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Can habitat surrogates predict the response of target species to landscape change?

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ABSTRACT

Surrogates are commonly used for monitoring biodiversity under a wide range of scenarios. However, surrogates are not often evaluated under diverse ecological conditions, and this hinders the identification of spatial and temporal boundaries of a surrogate's relationship with its biodiversity metric, including whether a surrogate can predict biodiversity responses to environmental change. We adapted a causal framework from the medical literature and applied this framework to investigate the consistency of a well-established habitat surrogate of arboreal marsupials: hollow-bearing trees. We tested the consistency of the relationship between hollow-bearing trees and arboreal marsupials across four long-term studies (>10 years) covering different habitat types and environmental disturbance. We also tested the ability of the change in hollow-bearing trees over time to predict the change in arboreal marsupials over time. We found a somewhat consistent relationship between hollow-bearing trees and relative abundance of arboreal marsupials, but the mechanistic details of this relationship varied both by location and by species of arboreal marsupial. Similarly, the surrogate approach was not able to predict trends over time, a result likely due to differences in natural temporal variation between the surrogate and target species of interest. Our investigation demonstrates that habitat surrogates can be very useful for certain aspects of monitoring programs, but that serious limitations prevail when trying to monitor changes over time, or if information on species-specific responses is required. Our new framework can be readily applied to any biodiversity surrogate with an established mechanistic link between the surrogate and biodiversity metric of interest.

1. Introduction

Ecological surrogates are widely adopted by ecologists, and sought after by practitioners, as substitutes for the difficult and costly task of measuring wholesale biodiversity (Noss, 1990; Dale and Beyeler, 2001; Angelstam and Dönz-Breuss, 2004; Sarkar et al., 2005; Rodrigues and Brooks, 2007; Butchart et al., 2010; Halpern et al., 2012; Noon et al., 2012). In this paper, we define an ecological surrogate as a measure that "reflects the biotic or abiotic state of the environment; represents the impact of an environmental change on a habitat, community or ecosystem; represents the abundance of a particular species; or is indicative of the diversity of a subset of taxa, or of wholesale diversity, within an area" (Lindenmayer et al., 2014).

A growing body of literature is dedicated to defining a wide range of ecological surrogates for actions such as designing reserves and monitoring biodiversity and effectiveness of management actions (McGeoch and Chown, 1998; Wessels et al., 1999; Lombard et al., 2003; Van Wynsberge et al., 2012; Koch et al., 2013; Kunkel et al., 2013). Yet, many surrogates are not validated or only validated under a narrow range of spatial and temporal conditions. Without subsequent evaluation, the temporal and spatial boundaries of a surrogate's effectiveness in reflecting the actual variable of interest remain unknown, and this potentially limits its broader application. The lack of an established framework to test key attributes of ecological surrogates in contrasting ecosystems, over time, or after a disturbance, contributes to this critical knowledge gap affecting the usefulness of many surrogates.

Few studies of ecological surrogates include a rigorous test of the spatial and temporal aspects of the surrogate relationship. Recent work has evaluated the effectiveness of surrogates in selecting reserve designs based on their ability to reflect the distribution of the patterns of interest, and compared results of different analytical methods to assess surrogacy relationships. For example,

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(Grantham et al., 2010) evaluated alternate methods (incidental representation, species accumulation index, and summed irreplaceability) for assessing a variety of taxonomic surrogates and found that different methods ranked the effectiveness of surrogates inconsistently.

Less work has been done to evaluate the effectiveness of ecological surrogates to monitor biodiversity, subgroups such as threatened species, or responses to management actions. Importantly, for a surrogate to be effective for monitoring, similar temporal trends should be present, which requires monitoring both the surrogate and outcome of interest (Favreau et al., 2006). Studies that do assess surrogates in multiple ecological scenarios often focus on only one aspect of the surrogate relationship, such as different spatial scales (Angelstam and Dönz-Breuss, 2004; Banks-Leite et al., 2013; Morelli et al., 2013). For example, Drever et al. (2008) found a consistent relationship between woodpecker richness and overall avian richness across 23 sites in British Columbia, yet cautioned that this relationship may break down during insect outbreaks when woodpeckers were likely to respond differently to the overall bird community. Other studies have attempted to test the limits of surrogates in different ways. Although these studies (and several others, e.g., (Warman et al., 2004; Sarkar et al., 2005; Altmoos and Henle, 2006; Favreau et al., 2006; Hess et al., 2006; Rodrigues and Brooks, 2007; Gollan et al., 2008; Dalleau et al., 2010; Grantham et al., 2010; Lewandowski et al., 2010; Van Wynsberge et al., 2012; Gillison et al., 2013; Di Minin et al., 2014; Lindenmayer et al., 2014)) provide specific examples of surrogate evaluation, they are each done in very different ways. What is lacking in ecology, therefore, is a general approach to the testing and evaluation of surrogacy relationships, and a simple framework to guide surrogacy testing for monitoring purposes.

Here, we adapt a causal framework from the medical surrogate literature (sensu (Atkinson et al., 2001)) to provide a stepwise process to guide the assessment of the relationships between a surrogate and variables of interest (hereafter termed targets) (Fig. 1) (Barton et al., 2015). In this framework, a mechanistic link between a potential surrogate and a target is identified (Fig. 1m); the relationship between the surrogate and target is tested in a variety of environmental conditions, such as different habitat types (Fig. 1A); the surrogate's response to disturbance is evaluated under a range of treatment types (Fig. 1B); the target's response to disturbance is evaluated under the same treatment types (Fig. 1B); and the relationship between the temporal trend of the surrogate and the temporal trend of the target is tested (Fig. 1C). By quantifying the relationship between the surrogate and the target under a range of spatial and temporal conditions, the strengths and limitations of the full surrogate model are able to be more fully understood. Critical to this framework, however, is a known mechanistic link between the surrogate and the target (Fig. 1m). Habitat surrogates often have a clear mechanistic link to the biodiversity metric being measured (Koch et al., 2013), and this provides the basis for why a consistent response to landscape change might be expected by both the surrogate and the biodiversity metric of interest.

Hollow-bearing trees have a clear mechanistic link with cavity-dwelling vertebrates globally, including birds, bats, invertebrates and a variety of terrestrial mammals through provision of shelter and nesting resources (Fischer and McClelland, 1983; Rose et al., 2001; Gibbons et al., 2002; Ranius et al., 2005), and thus are considered a keystone structure for biodiversity (Remm and Lõhmus, 2011). Furthermore, hollow-bearing trees are an established habitat surrogate for arboreal marsupials, which rely on hollows for roosting (Gibbons et al., 2002). Globally, numbers of hollow-bearing trees are declining in many forests and agricultural areas (Lindenmayer et al., 2012) often resulting in declines in the fauna dependent on hollows (Ranius et al., 2009). For this reason, they are monitored in different parts of the world to provide information about their associated fauna (Fischer and McClelland, 1983; Lindenmayer and Wood, 2010; Edworthy et al., 2012). We therefore expected a strong relationship between the availability of hollow-bearing trees and the presence and relative abundance of arboreal marsupials to persist under wide temporal and spatial conditions.

We tested the broader potential of hollow-bearing trees to act as a surrogate for arboreal marsupial presence and abundance using the causal framework outlined in Fig. 1. We used four long-term studies, each in a contrasting ecosystem, that have been monitored for both hollow-bearing trees and arboreal marsupials for at least 10 years. Each of these studies also included either fire or fragmentation as a distinct ecological disturbance during the monitoring period. Thus, we had an unparalleled opportunity to test the framework over a large spatial (~1000 km) and temporal scale (>10 years) on a key group of species that are of conservation concern (e.g., endangered Leadbeater's possum (*Gymnobelideus leadbeateri*), and the vulnerable squirrel glider (*Petaurus norfolcensis*) and yellow-bellied glider (*P. australis*)) to identify the boundaries of the surrogacy relationship. Using our large datasets, and the framework shown in Fig. 1, we addressed the following questions:

(Q1) Are hollow-bearing trees (or hollows) consistently a surrogate for the occurrence of arboreal marsupials (Fig. 1A)? In this context, we define "consistent" to be a repeated observation of a significant correlative relationship between the surrogate and target. We predicted that a relationship between the abundance of hollow-bearing trees and arboreal marsupials will occur consistently across space and time given the dependence of arboreal marsupials on hollows for daily roosting.

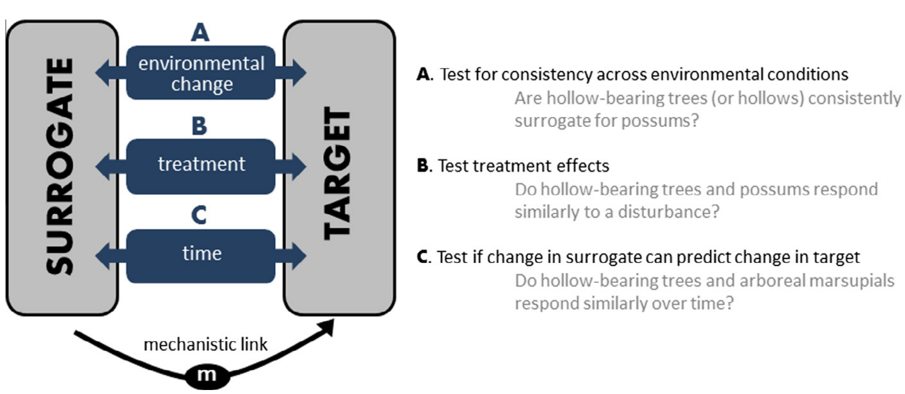

Fig. 1. A conceptual diagram describing the framework for evaluating the efficacy of an ecological surrogate in monitoring a target of interest.