although we cannot entirely rule out the possibility that taxonomic biases could arise if there is taxon-specific terminology use of our search terms (e.g., perhaps only plant biologists publish using the term *local adaptation* or only ornithologists use the term *parental care*), this seems implausible, because the terms we used were broad, colloquial terms used throughout subfields in biology. Regardless of the underlying reason, it is important to consider how such taxonomic imbalance may influence our understanding of general principles in ecology and evolution.

Citation bias. If geographic biases exist in the literature, they could be further exacerbated if authors tend to cite studies from one region over another. Even if there is no geographic bias in the proportion of studies on a particular topic, geographic biases could exist if studies from a particular region were cited more often. In this light, the heterogeneity among topics in the regional patterns of citation rates is striking. One might argue that studies of climate tolerance, density dependence, or interspecific competition are inherently more interesting in tropical systems. It is hard to understand, however, why parental care and sexual selection might be more interesting in temperate systems that they receive higher citation rates. This may reflect a bias among scientists in temperate regions, who outnumber those in tropical regions, to rely on more familiar examples when framing their own work.

The variation in citation rates among taxa suggests that the community may rely too heavily on studies of some taxa at the expense of attention to others. Across both regions, amphibian and mollusk studies were the most highly cited, whereas reptile and crustacean studies were the least cited. As with general taxonomic biases, it is important to acknowledge how such citation imbalances among taxa may influence the generalities we draw from the literature.

What is bias, and does it really matter? These data showed that, among 1800 papers sampled evenly from within seven temporal strata between 1991 and 2017, only .24 of them were focused on tropical systems. Furthermore, the proportion of tropical papers varied widely by subject matter and by taxon. Although the papers focused on tropical or temperate systems were cited at comparable rates, the papers focused on some taxa had substantially higher citation rates than those focused on other taxa. Do these results really reflect bias?

The answer might depend on what we consider our null hypothesis: What proportion of the literature should we expect to focus on the tropics? The simplest hypothesis might be an even distribution. We might build other expectations from the number of species found in the tropic or temperate zones (Macias-Ordonez et al. 2014) or the geographic distribution of ecologists and evolutionary biologists (Stocks et al. 2008). By either of the first two criteria, the tropics are underrepresented in the literature. The third criteria may match the data best and, in that case, we might be hard-pressed to consider the literature biased without a detailed statistical analysis of institutional affiliations of ecologists and evolutionary biologists.

The answer might depend not on the numbers of papers from each region, which are influenced by the personal predilections of scientists, funding opportunities, the availability of international collaborators, and logistics, but on the extent to which papers from each region are absorbed into our thinking. In this light, citation rates might be the better criterion. If we use this criterion, there is little evidence for widespread neglect of the tropics. Two lines of evidence support this claim. First, after adjusting for taxonomic biases, the average citation rates per paper were higher for tropical papers in five of the eight topics whose data we analyzed in the Bayesian framework. Second, we might argue that, for any given topic, if there is no bias, then the probability of a temperate paper's being cited, as compared with a tropical paper, is proportional to the representation of temperate papers in that topic. Were this the case, we would expect a positive correlation, across topics, between the probability that a temperate (tropical) paper is more heavily cited (figure 4) and the proportion of papers that are focused on temperate (tropical) systems (figure 1). There is indeed such a correlation (Spearman rank correlation among eight topics, $\rho = .82$, $p < .05$). Therefore, although tropical papers may be vastly underrepresented for a topic, the tropical papers on that topic are not being overlooked.

A better approach is to consider whether disparities in publication and citation rates might distort our understanding of a topic (Zuk 2016, Clarke et al. 2017). Taking this approach requires moving beyond counts of publications and citations to the assessment of results of empirical studies. For example, if studies of parental care indicate that the distribution of maternal, paternal, or biparental care is similar between temperate and tropical species within a group such as birds or mammals and if studies show that the duration of and investment in care follows the same theoretical predictions in both regions, then the small proportion of tropical studies of parental care (.17) may not be cause for concern. Obviously, to draw this conclusion, we need to have in hand a minimum number of tropical studies distributed comparably among taxa to the temperate studies. Whether there are enough such studies is a question that can only be answered by those who work in the topic, but for topics such as local adaptation, our results suggest there are likely too few.

The problem looms larger when there is reason to believe that tropical systems may operate qualitatively or quantitatively differently than temperate ones. This was the point raised by Clarke and colleagues (2017) in their critique of conclusions about biodiversity and ecosystem function. Our results suggest that this concern can be extended to other topics. Consider again the example of local adaptation. In general, the level of local adaptation depends on the spatial scale at which selective pressures diverge relative to the spatial scale of gene flow (for a review, see Richardson et al. 2014). If these scales are consistently different between tropical and temperate populations, then the very low representation of tropical systems in the literature on local adaptation may indicate that our understanding is distorted. This could well be the case, at least for animals, for which studies have shown that tropical species appear to have lower rates of gene flow among local populations than temperate species (Gascon et al. 1998). Along these same lines, there is a long history of hypotheses about latitudinal gradients in the nature and strength of biotic interactions and the spatial scale of divergence (and speciation; for a review, see Schemske et al. 2009); in this light, the dearth of tropical studies of local adaptation is even more striking. We can extend this concern to our results for density dependence, interspecific competition, and predator–prey interactions—not that these topics have not been studied in tropical systems but that tropical systems represent such a small proportion of what has been studied.

We can examine the potential importance of bias in taxonomic distributions of papers with the same criterion: Do the observed differences among taxa in their representation in the literature distort our understanding of a topic? We cannot answer this question without at least a minimum number of studies from a diversity of taxa. In this light, the few studies of parental care in mammals stand out. It is possible, of course, that papers published before 1991 were focused on mammals and that, in the period we surveyed, studies of birds were simply catching up. Even were this true, studies of avian care have surely used new techniques (e.g., assessing parentage) and tested new hypotheses (e.g., contrasts of investment in paternal care and investment in ornaments) in this period, and the dearth of mammalian papers remains striking.

Changing course. Our study inevitably leads to the difficult question of how we can reduce geographical bias. Just as the nature of the problem is multidimensional, so too may the solution require a variety of actions by the scientific community at different levels. First, given the observed geographical bias of studies published in journals indexed in the Web of Science, there is a clear need for additional work in the tropics. Authors studying tropical systems could cite this need and the associated literature to emphasize the importance of their work when submitting manuscripts. Next, our study has been focused on geographical bias in the number of papers published but does not address the deeper question of whether ecological and evolutionary mechanisms differ between regions. When choosing citations during manuscript preparation, authors should pay attention to whether the conclusions of prior studies differ between regions and should furthermore be aware that certain search engines themselves may be biased in their regional representation of papers. Along these same lines, because we have not yet tackled the question of whether ecological and evolutionary processes function the same in temperate and tropical systems, there is a clear need for more geographically comparative studies to address this key gap in knowledge. Finally, funding agencies should consider this need for more geographically comparative work as an avenue for targeted initiatives, because understanding whether our knowledge of fundamental ecological and evolutionary processes is affected by geographical bias in publications is a critical unanswered question.

Addressing the underrepresentation of the tropics in ecology and evolutionary biology is a serious challenge. Rapidly changing local climates and rapidly increasing human impacts give some urgency to addressing the imbalance. This cannot happen unless the larger scientific institutions in the temperate zones make it a priority to collaborate with their colleagues in tropical regions and help to train new cohorts of tropical biologists able to overcome the practical and financial challenges of learning more about tropical systems. Without such commitment, we may never know what we have missed.

Acknowledgments

This work was supported by National Science Foundation (NSF) IOS award no. 1257735 to KH and JT and NSF DEB award no. 1556884 to JT. Nicholas Ruhs, FSU STEM Research and Learning librarian, helped in obtaining the country of origin listing for journals indexed in the Web of Science.

Supplemental material

Supplemental data are available at *BIOSCI* online.

References cited

Archer CR, Pirk CWW, Carvalheiro LG, Nicolson SW. 2014. Economic and ecological implications of geographic bias in pollinator ecology in the light of pollinator declines. Oikos 123: 401–407.

Baker M. 2016. 1,500 scientists lift the lid on reproducibility. Nature News 533: 452.

Budden AE, Tregenza T, Aarssen LW, Koricheva J, Leimu R, Lortie CJ. 2008. Double-blind review favours increased representation of female authors. Trends in Ecology and Evolution 23: 4–6.

Burian RM. 1993. How the choice of experimental organism matters: Epistemological reflections on an aspect of biological practice. Journal of the History of Biology 26: 351–367.

Caro SP. 2012. Avian ecologists and physiologists have different sexual preferences. General and Comparative Endocrinology 176: 1–8.

Carpenter B, Gelman A, Hoffman MD, Lee D, Goodrich B, Betancourt M, Brubaker M, Guo J, Li P, Riddell A. 2017. Stan: A probabilistic programming language. Journal of Statistical Software 76. doi:10.18637/jss.v076.i01.

Cayuela L, Granzow de la Cerda Í, Méndez M. 2018. The state of European research in tropical biology. Biotropica 50: 202–207.

Clarke DA, York PH, Rasheed MA, Northfield TD. 2017. Does biodiversity: Ecosystem function literature neglect tropical ecosystems? Trends in Ecology and Evolution 32: 320–323.

Culumber ZW, Tobler M. 2017. Sex-specific evolution during the diversification of live-bearing fishes. Nature Ecology and Evolution 1: 1185.

Fanelli D, Costas R, Ioannidis JP. 2017. Meta-assessment of bias in science. Proceedings of the National Academy of Sciences 114: 3714–3719.

Feeley KJ, Stroud JT, Perez TM. 2017. Most 'global'reviews of species' responses to climate change are not truly global. Diversity and Distributions 23: 231–234.

Gascon C, Lougheed SC, Bogart JP. 1998. Patterns of genetic population differentiation in four species of Amazonian frogs: A test of the riverine barrier hypothesis. Biotropica 30: 104–119.

Ives AR. 2018. Informative irreproducibility and the use of experiments in ecology. BioScience 68: 746–747.

Jenner RA, Wills MA. 2007. The choice of model organisms in evo–devo. Nature Reviews Genetics 8: 311.

Ladle RJ, Todd PA, Malhado AC. 2012. Assessing insularity in global science. Scientometrics 93: 745–750.

Lee CJ, Sugimoto CR, Zhang G, Cronin B. 2013. Bias in peer review. Journal of the American Society for Information Science and Technology 64: 2–17.

Macedo RH, Karubian J, Webster MS. 2008. Extrapair paternity and sexual selection in socially monogamous birds: Are tropical birds different? Auk 125: 769–777.

McElreath, R. 2016. Statistical Rethinking: A Bayesian Course with Examples in R and Stan. CRC Press.

Macias-Ordonez R, Machado RG, Macedo RH. 2014. Macroecology of sexual selection: Large-scale influence of climate on sexually selected traits. Pages 1–32 in Macedo RH, Machado G, eds. Sexual Selection: Perspectives and Models from the Neotropics. Academic Press.

Miraldo A, Li S, Borregaard MK, Flórez-Rodríguez A, Gopalakrishnan S, Rizvanovic M, Wang Z, Rahbek C, Marske KA, Nogués-Bravo D. 2016. An Anthropocene map of genetic diversity. Science 353: 1532–1535.

Open Science Collaboration. 2015. Estimating the reproducibility of psychological science. Science 349: aac4716.

Parker TH, Forstmeier W, Koricheva J, Fidler F, Hadfield JD, Chee YE, Kelly CD, Gurevitch J, Nakagawa S. 2016. Transparency in ecology and evolution: Real problems, real solutions. Trends in Ecology and Evolution 31: 711–719.

Peirson EBR, Kropp H, Damerow J, Laubichler MD. 2017a. The diversity of experimental organisms in biomedical research may be influenced by biomedical funding. BioEssays 39: 1600258.

Peirson EBR, Bottino E, Damerow JL, Laubichler MD. 2017b. Quantitative perspectives on fifty years of the Journal of the History of Biology. Journal of the History of Biology 50: 695–751.

Pianka ER. 1966. Latitudinal gradients in species diversity: A review of concepts. American Naturalist 100: 33–46.

Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtova Z, Weber E. 2008. Geographical and taxonomic biases in invasion ecology. Trends in Ecology and Evolution 23: 237–224.

Richardson JL, Urban MC, Bolnick DI, Skelley DK. 2014. Microgeographic adaptation and the spatial scale of evolution. Trends in Ecology and Evolution 29: 165–176.

Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy, K. 2009. Is there a latitudinal gradient in the importance of biotic interactions? Annual Reviews of Ecology, Evolution, and Systematics 40: 245–269.

Schemske DW, Mittelbach GG. 2017. Latitudinal gradients in species diversity: Reflections on Pianka's 1966 article and a look forward. American Naturalist 189: 599–603.

Schiesari L, Grillitsch B, Grillitsch H. 2007. Biogeographic biases in research and their consequences for linking amphibian declines to pollution. Conservation Biology 21: 465–471.

Siepielski AM, Morrissey MB, Buoro M, Carlson SM, Caruso CM, Clegg SM, Coulson T, DiBattista J, Gotanda KM, Francis CD, Hereford J. 2017. Precipitation drives global variation in natural selection. Science 355: 959.

Stocks G, Seales L, Paniagua F, Maehr E, Bruna EM. 2008. The geographical and institutional distribution of ecological research in the tropics. Biotropica 40: 397–404.

Stroud JT, Feeley KJ. 2017. Neglect of the tropics is widespread in ecology and evolution: A comment on Clarke et al. Trends in Ecology and Evolution 32: 626–628.

Travis J. 2006. Is it what we know or who we know? Choice of organism and robustness of inference in ecology and evolutionary biology. American Naturalist 167: 303–314.

Watanabe, S. 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. Journal of Machine Learning Research 11: 3571–3594.

Zucker I, Beery AK. 2010. Males still dominate animal studies. Nature 465: 690.

Zuk M. 2016. Temperate assumptions: How where we work influences how we think. American Naturalist 188: S1–S7.

Zachary Culumber is an assistant professor at the University of Alabama, in Huntsville. Joseph Travis is a professor, Jaime Anaya-Rojas is a postdoctoral researcher, and William Booker, Alexandra Hooks, Elizabeth Lange, Benjamin Pluer, and Natali Ramírez-Bullón are graduate students at Florida State University, in Tallahassee.