Surrogates Underpin Ecological Understanding and Practice

LUKE S. O'LOUGHLIN, DAVID B. LINDENMAYER, MELINDA D. SMITH, MICHAEL R. WILLIG, ALAN K. KNAPP, KIM CUDDINGTON, ALAN HASTINGS, CLAIRE N. FOSTER, CHLOE F. SATO, MARTIN J. WESTGATE, AND PHILIP S. BARTON

A *surrogate* is a proxy measure for an attribute of true interest that is too difficult or costly to measure directly. Surrogacy is widely used in the environmental sciences, as well as in other disciplines, such as clinical medicine and pharmacology (Barton et al. 2015, Lindenmayer et al. 2015a). In medicine, for example, easily quantified properties of blood, such as cholesterol level, are regularly used to infer a patient's health, risk of disease, or response to a medical treatment (Barton et al. 2015). Similarly, ecologists often monitor attributes such as carbon stocks, species richness, or vegetation structure to infer the overall state of biodiversity, risk of undesired change, or response to a management intervention (Lindenmayer et al. 2015a).

Surrogates are often used in applied ecology to inform decisions about biodiversity management, atmospheric pollution, and conservation reserve selection (e.g., Rodrigues and Brooks 2007). However, proxy measures are also used widely in fundamental ecology. Ecosystem properties such as productivity, fire severity, and water quality are almost exclusively inferred from related but indirect measures (e.g., Keeley 2009). This implicit use of surrogacy is often not acknowledged outside of the applied disciplines. The conceptual and analytical frameworks developed to improve surrogacy in applied contexts therefore have much to offer research in fundamental ecology. Similarly, the causal frameworks and search for mechanism in fundamental ecology has much to offer applied surrogacy. In our view, integrating and communicating the lessons from each will lead to better outcomes for both.

Here, we consider how fundamental tenets from surrogate research, particularly those that deal with intrinsic uncertainty and risk, are underappreciated in broader ecological research. Our assertion is that explicit recognition of the use of surrogates will benefit all ecological research through improved evaluation of the accuracy, consistency, and certainty of the inferences drawn from measures, regardless of the context.

Understanding the limits of surrogacy

Financial, temporal, or logistical constraints may prohibit the direct measurement of a target of interest (Lindenmayer et al. 2015a), meaning statistically robust and informative surrogate measures are needed to make inferences about unmeasured quantities (see Lindenmayer et al. 2015b). Research on evaluating and validating surrogates has led to many positive outcomes for applied conservation, including early identification of ecosystem collapse, insights into rarely observed threatened species, and improved capacity to make effective management decisions (e.g., Rowland et al. 2018). However, surrogates are not perfect, and many surrogates may fail to provide useful information about a target of interest under some conditions, with potentially negative consequences. In medical research, for example, a relationship between arrhythmia and myocardial infarction led to the use of arrhythmia-suppressing drugs that ultimately increased death rates (Buyse and Molenberghs 1998). This example, as well as many others, provided a strong imperative for the development of reliable, accurate, and informative surrogates in medicine.

Evaluating surrogates in applied ecology is also important to ensure they provide useful information about a target. For instance, taxon-based surrogate schemes typically make an a priori selection of a surrogate (e.g., a particular bird species) assuming it is correlated with a target (e.g., the status of a broader avian assemblage; Lindenmayer et al. 2002). However, these relationships may be strongly nonlinear, scale dependent, context specific, or simply not present, such that the surrogate is informative and related to targets under some conditions but not others (e.g., Westgate et al. 2014). Understanding the mechanisms and theoretical underpinnings of surrogate–target relationships is essential to define the conditions under which a surrogate will be informative. Importantly, identifying where surrogates fail to provide the intended information about a target provides opportunities to develop new knowledge regarding causal mechanisms. Careful evaluation of surrogacy creates opportunities to improve understanding of the circumstances for which ecological relationships persist to the benefit of both fundamental and applied ecology.

Implicit use of surrogates in ecology

Surrogates have long been an important component of fundamental ecological research, although this is often not acknowledged. Many of the standard approaches for measuring key attributes of ecosystems are proxies for targets that are mostly unmeasurable. For instance, there is a wealth of fundamental research on the biotic and abiotic drivers of productivity and how productivity drives other biological patterns across a diverse array of ecosystems (see Zhu et al. 2016). However, there is often no practical way to directly measure total productivity, and so other measures, such as chlorophyll A, leaf litter biomass, or remotely sensed metrics (e.g., Normalized Difference Vegetation Index; NDVI), are used as proxies. Although the use of established surrogates for an ecosystem attribute such as productivity has tremendous value, it is naïve to think that the use of surrogates does not involve uncertainty or risk or present other problems associated with indirect measures and inference.

A key problem with the unacknowledged use of surrogates in fundamental ecology is that it ignores the variability, error, and context dependency inherent in the use of a proxy, thereby oversimplifying or potentially leading to a false level of confidence in results (Johnson and Lidström 2018). For example, NDVI is increasingly being used to test how forest productivity influences fauna because the link between NDVI and productivity is considered well established (Pettorelli et al. 2005). However, the key empirical research that supports NDVI as a robust surrogate for forest productivity shows wide-ranging correlations (r between 0.25 and 0.99) between NDVI and other measures of productivity (tree ring width, tree height, and litterfall) that are themselves often surrogates (Wang et al. 2004). Thus, there exists variation associated with both the context in which the relationship is determined and then where it is applied. However, NDVI is typically used without acknowledgement of uncertainty in how accurately it represents productivity or acknowledgment that the relationship between NDVI and productivity requires contextual validation.

The implicit use of surrogacy in fundamental research is by no means limited to productivity and includes widely used proxies for many well-researched ecological processes, patterns, or attributes. For instance, fire severity is a complex disturbance process related to the removal of plant biomass as a function of properties of a particular fire (e.g., burn size, temperature, and length), and it is almost exclusively represented by simple measures such as “scorch height” or “minimum twig diameter” (Keeley 2009). The abundance of particular carnivore species will often be inferred from counts of scats or tracks rather than direct observations (Heinemeyer et al. 2008). Thus, although researchers may present an assessment of the change in predator abundance in response to fire severity (and the uncertainty in that inference), what they may have actually modeled is a shift in scat density relative to fire “scorch height,” without recognition of the uncertainty of those surrogate–target inferences. In much of fundamental ecology, the simple measures used to infer these and other complex targets (e.g., ecological niche breadth, disturbance intensity, environmental stress, and resilience) are described but rarely acknowledged as surrogates.

Surrogates as a bridge between fundamental and applied ecology

A common perception in ecology is that fundamental and applied research are quite separate disciplines and that surrogate research is a subcomponent of applied ecology (figure 1a). A related idea is that knowledge transfer from fundamental to applied research is of greater importance than knowledge transfer in the opposite direction (figure 1a; Courchamp et al. 2015). We suggest that this model does not reflect the reality of surrogate use across both fields of research, underrepresents the diversity of surrogate research, and fails to consider the importance of knowledge transfer from surrogate to fundamental research (figure 1b). We propose that greater awareness of surrogates has the potential to increase the connection between fundamental and applied ecology, improve applied surrogacy through greater appreciation of mechanisms and theory, and strengthen fundamental research through greater acknowledgement of the need to evaluate and validate surrogate–target relationships.

We recognize that almost every association in ecological science includes considerable variability, error, and context dependency. Although a practical need to synthesize complexity into generalized theory exists, de-emphasizing uncertainty risks misinterpretation and overconfidence in inferred relationships (Johnson and Lidström 2018). This is where improved recognition of surrogate use in ecological research would be of greatest benefit. The surrogate literature offers approaches, tools, and language to account for and communicate the uncertainty intrinsic to using a measure of one entity to make an inference about another (see Lindenmayer et al. 2015b). Adopting the frameworks for evaluating and validating surrogates allows researchers to quantitatively formalize trade-offs between accuracy and cost-effectiveness and to more clearly justify the use of surrogates, whatever the context.

We contend that the use of surrogates should serve as an important bridge between the fields of fundamental and applied ecology. Ecosystems are complex, and surrogates are used to inform targets, irrespective of whether the target is a mechanistic process or the outcome of a conservation management intervention. Ecologists should seize the opportunity to clearly recognize surrogates in their research and appreciate that their research may speak to a much broader audience. Uniting theory and practice through a greater emphasis on surrogate ecology is particularly important for a changing world in which anthropogenic factors are increasingly determining the structure and functioning of ecosystems.

Acknowledgments

The work reported in this paper was funded by an Australian Research

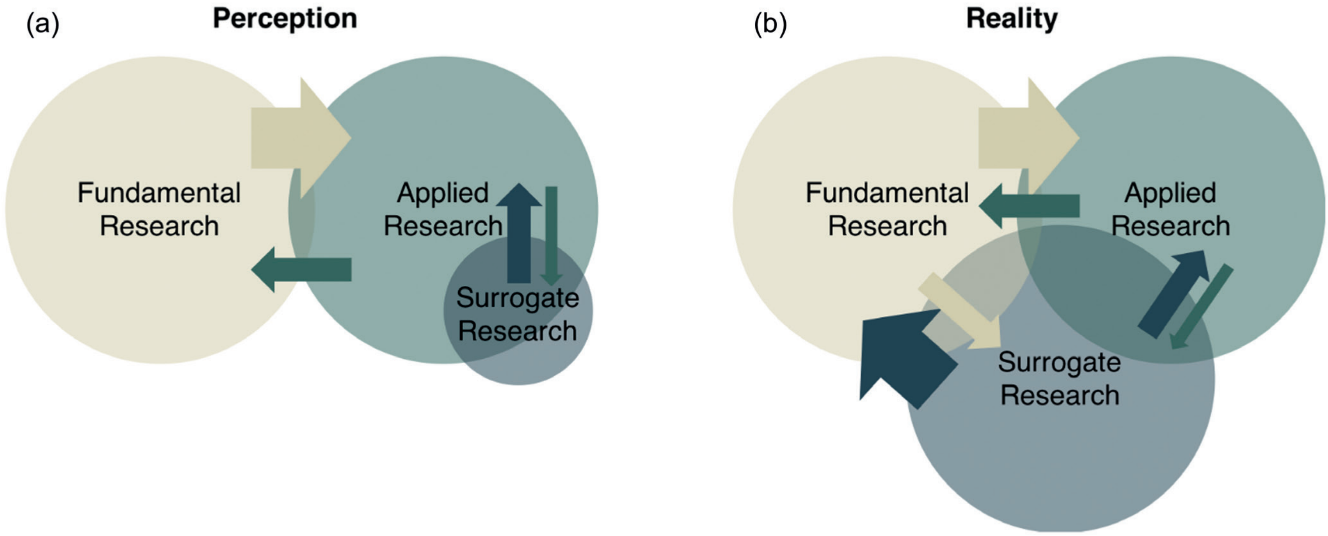

Figure 1. Conceptual diagrams representing the overlap of ideas and approaches in the distinct disciplines of fundamental, applied, and surrogate research. Arrow width indicates the importance of the knowledge transfers between research types. (a) The general perception is that applied research benefits more from fundamental research than vice versa and that surrogate research is a small component of applied research (modified from Courchamp et al. 2015). (b) We suggest that surrogate research is, in fact, part of both fundamental and applied research and that the transfer of surrogate knowledge to fundamental ecology is of considerable importance.

Council fellowship awarded to DBL. MRW was funded in part from a grant from the US National Science Foundation (no. DEB-1546686).

References cited

Barton PS, Pierson JC, Westgate MJ, Lane PW, Lindenmayer DB. 2015. Learning from clinical medicine to improve the use of surrogates in ecology. Oikos 124: 391–398.

Buyse M, Molenberghs G. 1998. Criteria for the validation of surrogate endpoints in randomized experiments. Biometrics 54: 1014–1029.

Courchamp F, Dunne JA, Le Maho Y, May RM, Thébaud C, Hochberg ME. 2015. Fundamental ecology is fundamental. Trends in Ecology and Evolution 30: 9–16.

Heinemeyer K, Ulizio T, Harrison R. 2008. Natural sign: Tracks and scats. Pages 45–75 in Long R, MacKay P, Zielinski W, Ray J, eds. Noninvasive Survey Methods for Carnivores. Island Press.

Johnson AF, Lidström S. 2018. The balance between concepts and complexity in ecology. Nature Ecology and Evolution 2: 585–587.

Keeley JE. 2009. Fire intensity, fire severity and burn severity: A brief review and suggested usage. International Journal of Wildland Fire 18: 116–126.

Lindenmayer DB, Manning AD, Smith PL, Possingham HP, Fischer J, Oliver I, McCarthy MA. 2002. The focal species approach and landscape restoration: a critique. Conservation Biology 16: 338–345.

Lindenmayer D, Barton P, Pierson J, eds. 2015a. Indicators and Surrogates of Biodiversity and Environmental Change. CSIRO.

Lindenmayer D, et al. 2015b. A new framework for selecting environmental surrogates. Science of The Total Environment 538: 1029–1038.

Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology and Evolution 20: 503–510.

Rodrigues ASL, Brooks TM. 2007. Shortcuts for biodiversity conservation planning: The effectiveness of surrogates. Annual Review of Ecology, Evolution, and Systematics 38: 713–737.

Rowland JA, Nicholson E, Murray NJ, Keith DA, Lester RE, Bland LM. 2018. Selecting and applying indicators of ecosystem collapse for risk assessments. Conservation Biology. doi:10.1111/cobi.13107

Wang J, Rich PM, Price KP, Kettle WD. 2004. Relations between NDVI and tree productivity in the central Great Plains. International Journal of Remote Sensing 25: 3127–3138.

Westgate MJ, Barton PS, Lane PW, Lindenmayer DB. 2014. Global meta-analysis reveals low consistency of biodiversity congruence relationships. Nature Communications 5: 853–858.

Zhu Z, et al. 2016. Greening of the Earth and its drivers. Nature Climate Change 6: 791–795.

Luke S. O'Loughlin (luke.oloughlin@anu.edu.au), David B. Lindenmayer, Claire N. Foster, Chloe N. Sato, Martin J. Westgate, and Philip S. Barton are affiliated with the Fenner School of Environment and Society at the Australian National University, in Canberra. Melinda D. Smith and Alan K. Knapp are affiliated with the Department of Biology's Graduate Degree Program in Ecology at Colorado State University, in Fort collins. Michael R. Willig is affiliated with the Center for Environmental Sciences and Engineering and the Department of Ecology and Evolutionary Biology at the University of Connecticut, in Storrs. Kim Cuddington is affiliated with the Department of Biology at the University of Waterloo, in Ontario, Canada. Alan Hastings is affiliated with the Department of Environmental Science and Policy at the University of California, Davis.

doi:10.1093/biosci/biy080