

Opinion

Transformative Research Is
Not Easily Predicted

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Transformative research (TR) statements in scientific grant proposals have become mainstream. However, TR is defined as radically changing our understanding of a concept, causing a paradigm shift, or opening new frontiers. We argue that it is rarely possible to predict the transformative nature of research. Interviews and surveys of 78 transformative ecologists suggest that most TR began with incremental goals, while transformative potential was recognized later. Most respondents thought TR is unpredictable and should not be prioritized over ‘incremental’ research that typically leads to breakthroughs. Importantly, TR directives might encourage scientists to overstate the importance of their research. We recommend that granting agencies (i) allocate only a subset of funds to TR and (ii) solicit more realistic proposal statements.

Trends

We argue that transformative research is inherently unpredictable.

Emphasizing transformative research actually may hinder scientific discovery.

‘Do you think Bob Paine knew he was being transformative when he started ripping sea stars off rocks? No!’.

Funding agencies should concentrate on the ‘goals’ of the research rather than the ‘outcome’.

Transformative Research As an Unrealistic and Potentially Harmful Goal

Internationally, granting agencies recently have required proposers and reviewers to identify how proposed research would be transformative. We argue that **transformative research** (TR; see [Glossary](#)) is inherently unpredictable at the proposal phase and typically becomes recognizable late in the scientific process. Further, it often arises from **‘incremental’ research** (IR), which is considered its opposite. This dichotomy was noted by Kuhn and Hawkins [1], who argued that scientific knowledge proceeds incrementally, occasionally punctuated by paradigm-shifting discoveries. Paradoxically, emphasizing TR actually can hinder scientific discovery. Under zero-sum funding, if breakthroughs result from incremental advances, reapportioning funding in favor of putative TR actually can decrease breakthroughs. Further, prioritizing TR might encourage scientists to overstate the importance of proposed research. Overhyping research expectations could undermine public trust in science, now more important than ever to uphold [2].

As a caveat, we believe it is important to contemplate the potential of proposed research to be groundbreaking. However, we question whether the lofty definition of TR as radically changing our understanding of a concept, causing a paradigm shift, or opening new frontiers is predictable at the proposal phase, and thus question whether funding decisions should strongly depend on TR statements.

Directives for TR in Grant Proposals

Prioritization of TR has become pervasive among granting agencies including the European Research Council (ERC), Canadian Natural Sciences and Engineering Research Council (NSERC), Academy of Finland, US National Institutes of Health (NIH), US Department of Defense (DoD), and US National Science Foundation (NSF). These agencies often use synonyms for TR such as ‘high-risk’, ‘pioneering’, or ‘breakthrough’ research. For example, the ERC supports ‘pioneering proposals addressing new and emerging fields of research or

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proposals introducing unconventional, innovative approaches and scientific inventions' [3]. One goal of NSERC's Discovery Frontiers grants is to 'conduct transformative, paradigm-changing research' [4].

The US NSF has made the pursuit of TR a top priority by asking for TR statements in every major research proposal solicited. This is one of our own motivations for exploring the issue of TR in proposals, but we believe that our findings and recommendations are relevant internationally. Here, we use the NSF as an example of how TR became a focus of granting agencies. In 2005, the US National Academy of Science (NAS) reported that the US lagged other countries in scientific advances [5]. This spurred the National Science Board (NSB) to propose ways that NSF could nurture risky, potentially 'transformative' science [6]. NSB argued that 'high-risk/high-impact' research should be an important component of any funder portfolio. NSB recommended 'a new, distinct, and separate Foundation-wide program to solicit and support transformational . . . proposals'. While stressing the importance of TR, the NSB cautioned that distinguishing TR from IR is often possible only in hindsight, and 'did not see a need to adjust or to modify the current merit-review mechanism at NSF'. In response, NSF, which funds approximately 24% of US academic research (www.nsf.gov/about), required all proposers to address how each proposal was transformative [7]. The author guidelines were reworded (in bold), 'How important is the proposed activity to advancing knowledge and understanding within its own field or across different fields? . . . To what extent does the proposed activity suggest and explore creative, original, **or potentially transformative** concepts?' [8].

A Tale of Two Transformative Ecologists

This opinion piece began with a conversation among the coauthors. Sarah Gravem had suggested that a planned experiment was insufficiently 'transformative'. Bruce Menge retorted, 'Do you think Bob Paine knew he was being transformative when he started ripping sea stars off rocks? No! We won't know if something is important until we test it.' Menge was mentored by two iconic and transformative ecologists, Robert T. Paine and Joseph H. Connell. During Menge's PhD, Paine developed the 'keystone' species concept [9,10], which experimentally demonstrated top-down effects by predators in nature and challenged the paradigm that competition drove species coexistence and diversity (e.g., [11–14]). His work on the keystone species concept influenced many fields of research throughout the sciences (Figure 1A; see Supplemental Information 1 online for figure methods; see <http://bit.ly/2uJCqA1> for an interactive version). Nevertheless, the transformative impact of his work grew slowly (Figure 1B).

Did Paine predict the transformativeness of this research when he began his experiments? With his 2016 passing, we will never know. Shortly beforehand, Paine commented to J. Estes (personal communication) that upon seeing the Washington coastal intertidal community, he recognized it was an 'ecological gold mine'. However, he did not indicate he predicted his results. Paine later realized the implications of his result for other systems, but nonetheless the significance of his findings was long underappreciated.

In 1970, Menge took a postdoctoral position with Joseph Connell and William Murdoch at University of California Santa Barbara. Connell's [15] paper on barnacle competition is a long-standing textbook example and was perhaps the first demonstration of the power of field experiments. It is doubtful that Connell expected his research to be transformative. Connell's interest was the topic of population regulation rather than competition. While walking the intertidal at Millport, Scotland, he noticed that each footfall covered 100s of barnacles, far more than the 40 rabbits trapped in his entire Master's research. He also realized that the tiny, immobile barnacles allowed manipulative experiments. Like Paine's work, realization of the importance of Connell's paper took time, but both studies were clearly transformative.

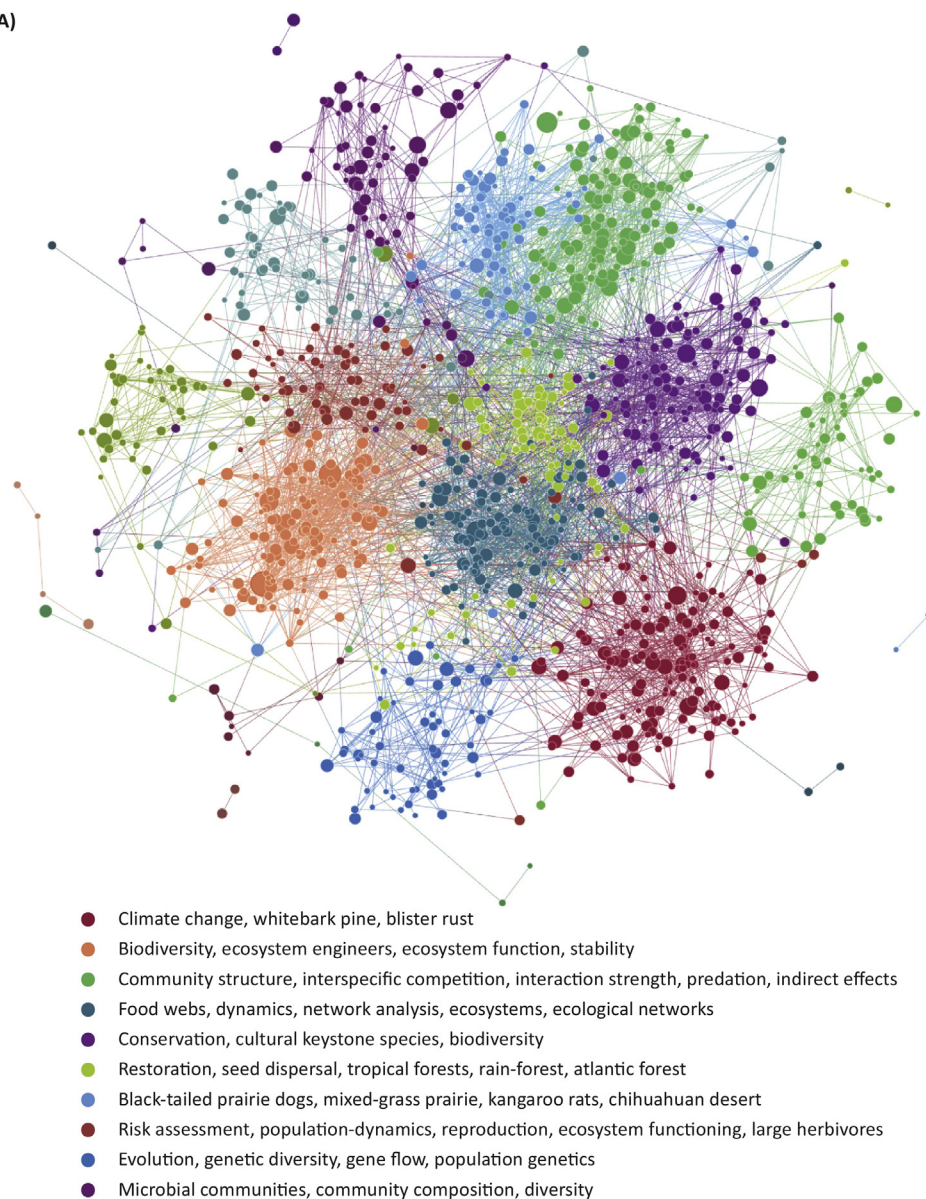
Glossary

Breakthrough research: also known as high-risk research. It is transformative, ambitious, and mold-breaking research. Its significance can be based on tackling exceptionally wide and complex research problems, on challenging existing theories and scientific paradigms, on radically new ways of using methods, as well as on unprejudiced combination and interdisciplinary integration of different research perspectives [39].

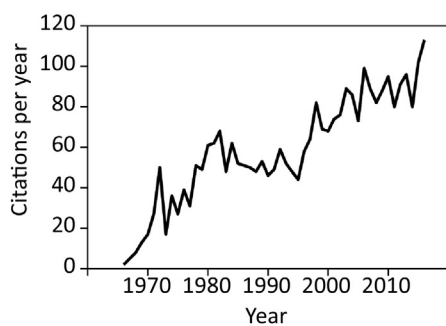
Incremental research (IR): research building upon the results of previous studies or testing long-standing hypotheses and theories [6].

Transformative research (TR): research driven by ideas that have the potential to radically change our understanding of an important existing scientific or engineering concept or leading to the creation of a new paradigm or field of science or engineering. Such research also is characterized by its challenge to current understanding or its pathway to new frontiers (as defined by NSB [6]).

(A)



(B)



Trends in Ecology & Evolution

(See figure legend on the bottom of the next page.)

Our Approach: Investigating the Predictability of TR

Here, we focus on TR in ecology, acknowledging that in this field TR can be especially rare, as Paine himself argued [16]. To investigate the usefulness of the transformative proposal criterion for promoting scientific progress, we interviewed groundbreaking authors, and surveyed opinions of 72 highly cited ecologists. We asked: (i) When do researchers realize their research is transformative? (ii) Can a researcher predict TR? (iii) Do scientists agree that TR statements are useful metrics in judging proposals? (iv) Should TR be prioritized over IR? (v) Is prioritizing funding for TR potentially harmful?

Case Studies

The authors collectively identified six important ecological advances to be used as case studies. We interviewed the authors about the process of doing TR, including Stephen R. Carpenter [17], Camille Parmesan [18], John W. Laundré [19], Joan A. Kleyvas [20], William J. Ripple [21], and Daniel I. Bolnick [22] (see Supplemental Information 2 online for interview questions). These choices represent studies that have transformed our personal understanding of ecology but we do not suggest that they are the six most transformative ecology studies. In addition, our examples are biased toward US ecologists because of our location, but we believe the results and our recommendations are relevant worldwide.

Survey

We identified transformative ecologists using a Web of Science search of all records (1965–2016) using the keyword ‘ecology’ from the following journals: *Journal of Ecology*, *Ecology*, *Ecology Letters*, *Ecological Monographs*, *American Naturalist*, *Functional Ecology*, *Proceedings of the Royal Society of London – Biological Sciences*, and *Oecologia*. We selected papers with 650 or more citations, excluding reviews and methods papers, and contacted the first authors. We also contacted first authors of papers in the Western Society of Naturalists’ list of Top 100 influential papers in Ecology [23]. 72 of the 110 authors contacted completed our survey (see Supplemental Information 3 online for more information). We acknowledge that citation numbers are an imperfect way of indicating TR, but our goal was to contact a group of influential authors for surveying purposes, not to exhaustively identify TR.

Interview Results

In general, the authors said that their transformative studies began as incremental investigations whose importance they only appreciated later. Parmesan’s sentiment that ‘it was more a matter of being in the right place at the right time’ (Box 1) was echoed by many authors. Many studies had minimal funding. For example, Laundré (see Supplemental Information 4 online) was supported by a small citizen science project, and Ripple (Box 2) used discretionary funds. Of the authors interviewed, only Carpenter had agency funding before his research on trophic

Figure 1. The Reach of Paine’s Transformative Research. (A) Network visualization of journal articles from 1991 to 2016 that included the term ‘keystone species’ in the title, abstract, or keywords identified by Web of Science (keywords and abstracts became available in 1991). Every node is an article and is sized by the number of citations per year. Nodes are linked if they share similar keywords. Groups of documents that are more linked formed 22 clusters of ‘keyword themes’ indicated by color and labeled by keywords most commonly shared in the group. Clusters that contain 10 or more articles are labeled. The broad representation from different scientific fields visually emphasize the cross-disciplinary reach of Paine’s transformative research. For example; certain clusters pertain specifically to the genesis of the keystone concept (e.g.; community structure; food web dynamics); while others in different fields of study (e.g.; microbiology; evolution; and genetics) highlight the breadth of Paine’s work; and the network illustrates the reach of his transformative discovery. See <http://bit.ly/2uJCqA1> for an interactive version. (B) The citation rate per year in Web of Science of Paine’s 1966 transformative paper [9] that experimentally demonstrated the keystone species effect. This shows that the transformative impact of the research began modestly and grew over time. For a Figure360 author presentation of Figure 1, see the figure online at <http://dx.doi.org/10.1016/j.tree.2017.08.012#mmc1>

Box 1. Case Study: Dr Camille Parmesan's Work on Species' Responses to Climate Change

Dr Parmesan is a professor at the University of Plymouth and an Intergovernmental Panel on Climate Change (IPCC) contributor. Her early work focused on the ecology of a butterfly species (*Euphydryas editha*) in the American Southwest. Initially, she examined range shifts of a single butterfly species, expecting to find fluctuations due only to local extinctions and extensions among specific ecotypes. Instead, she found the now well-known shifts northward and toward higher elevations in the species' range [18]. During this time, climate scientists were examining the trend in rising global temperatures, but had not yet made connections to how this would affect organisms. Parmesan's 1999 paper [40], funded by a postdoctoral position at the National Center for Ecological Analysis and Synthesis (NCEAS), found that the concerted movement of European butterfly species northward closely correlated with the observed northward shift in continental isotherms. This paper caught the attention of both the scientific community and policy makers, and finally convinced many that the effects of climate change were nontrivial. A later global meta-analysis [41] provided the most conclusive evidence for northward species range shifts. These papers were instrumental in spawning the field of global change biology that has yielded thousands of studies to date. For her part, Dr Parmesan did not believe that researchers can be deliberately transformative; it is simply a matter of being in the right place at the right time.

cascades in lakes (see Supplemental Information 5 online). The insightful moments also typically occurred after the study was underway. A chance glance at a poster in the Yellowstone visitor center spurred Ripple's ideas on terrestrial trophic cascades. Laundré noticed during data collection that despite abundant deer, few were eaten by mountain lions, launching the idea of the 'ecology of fear' (see Supplemental Information 4 online). Several were unaware of the transformative potential of their work until the analysis, or even until the publication stage. For example, Kleypas stated that the impact of her ocean acidification research 'didn't hit [her] until [she] had put together the results of the study' (see Supplemental Information 6 online). However, despite publishing what many consider TR, none of the six authors believed that scientists can be deliberately transformative (Boxes 1 and 2; see Supplemental Information 4–7 online).

Survey Responses**When Do Researchers Typically Realize Their Research Was Transformative?**

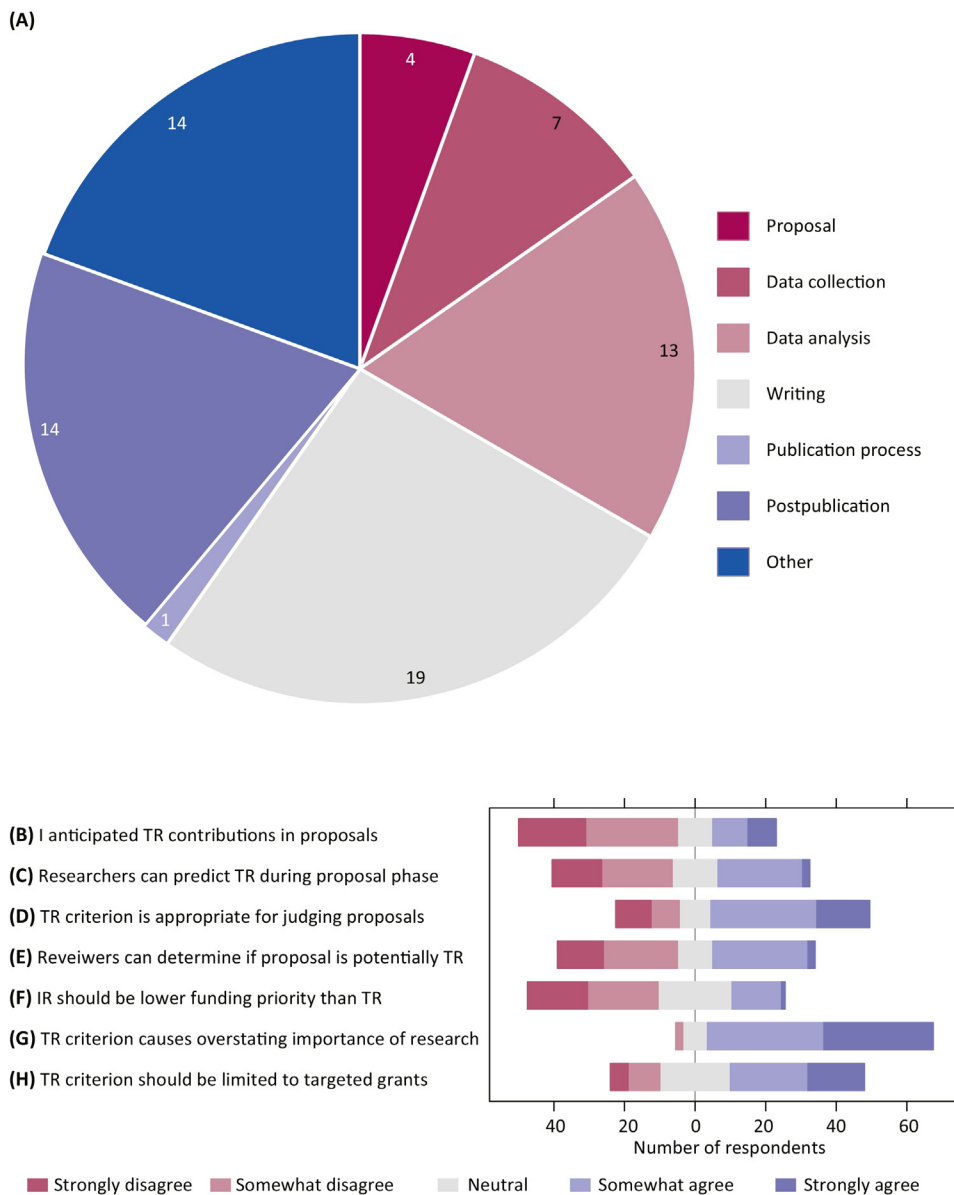
Typically, researchers we surveyed realized the transformative nature of their work during later research stages, including data analysis (18.1% of the time), writing (26.4%), and

Box 2. Case Study: Dr William Ripple's Work on Predators Initiating Trophic Cascades

In the early 1990s, discussion regarding the role of herbivory and predation in controlling communities was ongoing following the conceptual framework outlined by Hairston and colleagues' Green World Hypothesis [42]. Despite McLaren and Peterson's [43] early work on Isle Royale, trophic cascades were thought to be nonexistent or very weak in terrestrial compared with aquatic systems [44]. In their 2000 paper [21], William Ripple and Eric Larsen explicitly described trophic interactions as a trophic cascade in a terrestrial system, and inspired a surge of research across disciplines [45]. Using university travel funds, they visited Yellowstone in 1998 to investigate whether ongoing recruitment failure of aspen since the 1930s was correlated with climate change, fire suppression, or an increase in browsing elk populations following relaxation of hunting pressure. The potential role of apex predators in regulating aspen recruitment was considered only after Ripple saw a photograph of a wolf standing among young aspen in the visitor's center. Tree core data revealed that the truncated age structure of aspens in the park was tightly correlated with the extirpation of wolves from the park by 1926 [21]. The paper was published in *Biological Conservation* only after extensive revisions. The paper received widespread attention among scientists and the public, as Yellowstone is a highly valued area with many invested stakeholders.

Follow-up research demonstrated that wolf reintroduction in 1995 led to a decrease in elk browsing and a subsequent increase in aspen recruitment and canopy cover. Cascading effects of large carnivores on herbivore density and plant recruitment have now been demonstrated in multiple terrestrial ecosystems [46]. Research on trophic downgrading (the anthropogenic extirpation of large carnivores) and its effects on overall ecosystem health, function, and diversity is now a major interdisciplinary research focus [47].

Ripple said that his initial observations were conducted at a serendipitous time, and that the availability of other data sets on predator abundance and tree recruitment in the park dating back to the early 20th century helped connect his observations. During his initial, nearly unfunded, fieldwork in Yellowstone, Ripple did not expect to spur almost two decades of intensive research on terrestrial trophic cascades. While Ripple believes that the transformative nature of research cannot be predicted, he does believe that it is possible to increase your chances and that 'asking big questions can get you big answers'.



Trends in Ecology & Evolution

Figure 2. Responses by 72 Highly Cited Ecologists to an Email Survey Regarding Their Views on Transformative Science and Its Role in Funding Decisions. (A) Survey responses to the question ‘During which phase did the transformative potential for your research become solidified?’ by highly cited ecologists. Numbers indicate sum of the responses. Only four identified the transformative potential of their research during the proposal stage, whereas 20 realized it during data collection and analyses and 34 realized it during writing, publication, or postpublication. (B–H) Likert-scale responses by transformative ecologists to survey questions on transformative and incremental research (TR and IR, respectively). Neutral responses (gray) are centered in the figure, with frequency of strongly disagree and disagree to the left of center (dark red and red, respectively) and of agree and strongly agree (blue and dark blue, respectively) to the right of center. Ecologists generally disagree with the statements ‘I anticipated transformative research contributions in proposals’ and ‘researchers can predict transformative research during the proposal phase’. They generally agreed that ‘transformative research is appropriate for judging proposals’ but there was no consensus on whether ‘reviewers can determine if a proposal is potentially transformative research’. Ecologists generally strongly disagree that ‘incremental research should be lower funding priority than transformative research’ and strongly agree that the ‘transformative research criterion causes overstating importance of research’. Moving forward, ecologists think that the ‘transformative research criterion should be limited to targeted grants’. Full text of questions and counts are included in Supplemental Information 3 online.

For a Figure360 author presentation of Figure 2, see the figure online at <http://dx.doi.org/10.1016/j.tree.2017.08.012#mmc2>

postpublication (19.4%), but rarely at the proposal stage (5.6%; [Figure 2A](#) and Supplemental Information 3 online). Similarly, the majority (61%) had not anticipated their contributions to ecological progress during the proposal phase, though some did (23%; [Figure 2B](#) and Supplemental Information 3 online).

Can a Researcher Predict If His or Her Research Will Be Transformative?

On average, survey respondents ‘somewhat disagreed’ that TR is predictable at the proposal phase ([Figure 2C](#) and Supplemental Information 3 online). One respondent asserted that predicting TR was impossible: ‘The most transformative ideas will *not* be ones predicted in proposals. If you can predict them, they are unlikely to be transformative. The most transformative ideas are the surprises in your data or observations. Surprises are by definition not predictable.’ This sentiment was actually acknowledged by the NSB and NSF: NSB suggested that identifying TR is only possible in hindsight [6], and the then NSF Director Arden Bement noted ‘Most transformations resulting from research are recognized *post hoc*, not *a priori*’ [24]. Similarly, Trevors *et al.* [25] commented ‘Transformative research is often elusive, requires different approaches and sometimes depends on luck. [It] concerns intangibles such as human intuition, curiosity, serendipity, unpredictable events, correcting previous knowledge, implausible hypotheses, a well-prepared mind and often interpersonal communication.’

Are TR Statements Useful in Reviewing Proposals?

Although most respondents disagreed that researchers can predict TR in proposals and most did not predict their own TR ([Figure 2A–C](#) and Supplemental Information 3 online), respondents ‘somewhat agreed’ that the TR statements are appropriate for judging ecological proposals ([Figure 2D](#) and Supplemental Information 3 online). One respondent, an active proposer and grant reviewer, said ‘I agree that ideally we need funding for both IR and TR proposals. But the reality is that research funding is quite limited. Given these constraints, should priority be given to research that has the potential to be transformative? I think a strong case can be made that this is one valid criterion.’

Thus, we have a conundrum. Most researchers feel that they cannot predict TR in proposals, but also feel TR statements are useful in the funding process. But can reviewers reliably evaluate transformative potential? No consensus emerged on this issue ([Figure 2E](#) and Supplemental Information 3 online). Concern about reviewer abilities to judge potentially transformative proposals was one of the original reasons that TR statements were recommended [6]. However, Hossenfelder [26] argued that encouraging reviewers to favor potentially TR ‘will not work very well . . . If you random[ly] sample [reviewers], you’re more likely to get conservative opinions just because they’re more common. As a result, [TR] projects are unlikely to be reviewed favorably. [Reviewers] still have to evaluate if the high risk justifies the potential high payoff. And assessment of tolerable risk is subjective.’

Should TR Funding Be Prioritized over Incremental Research Funding?

Transformative requirements can be detrimental to the IR from which many major paradigm-shifting ideas materialize. By placing emphasis on TR, funding agencies might stifle the IR needed to lay the groundwork required to facilitate proposals that can define a new field or challenge major paradigms. Our survey revealed broad sentiment among ecologists that IR should not be a lower priority than TR ([Figure 2F](#) and Supplemental Information 3 online). For example, one respondent commented ‘thousands of us make incremental steps, . . . that collectively move the dial on our science . . . I believe that emphasis on novelty and [TR], while well intended, has neutral or more likely negative effects on our path forward. It creates a false dichotomy between “novel” and “incremental” science.’

Incremental research is often viewed as a loaded term. It implies that studies that do not shift paradigms, redefine a field, or create new technology are less important, or at least less worthy of funding. For example, former NSF director Bement [24] commented ‘if it’s “safe science,” NSF should not fund it.’ However, most paradigm shifts would not be possible without a wealth of background knowledge and field-defining research. Kuhn and Hawkins [1] suggested that most science was incremental, or what they called ‘normal’. Many agree that incremental advances are often prerequisites of TR [6,27–30]. The necessity of IR was even featured on Freakonomics Radio [28], where economist Ed Gleaser pointed out that Nobel Prizes are not typically given for single TR papers. Rather, they are often given for a body of IR, often represented by dozens of papers, by a particular person. If in fact transformations arise from IR, then the transformative criterion is actually redundant with the solicitation of IR [31]! This is reflected by mixed evidence that soliciting TR led to increases in transformative outcomes compared with the typical model [33].

Is Prioritizing Funding for TR Potentially Harmful?

Our results suggest that predicting TR at the proposal stage is not only difficult, but also that prioritizing it can be potentially harmful. Survey-takers expressed strong consensus that emphasizing the importance of TR in proposals causes researchers to overstate the potential importance of their work (Figure 2G and Supplemental Information 3 online). With limited funding, incentivizing ‘promise inflation’ can be harmful to the ‘honest scientists who . . . propos[e] to [make] an important contribution to the solution of an important problem. They risk being dismissed as small-timers with no vision’ [27]. One respondent commented that transformative statements can be more of an ‘essay contest’ than truthfully representing the likely impact of proposed research. Survey results echo this idea. Respondent Dr Lauri Oksanen stated, ‘If folks are requested to emphasize the transformative aspects of a proposal, the likely result is self-bragging and a soup of fashionable terms.’ Holbrook [31], an organizer of an NSF workshop on TR, expressed the opinion that grant writing has turned into a game where ‘transformative’ is a buzzword not taken seriously by proposers, reviewers, or authors.

The transformative requirement might also be especially detrimental to ecology relative to other fields. One respondent remarked, it ‘is certainly a death-knell for long-term research projects.’ Unfortunately, successful long-term ecological research requires lengthy periods of data collection, which can lead to their categorization as ‘incremental’. For example, Hubbell’s [33] *Unified Neutral Theory of Biodiversity and Biogeography* was an unanticipated but transformative consequence of long-term monitoring and mapping of tropical trees in Panama. This is especially concerning because long-term ecological research contributes relatively more to ecological knowledge and to public policy [34].

Looking Ahead

Recommendation (i): Allocate Only a Subset of Grant Funds to Potentially Transformative Research

This strategy has been adopted by several granting agencies (e.g., ERC, NSERC, Academy of Finland, US NIH, and DoD). Targeted allocation of funding for TR, in our view, would both encourage TR and support IR, leading to transformations. Further, survey-takers agreed that the TR requirement should be limited to only a subset of funds (Figure 2H, see Supplemental Information 3 online). Such a strategy would not significantly affect funding for typical incrementally focused proposals, would encourage long-term research, and would not incentivize grant writers to inflate the importance of their research. This last benefit is important; public trust in science and scientists has waned [35], in part due to antiscience polarization tactics [36,37]. In this atmosphere, overhyping the likely importance of one’s research can be damaging. This recommendation is particularly relevant for the NSF because the TR requirement is ubiquitous

Box 3. Recommendations for Granting Agencies

Allocate only a subset of grant funds to potentially transformative research.

Solicit realistic proposal statements regarding research goals.

among NSF-funded programs. The NAS, NSB, and others originally recommended that the NSF allocate a fraction of the agency research budget to TR [5,6,27]. Since NSF implemented the ubiquitous TR requirement with ‘constructive ambiguity’, intending to assess its efficacy in the future [6,24,29], we believe the time for reassessment has come.

Recommendation (ii): Solicit Realistic Proposal Statements Regarding Research Goals

We do not criticize the goal of fostering TR itself, but feel identifying it is unrealistic for most proposals. As our results suggest, and as granting agencies acknowledge [6,25,38,39], predicting TR is not usually possible. Thus, we suggest that granting agencies should adopt a broader definition of TR or use a different term that is more realistic. Currently, proposal solicitations of NSF, and to some extent ERC, focus on the potential transformative ‘outcomes’ of all proposed research, which seem inherently unknowable (e.g., ‘changing’ our understanding, ‘creating’ paradigms or fields, ‘pathways’ to new frontiers, scientific ‘inventions’). This creates a straw man for reviewers to criticize as being either too far-fetched or too uncertain to fund. Rather, we suggest that funding agencies concentrate on the ‘goals’ of the research rather than the ‘outcome’. For example, the Academy of Finland uses the term **breakthrough research** [39]. Breakthrough research is rooted in the goals of ‘tackling’ problems, ‘challenging’ theories and paradigms, ‘using’ methods, and ‘integrating’ perspectives. We suggest that judging proposals by their goals rather than their potential outcomes is both realistic and easier for reviewers to evaluate.

Concluding Remarks

We suggest (i) TR is usually realized in later stages of research; (ii) researchers cannot predict TR, especially in proposals; (iii) TR predictions are not useful in judging proposals; (iv) TR funding should not detract from IR funding; and (v) requiring TR statements incentivizes disingenuousness and can stifle certain types of research. Though we wholeheartedly agree that proposals should explore the novelty, utility, or advanced contributions the research can provide, we recommend that only a subset of solicitations request TR statements while most should solicit more realistic statements of research goals. We believe that our findings and recommendations are relevant for granting agencies worldwide as they determine how to allocate funding among different research endeavors (see Box 3).

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Supplemental Information

Supplemental information associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tree.2017.08.012>.

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