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Integrating age structured and landscape resistance models to disentangle invasion dynamics of a pond-breeding anuran

Giovanni Vimercati[a,*], Cang Hui[b,c], Sarah J. Davies[a], G. John Measey[a]

[a] Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa
[b] Centre for Invasion Biology, Department of Mathematical Sciences, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa
[c] Mathematical and Physical Biosciences, African Institute for Mathematical Sciences, Cape Town 7945, South Africa

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ABSTRACT

Modelling population dynamics of invasive species may help to propose effective management countermeasures. Invasion dynamics generally show recursive patterns across species and regions, where initial lag is followed by spread and eventual dominance phases. However, timing and modes of these phases are highly variable, emerging from the interplay between traits of the invader and characteristics of the invaded landscape. Disentangling this interplay is particularly arduous in species with complex life-histories, where an individual passes through different life stages that alter physiology, behaviour and interactions with the environment. Here, we describe an age structured model that can be utilized to simulate population dynamics of invasive pond-breeding anurans. The model follows a spatially structured population approach, each pond representing a discrete habitat patch that exchanges individuals with other similar patches, and simulates change in survival and dispersal behaviour as a function of age. It also integrates dispersal with landscape complexity through landscape resistance modelling to depict functional connectivity across the pond network. Then we apply the model to a case study, the invasion of the guttural toad *Sclerophrys gutturalis* in Cape Town, first detected in 2000. Age-structured demographic and spatial dynamics of the focal population are reconstructed in a network of 415 ponds embedded in a heterogeneous landscape. Parameterization is conducted through field and laboratory surveys, a literature review and data collected during an ongoing extirpation from 2010. We use the model to explore: i) occurrence and duration of lag phase; ii) whether the spatial spread fits an accelerating or a linear trend; iii) how simulated dynamics match field observations. Additionally we test model sensitivity to demographic and behavioural traits. We found a lag phase in both demographic and spatial dynamics; however the lag duration of these dynamics does not coincide, where invaders start to spread across the pond network five years before the demographic explosion. Also, we found that the spatial spread fits an accelerating trend that causes complete invasion of the network in six years. Such dynamics noticeably match field observations and confirmed patterns previously detected in other invaders characterized by high dispersal abilities. Sensitivity analysis suggests that it would have been preferable to quantify initial propagule size and post-metamorphic survival in the field; both timing and modes of invasion are particularly sensitive to these parameters. We conclude that the model has potential to forecast amphibian invasion dynamics and test management countermeasures.

1. Introduction

The study of amphibian population dynamics and their drivers is essential from a conservation perspective. Amphibia are the most threatened group of vertebrates (Stuart et al., 2004; Wake and Vredenburg, 2008), where several native populations are currently declining across the globe (Houlahan et al., 2000; Green, 2003) and some populations have already headed toward extinction (Wake and Vredenburg, 2008; Howard and Bickford, 2014). This trend is mainly caused by anthropogenic activities such as land-use change, greenhouse gas emissions and accidental introductions of pathogens and invasive species (Blaustein and Kiesecker, 2002; Collins and Storfer, 2003; Grant et al., 2016). Amphibians them-

* Corresponding author.
E-mail addresses: gvimercati@outlook.com (G. Vimercati), chui@sun.ac.za (C. Hui), sdavies@sun.ac.za (S.J. Davies), john@measey.com (G.J. Measey).

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selves can be invasive (Kraus, 2009) and their introduction and establishment are predicted to increase in the coming years as a consequence of globalization and international trade (Kraus and Campbell, 2002; Reed and Kraus, 2010). Since ecological and social-economic impact of these invasive populations can be severe (Measey et al., 2016; Kumschick et al., 2017), it is important to reconstruct their demographic and spatial dynamics in order to predict invasion potential and perform adaptive management.

Demographic and spatial invasion dynamics inferred by field surveys or mathematical models indicate recursive patterns across taxa and regions (Essl et al., 2012; Larkin, 2012; Van Wilgen et al., 2014; Hui and Richardson, 2017); however traits of the invader and characteristics of the invaded environment may significantly influence timing and modes of such dynamics (Hastings et al., 2005; Jongejans et al., 2011; Larkin, 2012; Roques et al., 2016; Hui and Richardson, 2017). For example, at the onset of an invasion, most alien populations show a lag phase consisting of a low number of invasive individuals and/or invaded patches (Crooks and Soule, 1999; Crooks, 2005; Essl et al., 2012). The lag duration may however range between three and hundreds of generations with factors such as propagule pressure or population growth rate often hypothesized to play a role (Schreiber and Lloyd-Smith, 2009; Larkin, 2012; Aagaard and Lockwood, 2014). Similarly the phase of spatial spread may be considerably variable, where it may fit an accelerating and sigmoid, or a linear and decelerating relationship (Crooks, 2005; Aikio et al., 2010; Kelly et al., 2014). Long range dispersal events, environmental heterogeneity or evolutionary phenomena may all contribute to such variation (Higgins and Richardson, 1999; Schreiber and Lloyd-Smith, 2009; Jongejans et al., 2011; Marco et al., 2011). Since predicting timing and modes of an invasion may have an important role to respond quickly through effective countermeasures (Higgins and Richardson, 1999), complexity of invasion dynamics should never be underestimated. Each invasion should preferentially be modelled by incorporating species-specific characteristics and environmental features (Schreiber and Lloyd-Smith, 2009; Roques et al., 2016).

Most amphibian populations are not homogenously distributed across the landscape; instead they occur at greater densities in or around habitat patches that allow or facilitate survival and reproduction, such as wetlands and water bodies (Marsh and Trenham, 2001). Therefore their dynamics, especially in the case of pond-breeding species, can be profitably visualized through a spatially structured "ponds-as-patches" approach (Marsh and Trenham, 2001) where: i) each breeding site is considered a single discrete habitat patch that exchanges individuals with other analogous patches (Skelly, 2001; Smith and Green, 2005); ii) the number of individuals at each pond is exclusively due the birth/death rate within pond and the exchange rate among ponds (Marsh and Trenham, 2001; Pontoppidan and Nachman, 2013). Reproduction and survival in and around a pond may be affected among other factors by pond size, occurrence of predators and/or competitors, abundance of trophic resources or pollutants (Skelly, 2001; Van Buskirk, 2005; Hamer and Parris, 2013). Similarly, exchange rate among ponds may vary as a function of pond–pond distance, availability of ponds, habitat and landscape heterogeneity and species vagility (Decout et al., 2012; Willson and Hopkins, 2013; Hillman et al., 2014).

The capacity to incorporate this variation is essential in our effort to model population dynamics; but this may be particularly challenging considering that in most amphibians each individual passes through different life stages (e.g. egg, larval, metamorph, juvenile, adult) which ontogenetically alter physiology and behaviour. Age structured models are a powerful approach to depict this complexity because they incorporate changes in survival and reproduction as a function of age (Caswell et al., 2003; Govindarajulu et al., 2005). Such a bottom-up approach explores emergent properties of a population by modelling interactions within (e.g. competition) and among (e.g. cannibalism) discrete age classes (Gamelon et al., 2016). Age structured models also allow application of differential dispersal dynamics to each age class by reconstructing how virtual organisms disperse across the landscape according to their life stage (Neubert and Caswell, 2000; Steiner et al., 2014). Dispersal is generally affected by the interplay between landscape complexity (also see structural connectivity in Baguette and Van Dyck, 2007) and species-specific vagility (Hillman et al., 2014) linked to physiological and behavioural traits. An effective way to simulate such interplay is landscape resistance modelling, where functional connectivity (Stevens et al., 2005; Baguette and Van Dyck, 2007) across a landscape is modelled, combining the cost for an individual to move between habitat patches and detailed information about the landscape itself (Adriaensen et al., 2003). Since landscape complexity may strongly affect efforts to model amphibian populations (Ficetola and De Bernardi, 2004; Willson and Hopkins, 2011), the incorporation of landscape resistance modelling into an age-structured approach seems appropriate to simulate among-patch dynamics (Stevens et al., 2005; Baguette and Van Dyck, 2007).

In this paper, we describe a novel model that integrates age structured and landscape resistance approaches to reconstruct population dynamics of invasive pond-breeding anurans. The model is applied to a case study, the ongoing invasion of guttural toads *(Sclerophrys gutturalis)* in Cape Town, South Africa. Field data collected during management attempts, laboratory surveys and a literature review were employed to parameterize the model. Considering both demographic and spatial dynamics of the invasive population, we explore: i) occurrence and duration of lag phase; ii) whether the spatial spread fits an accelerating or a linear trend; iii) to what extent these dynamics match field observations. Additionally, we estimate sensitivity of the proposed model to demographic and behavioural traits. We conclude by discussing future implementations of the model to forecast amphibian invasive dynamics and test alternative management countermeasures.

2. Methods

2.1. Case study

The guttural toad (*Sclerophrys gutturalis)* is domestic exotic in South Africa (Measey et al., 2017) being native in most of the country but not in Cape Town, where an invasive population has recently established. The invaded area is characterized by a peri-urban landscape which provides numerous suitable breeding sites, namely artificial ponds, for the toads (Fig. 1). The invasion is occurring within the range of the congeneric species western leopard toad (*Sclerophrys pantherina*), currently listed as Endangered by the IUCN (SAFRoG & IUCN SSC-ASG 2010) and endemic to two restricted areas of south-western South Africa (Measey and Tolley, 2011). Moreover, invasions of toads in particular are known to have relevant environmental and economic impacts (Measey et al., 2016). Following the recognition of the invasion, the City of Cape Town (CoCT) started a sustained extirpation program (i.e. eradication at local scale, Panetta, 2007) in 2010 by opportunistically removing toads at any life stage (adult, juvenile, metamorph, tadpole and egg) from garden ponds, public open spaces and roadways. The removal from the ponds was particularly arduous because they were all located in private properties not always accessible to the eradicators. Despite the removal of more than 5000 post-metamorphic individuals and many thousands of tadpoles and eggs (Measey et al., 2017), the invasive population is still in expansion.