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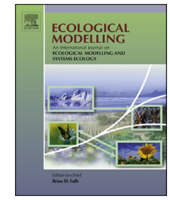

Review

Physiological limits in an ecological niche modeling framework: A case study of water temperature and salinity constraints of freshwater bivalves invasive in USA

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ABSTRACT

Ecological niche modeling has emerged as a notable tool in invasive species risk assessment. However, the advances of the ecological niche theory, the basis of ecological niche modeling, are not matched by availability of detailed biological data. Thus, we proposed a conceptual framework to refine the boundaries of ecological niche, differentiating the species' existence status (survival, growth, and reproduction) based on physiological limits of major life history characteristics. We discussed differences between the classic and the proposed frameworks and emphasized the importance of the time axis in understanding species' existence status. We exemplified the implementation potential of this framework by reviewing published studies of physiological limits (temperature and salinity) for survival, growth, and reproduction of invasive freshwater bivalves in USA. We found considerable amount of physiological information through the literature review, though there is a research bias toward more influential invasive species (vs. less influential invasive species), temperature tolerance (vs. salinity tolerance), and survival limits (vs. growth and reproduction limits); filling the knowledge gaps will strengthen the potential of the proposed framework. Our framework addresses the lack of long-term field data, but is limited in that one can only identify unsuitable instead of suitable conditions for species, given incomplete understanding of species' physiological tolerance. Future studies may consider developing new algorithms that utilize physiological limits as priors in a Bayesian approach.

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1. Introduction

Invasive species are well-known for their negative effects, including economic and biodiversity losses (Clavero and García-Berthou, 2005; Gallardo et al., 2016; Pimentel et al., 2005; Shine, 2010; Simberloff et al., 2013). Prevention, as an effective management strategy of invasive species (Leung et al., 2002; Simberloff et al., 2013), relies on risk assessments that provide information about a species' potential of invasion (Vander Zanden and Olden, 2008). One way of inferring a species' invasive potential is to generate a risk map that indicates suitability of habitat or probability of occurrence based on environmental conditions (Jiménez-Valverde et al., 2011; Tingley et al., 2014). Two major approaches are used to estimate the relationship between species' potential distribution and environmental conditions: (1) correlative models that are based on known occurrences of species and (2) mechanistic models that are based on species' biological performance (Buckley et al., 2010; Dormann et al., 2012; Kearney and Porter, 2009; Phillips and Dudik, 2008). The former, ecological niche models (ENMs), relating known species occurrences to abiotic variables, emerged as a promising tool for predicting invasive species' potential distribution before invasion occurs and assessing the most vulnerable areas, thus facilitating prevention practices (Peterson, 2003; Thuiller et al., 2005). Benefiting from accumulation of and open access to biodiversity data (e.g., GBIF) and environmental data (e.g., Worldclim), ENMs can efficiently serve as a risk assessment tool (Jiménez-Valverde et al., 2011), or at least as "first-step screening" (Hulme, 2006), especially when facing high number of candidate invasive species in a region.

ENMs are based on the niche concept defined by Hutchinson as a "combination of environmental factors that is necessary and sufficient for species' indefinitely persistence" (Hutchinson, 1957; Hutchinson, 1978). However, the term "environmental" is ambiguous and can be interpreted in different ways based on focal species or question being studied. To increase the clarity of niche in ENMs, a separation of abiotic (or scenopoetic) and biotic (or bionomic) variables has been proposed (Soberón and Peterson, 2005; Soberón, 2007). The two categories of variables are assumed to exhibit scale-dependency, with abiotic variables affecting species' distributions at broad spatial scales [e.g., 1–100 km^2 (Soberón, 2007) and 50 km^2 (Pearson and Dawson, 2003)] and biotic variables affecting species' distributions at fine spatial scales [e.g., less than 1 km^2 (Bidegain and Juanes, 2013; Pearson and Dawson, 2003)]. Abiotic variables have been used intensively in ENMs (Peterson et al., 1999; Peterson and Vieglais, 2001) and have benefited from rapid accumulation of datasets with global coverage (e.g., climate and land cover). The niche being estimated with abiotic variables is referred to as the abiotic fundamental niche (or Grinnellian niche), hereafter "fundamental niche" (Soberón, 2007).

The status of species in Hutchinson' conceptualization of the niche is indefinite persistence (Hutchinson, 1957; Hutchinson, 1978), and was later interpreted differently by scholars and given meanings such as survival of species, growth, reproduction, or positive intrinsic growth rate, or any combinations of these aspects (Table 1). These derived interpretations reflect the advances in understanding species' distributions in geographic space. However, species are usually represented in ENMs through occurrence records, and less commonly abundance data. Neither occurrence nor abundance data are ideal for a close estimation of the fundamental niche, which may be achievable only by studying population growth or using mechanistic modeling based on detailed, species specific energy and water needs (Kearney, 2006; Kearney and Porter, 2004; Soberón, 2007); nevertheless, population growth or species' energetic requirements data are not readily available, except for a few well-studied species (Kearney and Porter, 2004). In other words, the advancement of niche theory has not been matched by growth of sources of information to help understand and improve species' distribution estimates, which is one of the original and fundamental goals of niche theory (Hutchinson, 1957; Hutchinson, 1978).

A simplified way to conceptualize the fundamental niche is to determine the boundary that separates suitable from unsuitable conditions, as defined by Hutchinson, though the limitation of this framework is the assumption of equal probability of species' existence inside and zero probability outside the fundamental niche (Hutchinson, 1957). A step further could be to quantify the fitness of a species across a gradient of abiotic conditions, which is biologically more meaningful, however relies more heavily on complex information (Barve et al., 2014). Thus, in lieu of availability of adequate data, we propose a framework that refines the classic ecological niche boundary using species' relevant physiological limits to obtain more accurate estimations of species' distribution. Specifically, we propose to differentiate species' existence status based on major life history characteristics that are possible given species' physiological limits and abiotic conditions in geographic space. Physiological responses to abiotic conditions are observed at individual level, but should be informative of the status of species when the goal is to estimate the fundamental niche with abiotic variables. Therefore, we assume that conditions that fulfill individual survival, growth, and reproduction will lead to positive population growth, thus species' indefinite existence. Our objectives are to (1) build a bridge between the classic ecological niche concept defined by Hutchinson and our proposed refined framework, (2) review available physiological information for a group of invasive species, and (3) illustrate the applicability of our proposed framework in ENMs and invasive species distribution estimates.

2. Considering physiological limits in ecological niche modeling framework

2.1. Definition and justification

We define broadly the physiological limits as environmental (abiotic) conditions that permit normal functioning of organisms and supporting major life history characteristics, i.e., survival, growth, and reproduction, and consequently determine species' existence in geographic space, or distribution.

Physiology is one of earliest scientific disciplines in biology (Scheer, 1963), thus information about species' physiological limits is expected to be available in the literature (Addo-Bediako et al., 2000; Araújo et al., 2013; Hoffmann et al., 2013; Lutterschmidt and Hutchison, 1997). Species' distributions can be limited by physiologically intolerant conditions through death or negative effects on reproduction and life cycles (Gaston, 2003). The effect of phys-

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