LRH: Bruna *et al.*

RRH: Replicability in Tropical Biology

A Proposal to Advance Theory in Tropical Biology by Promoting Replication

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1 A hallmark of science is *replicability* (Voelkl *et al.* 2020). Replication is collecting new data to
2 test a claim from prior research (Nosek & Errington 2020b). Replication advances credibility of
3 research by increasing confidence in the reliability of a finding, improving the precision of
4 estimated effects, or identifying how our understanding of conditions needed to observe a finding
5 might be limited. Corroborating findings with replication helps eliminate mistakes and
6 questionable research practices and speeds scientific progress (Fraser *et al.* 2018, Redish *et al.*
7 2018), which is why it is fundamental to the scientific method (Popper 2005).

8 A surge of efforts to replicate the results of fundamental studies in fields ranging from
9 chemistry (Bergman & Danheiser 2016) to the biomedical sciences (Errington *et al.* 2014,
10 Amaral *et al.* 2019) reflects a general concern that this core principle of science may not be
11 operating as well as expected in practice. For example, the Open Science Collaboration (2015)
12 replicated 100 psychology findings and observed successful replication of results for less than
13 40% of them. Observing differences between original studies and replications can be beneficial,
14 however, by leading to the development of generative theory to account for the observed
15 differences. For example, in exploring a failure to replicate one could identify previously
16 unappreciated factors critical for observing the phenomenon of interest (Open Science
17 Collaboration 2015). Of course, it is also possible that the original result was a false positive, in
18 which case nothing would explain why the original study observed a finding but the replication
19 did not. Over time replications either build confidence in and mature the theoretical
20 understanding of a phenomenon, or they render the finding irrelevant because the conditions for
21 demonstrating replicability cannot be identified (Nosek & Errington 2020b).

22 Field-based sciences such as Ecology, Behavior, and Evolution (EBE) could benefit from
23 promoting replication (Kelly 2006, Huang 2014, Nakagawa & Parker 2015, Fidler *et al.* 2017),

but the response of the EBE community to these calls has ranged from tepid to skeptical (Schnitzer & Carson 2016, Senior Editors 2016). The reasons echo those put forward by scientists in other fields: a lack of incentives or professional rewards for carrying out replications, few journals willing to publish the results of replicated studies, and concerns about efficient use of scarce research funding (Nakagawa & Parker 2015, Schnitzer & Carson 2016, Fidler *et al.* 2017). In addition to these practical obstacles, however, many suggest a more fundamental conceptual one – that research in EBE is inherently impossible to replicate because it is carried out under unique biotic and abiotic conditions (Schnitzer & Carson 2016, Ives 2018).

To be clear, there is no such thing as exact replication regardless of discipline and research context – there will always innumerable differences resulting from changes in season, laboratory conditions, historical circumstances, or the identity of participants. This is certainly true in an EBE context, in which the biotic and abiotic conditions under which field studies are conducted will never be identical. But scientific claims are not historical ones, for which a finding is presumed to apply only in the original context. Scientific claims are statements about regularities one expects to observe across contexts when certain conditions are met. That is why replication is formally defined as attempting to reproduce a previously observed result with procedures that provide no *a priori* reason to expect a different outcome (Schmidt 2009, Open Science Collaboration 2015, Nosek & Errington 2017). This is why replications in EBE do not have to be conducted under biotic and abiotic conditions identical to those of the original study; given our present understanding of the phenomenon, the new environmental context should not reveal something different from the original one (Nosek & Errington 2020b). Of course, our ‘present understanding’ can be wrong, which is why a replication that does not produce the same finding as the original study can be so useful for testing and advancing theory – it forces one to

assess whether the original study could have been a false positive, if the replication might have been a false negative, or to generate hypotheses for why the studies had different outcomes. This assessment may be especially important in the context of management or conservation, where one seeks confidence in the original conclusions, rather than broad theoretical generality.

The assertion that EBE research can't be replicated may stem from confusion regarding precisely what constitutes a "replication", especially with regards to geography and species identity (reviewed in Nakagawa & Parker 2015, Fraser *et al.* 2020). If the original claim is explicitly bounded by geography or species identity, then to qualify as a replication the methodology must respect those restrictions. If the original claim is more general, however, then the replication can in theory transcend geography and species identity within limits concordant with the extent of the original claim's generality (Table 1). While replications are perhaps most straightforward to conceptualize when using species and methods identical to those in original study, they can be conducted with other systems *if the replication design actively confronts the present understanding with a test that provides diagnostic information increasing or decreasing confidence in the original claim*. Put another way, a replication is a theoretical commitment to specify a study design for which one expects the same outcome as the prior findings given our understanding of the phenomenon of interest (Nosek & Errington 2020b).

While expanding the domain of valid replications to include novel systems is conceptually exciting, this also requires exceptional rigor and *a priori* consensus regarding the study design and expected outcomes (Nosek & Errington 2020a). This challenge is further exacerbated if the theoretical expectations of the original study are underspecified, making it unclear if the claim should in fact recur in different locations or species. Ambiguous expectations lead to asymmetric inference – while observing consistent evidence builds confidence in the

original finding, failing to do so doesn't decrease confidence. Such asymmetric tests are therefore not replications. They are tests of generalizability (Nosek & Errington 2020b), which are useful for understanding the breadth and boundaries of a phenomenon but do not directly confront the original conclusion. In fields that have historically emphasized tests of generalizability, such as EBE, positive results can appear to establish the broad applicability of a phenomenon without ever actually testing its replicability – especially given the biases against publication of null results (reviewed in Fidler *et al.* 2017). Advancing theory in our discipline requires both testing predictions in new systems and assessing the validity of studies on which theory was built by attempting to replicate them (Cassey & Blackburn 2006, Nakagawa & Parker 2015, Fidler *et al.* 2017).

Shifting the current research paradigm to one that values such replications requires two things: an EBE community that recognizes their value (Fraser *et al.* 2020) and providing the incentives to carry them out (Nakagawa & Parker 2015, Fidler *et al.* 2017). Academic societies are uniquely poised to both promote the value of replications and provide the needed incentives. We therefore propose that the Association for Tropical Biology and Conservation (ATBC) spearhead a Reproducibility Project in Tropical Biology – the first such effort in environmental biology – to encourage replicating some of the most important studies in our field.

The Reproducibility Project in Tropical Biology (RP:TB)

The Reproducibility Project¹ we envision would have four major objectives. **First**, to determine the extent to which the results of studies in Tropical Biology can be replicated.

¹ While the focus of this project is the replication of experiments, we named our effort the “Reproducibility Project: Tropical Biology” to be consistent with other similar initiatives (e.g., the Reproducibility Project: Cancer Biology (<https://www.cos.io/rpcb>), and the Reproducibility Project: Psychology (<https://osf.io/ezcuj/wiki/home/>)).

Second, to identify obstacles to conducting effective replications of these studies, including such factors as insufficiently detailed methods in the original article, the extinction of species or loss of study site, changes in local, landscape, or global environmental conditions, or advances in statistical or analytical methods. **Third**, to quantify predictors of replication success, such as the location and species with which the experiment was conducted and the extent to which the original study site and system has been modified by human activities. **Fourth**, to build capacity by training early-career scientists and promoting collaboration between tropical biologists – especially North-South and South-South collaborations. Addressing some of these objectives should be relatively straightforward (e.g., 1, 4). The statistical power required for others (e.g., 2, 3) may require increasing the number of replications, prioritizing replications using the original study design and system to reduce the number of variables under consideration, or both.

Why should the ATBC lead this initiative? With almost 1000 members in over 65 countries, the ATBC is ideally positioned to bring together and support the scientists who want to implement replications in a diversity of ecosystems throughout the tropics. In addition, as publisher of *Biotropica* the ATBC can provide an important incentive to participating scientists – the guaranteed publication of results, irrespective of the outcome. Finally, by working in collaboration with the Center for Open Science – which helps coordinate the reproducibility projects in psychology and cancer biology – the ATBC would be able to provide participants the necessary infrastructure for collaboration and project management, training in data management and statistical analysis, and support for pursuing funding to carry out replications.

What studies should be priorities for replication?

In developing the idea for this initiative, we consulted a diverse group of tropical

biologists and asked what studies they considered worthy of replication because of their importance to the theoretical underpinnings of our field or their importance for advancing the conservation and management of tropical ecosystems. We then narrowed the nominated studies to a list of 15 that we suggest as priorities for replication (Table 2). Some of these focus on species with broad distributions (e.g., Janzen 1967, Augspurger 1983), making it possible to repeat the original study in the same location or with the same species in a new site. In others the focal assemblage is unlikely to be identical outside of the original study site, but having some species in common and easily implemented methods (e.g., Dirzo *et al.* 1992) means they meet the criteria for confronting the original claim with a new test (Table 1).

It is important to emphasize that we are not arguing these studies are the most important ones in tropical biology, nor that they are the only ones that merit replication. The list is neither geographically nor disciplinarily representative of the field. It is meant to spark discussion (or better still disagreement) and provide examples of the types of studies we feel should be replicated. That is why there is a mechanism for supporting the replication of studies not on this list. Frankly, however, we prefer the list of studies be generated bottom-up by the ATBC community. For example, we propose there could be a series of ATBC workshops in which participants working in a diverse range of subdisciplines and locations come together with representatives from the Center for Open Science to discuss the criteria for inclusion and propose a list of studies. This would be followed by an opportunity for the entire membership of the ATBC to provide feedback on the proposed studies and nominate alternatives.

How would the Reproducibility Project: Tropical Ecology be Implemented?

We envision a 10-year Reproducibility Project with two principal phases. In Phase 1 the

ATBC would solicit and select Principal Investigators (PIs) to guide the replication of five studies on our priority list. These PIs – with the assistance of the Center for Open Science, an ATBC Committee, and *Biotropica*'s Editors – would develop and post the guidelines for replicating a study, including the protocols, data collection sheets, and scripts for statistical analyses to be used by participating researchers. The ATBC would then help PIs recruit a network of researchers in different locations to replicate the study. Implementing a local replication requires working with the PI's to pre-register the study (Chambers *et al.* 2014, Nosek & Lakens 2014) with *Biotropica*'s Editorial Board, which peer reviews the design and provisionally accepts a *Registered Report* for publication prior to any data collection. This model, which has been adopted by a number of journals participating in Reproducibility Projects (see <https://cos.io/rr>), both enhances the credibility of projects and provides incentive for participation because it guarantees publication of results regardless of statistical significance or magnitude of the effects (Chambers *et al.* 2014, Nosek & Lakens 2014). Moreover, this model facilitates engagement of experts in the design of the methodology and leads to consensus on what constitutes a replication test of a study before the results are known (Nosek & Errington 2020a). This is valuable both for improving the quality of replication designs and to address the potential for pre-existing beliefs to motivate accepting or dismissing a replication's outcome. Once the data have been collected, the PI's will work with the research teams to analyze and archive it and prepare the results-included *Registered Report* for submission to *Biotropica*.

When all of the replications have been completed, the PIs will conduct a meta-analysis of the entire network's results – also to be published in *Biotropica* – with all network members as co-authors. We anticipate these meta-analyses will be high-impact advances given the geographic scope, methodological consistency, and the conceptual importance to the field of the

selected studies. That all participants would be authors or co-authors of two publications irrespective of their replication's outcome is a critical incentive we hope would encourage those who might otherwise be hesitant about repeating the work of others to participate.

Phase Two (years 5-10) would expand the Reproducibility Project by inviting researchers from ATBC's global community of members to either replicate other studies on the proposed list or nominate alternative studies they deem critical for replication. These proposed replications could either be conducted by networks or by individual researchers wishing to implement the approved protocols of important studies that at their field sites. Phase 1 would demonstrate to the community that replication is straightforward to implement, yields novel insights, and has tangible professional benefits. Phase 2 would consolidate a cultural shift in which replication is viewed as integral to research and training in tropical biology and stimulate the community to identify studies they view as worthy of replication.

How much would a Reproducibility Project cost?

The amount of funding needed to support the RP:TB will depend in part on the studies selected for replication and number of nodes in each replication network. That said, we estimate the RP:TB could be implemented for approximately \$800,000 plus institutional overhead. This amount is comparable to that of grants awarded by many private foundations and government agencies, and only a fraction of what is spent annually on tropical research worldwide. The majority of these funds (>80%) would go to support research, with the remainder used to support a small RP:TB coordination team, defray publishing and data archiving fees, and for program evaluation. Of course, there is no need for scientists interested in implementing replications as part of their research or teaching programs to wait for the ATBC and *Biotropica*'s Editorial

Board to consider and implement an RP:TB and pursue the funds support it. We encourage those interested in organizing and conducting replications now to do so, and ask that they contact us for additional information on project pre-registration and the support COS and ATBC are able to provide their efforts.

Broader Impacts of the Reproducibility Project in Tropical Biology

Some of the most important advances in tropical biology have come from researchers forming networks to systematically collect observations of tree growth and diversity in permanent plots (Menke *et al.* 2012, Anderson-Teixeira *et al.* 2015, Poorter *et al.* 2016, Rovero & Ahumada 2017). The same is likely to be true as tropical biologists embrace “distributed experiments” (Fraser *et al.* 2013, Borer *et al.* 2014), in which the same experimental manipulation is implemented at geographically and ecologically disparate locations (e.g., Romero *et al.* 2020). The Reproducibility Project in Tropical Biology (RP:TB) we envision complements these efforts with a new means by which researchers throughout the tropics can collaborate to test and advance theory. Because many of the experiments proposed for replication are inexpensive to implement and monitor, and financial obstacles to individual participation will be eliminated when the RP:TB is finally funded, we expect this initiative will greatly expand the diversity of researchers participating in or leading networks. We especially hope the RP:TB will serve to stimulate much needed North-South and especially South-South collaboration (Stocks *et al.* 2008). The ATBC-organized workshops and symposia emerging from the project will also serve as an important tool for capacity building and the professional advancement of early career scientists, as will the integration of reproducibility projects and a culture of open science in field courses and other educational programs. Finally, the data from replications will be highly

valuable for quantifying the generality, impact, magnitude, speed, and consequences of human-induced alteration of ecosystems. Nowhere is this need more critical than in tropical ecosystems, which are home to majority of the world's biodiversity and human population, play a critical role in global climate, and are being transformed by humans at an unprecedented rate and scale.

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AUTHIR CONTRIBUTIONS

Conceptualization: EMB, BMN, TME, RC

Writing – original draft: EMB

Writing – review & editing: RC, TME, BMN

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TABLE 1. Examples of replications vs. generalizability tests with tropical systems. Replications in EBE were often characterized by how closely the species and location matched those of the original study^a; we use the more conceptually generative definition of a replication: a study for which any outcome is diagnostic evidence of about a claim from prior research (Nosek & Errington 2020b).

Approach	<u>Potential Replications</u>		<u>Generalizability Tests</u>	
	Duplicates the original experimental or sampling methods with the same species or populations in the original location.	Duplicates the original experimental or sampling methods using the same species or populations but in a different location.	Tests of the same hypothesis using the original methods but in different species or systems	Tests of the same hypothesis using new methods
Examples using Janzen (1967)	Removal of <i>Pseudomyrmex ferruginea</i> from <i>Vachellia cornigera</i> (formerly <i>Acacia</i>) in Guanacaste National Park in Costa Rica.	Removal of <i>P. ferruginea</i> from <i>V. cornigera</i> in Southern Mexico using original methods	Removal of <i>P. ferruginea</i> from <i>V. collinsii</i> using original methods or Removal of <i>Crematogaster laevis</i> ants from <i>Tococa bullifera</i> using methods based on the original study	Comparing herbivory on plants after manipulating ant access to extrafloral nectaries
Examples using Dirzo et al. (1992)	Sample herb communities in gaps of different sizes and ages in the lowland forests of Los Tuxtlas, Mexico.	Sample herb communities in gaps of different sizes and ages in the lowland forests of the Maya Biosphere Reserve, Guatemala.	Sample herb communities in gaps of different sizes and ages in lowland forests of Borneo or Brazil using original methods or Sample herb communities in gaps of different sizes and ages in dry forests or cloud forests	Sample tree communities in gaps of different sizes and ages or Sample herb communities on landslides of different ages or sizes

^a e.g., "direct", "partial", or "conceptual" replication; reviewed in Kelly (2006), Nakagawa and Parker (2015), and Fidler *et al.* (2017).

TABLE 2. Proposed list of studies to be replicated as part of the ATBC Reproducibility Project in Tropical Biology.

<i>Interspecific Interactions and Population Dynamics</i>	
Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. <i>Ecological Monographs</i> 53:209-233.	The coevolutionary arms race between plants and herbivores has led to the evolution of thousands of defensive chemical compounds, including many used by humans as pharmaceuticals (e.g., quinine, taxol, opiates). Coley demonstrated how plant characteristics interact with local environmental conditions in forests to influence these plant defenses; replicating it in other locations is critical to both refining plant evolutionary theory and improving bioprospecting for novel pharmaceutical or pesticide compounds.
Augspurger, C. K. 1983. Seed dispersal of the tropical tree, <i>Platypodium elegans</i> , and the escape of its seedlings from fungal pathogens. <i>Journal of Ecology</i> 71:759-771.	Though this study was intended to test a fundamental theory explaining where seedlings become established, it also demonstrated fungal pathogens were an important and underappreciated mechanism influencing where seedlings became established. However, we know little about variation in pathogen effects at large scales or how climate change has altered their impacts, even for tree species that are central to community-based conservation strategies in the tropics (e.g., mahogany, Brazil nut). Replicating this study fill this data void.
Janzen, D. H. 1967. Interaction of the bull's-horn acacia (<i>Acacia cornigera</i> L.) with an ant inhabitant (<i>Pseudomyrex ferruginea</i> F. Smith) in eastern Mexico. <i>The University of Kansas Science Bulletin</i> 47:315-558.	Over 300 species of tropical plants worldwide house ants in specialized structures in return for ants ferociously defending them against herbivores - an interaction that has fascinated naturalists since the early 1600s. This study, conducted in Central America with the tree genus <i>Acacia</i> , was the first to demonstrate unequivocally and experimentally that this was

indeed a mutualism. Acacia are used by humans worldwide for timber and other uses and are critical stocks of carbon in African savannas; understanding why Acacia trees live or die has direct implications for individual livelihoods and conservation strategies. However, perhaps this study's greatest impact was in demonstrating ant-plant systems are ideal ones for experimentally studying the structure, breakdown, and recovery of mutualistic interactions in ways that are impossible with other mutualist systems (e.g., pollination, seed dispersal). Replicating this study will allow ecologists to infer how human activities have affected ecologically critical mutualistic interactions.

Marquis, R. J. 1984. Leaf herbivores decrease fitness of a tropical plant. *Science* 226:537-539.

This study was one of the first to show that herbivory can lead directly to reduced seed production in plants. Consequently, subsequent studies modeling the long-term viability of endangered plant species or those harvested for use by humans have usually incorporated either direct or indirect measurements of herbivory or its impact. Replicating this study will help assess under what circumstances these labor-intensive and challenging measurements are actually necessary.

Tropical Environments and Organismal Responses to Environmental Conditions

Chazdon, R. L., and N. Fetcher. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology* 72:553-564.

Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical

The limited amount of sunlight reaching the understory of tropical forests - less than 2% - is the factor limiting the growth and survivorship of forest plants. These studies mapped understory light levels and documented how plants respond physiologically to variation in the light environment. Though considered seminal, they have yet to be replicated. Consequently, it remains poorly understood how altered forest structure resulting from deforestation or drought changes forest

<p>trees. <i>Oecologia</i> 98:3-4, 419-428.</p>	<p>microclimate and how plants respond to these changes.</p>
<p>Ewel, J. J. 1976. Litterfall and leaf decomposition in a tropical forest succession in Eastern Guatemala. <i>Journal of Ecology</i> 64:293-308.</p>	<p>40% of the world's tropical forests are not "primary forest", but rather "successional" forest regenerating in areas abandoned after agriculture or deforestation. How these areas were used prior to being abandoned strongly influences nutrient cycling in regenerating forests, which in turn influences their species diversity and hence capacity to sequester carbon. Replicating this study globally will provide the most robust data to date on these issues, informing the principal international policy mechanisms</p>

Species Diversity and Dynamics

<p>Dirzo, R. C. C. Horvitz, H. Quevedo, M. A. Lopez. 1992. The effects of gap size and age on the understorey herb community of a tropical Mexican rainforest. <i>Journal of Ecology</i> 84(4): 809-822.</p>	<p>These studies were fundamental in describing how 1000s of species are able to coexist in tropical ecosystems when presumably competing for the same resources. Revisiting their conclusions is essential in light of the myriad ways tropical ecosystems are being altered, since most conservation policies are based on the original results. For instance, deforestation and droughts increase forest disturbance, which can cause species that thrive in them to increase in abundance while others go extinct.</p>
<p>Gentry, A. H., and C. Dodson. 1987. Contribution of nontrees to species richness of a tropical rain forest. <i>Biotropica</i> 19:149-156.</p>	
<p>Jankowski, J. E., A. L. Ciecka, N. Y. Meyer, and K. N. Rabenold. 2009. Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. <i>Journal of Animal Ecology</i> 78:315-327.</p>	<p>Similarly, warming climates are predicted to cause species found only at high elevations to be pushed "off mountaintops" to extinction. Finally, the interaction of changing landscapes and climates can influence animal behavior responsible for mating success; without understanding changes in species behavior, abundance, and distribution it is impossible to design</p>

Ryan, M. J. 1983. Sexual selection and communication in a Neotropical frog, *Physalaemus pustulosus*. *Evolution* 37:261-272.

conservation and management plans to proactively protect threatened biodiversity.

Anthropogenic Impacts on Tropical Systems

Bruna, E. M. 1999. Seed germination in rainforest fragments. *Nature* 402:139-139.

Carvalho, K. S., and H. L. Vasconcelos. 1999. Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. *Biological Conservation* 91:151-157.

Holl, K. D. 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: Seed rain, seed germination, microclimate, and soil. *Biotropica* 31:229-242.

Menke, S., K. Bohning-Gaese, and M. Schleuning. 2012. Plant-frugivore networks are less specialized and more robust at forest-farmland edges than in the interior of a tropical forest. *Oikos* 121:1553-1566.

Deforestation and the resulting isolation of 'islands' of forest surrounded by agriculture is possibly the leading cause of extinction in the tropics. The following studies have provided some of the most important and widely-applied insights to date on how plants and animals that remain in these forest fragments are influenced by the dramatic changes to their environment. Replication - especially in the understudied forests of equatorial Africa - will help ensure that the results of these studies are truly applicable to other regions or if resources are better allocated to mitigating the impacts of deforestation on other species and ecological processes.