

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



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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.

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## 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-

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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 homogeneously 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

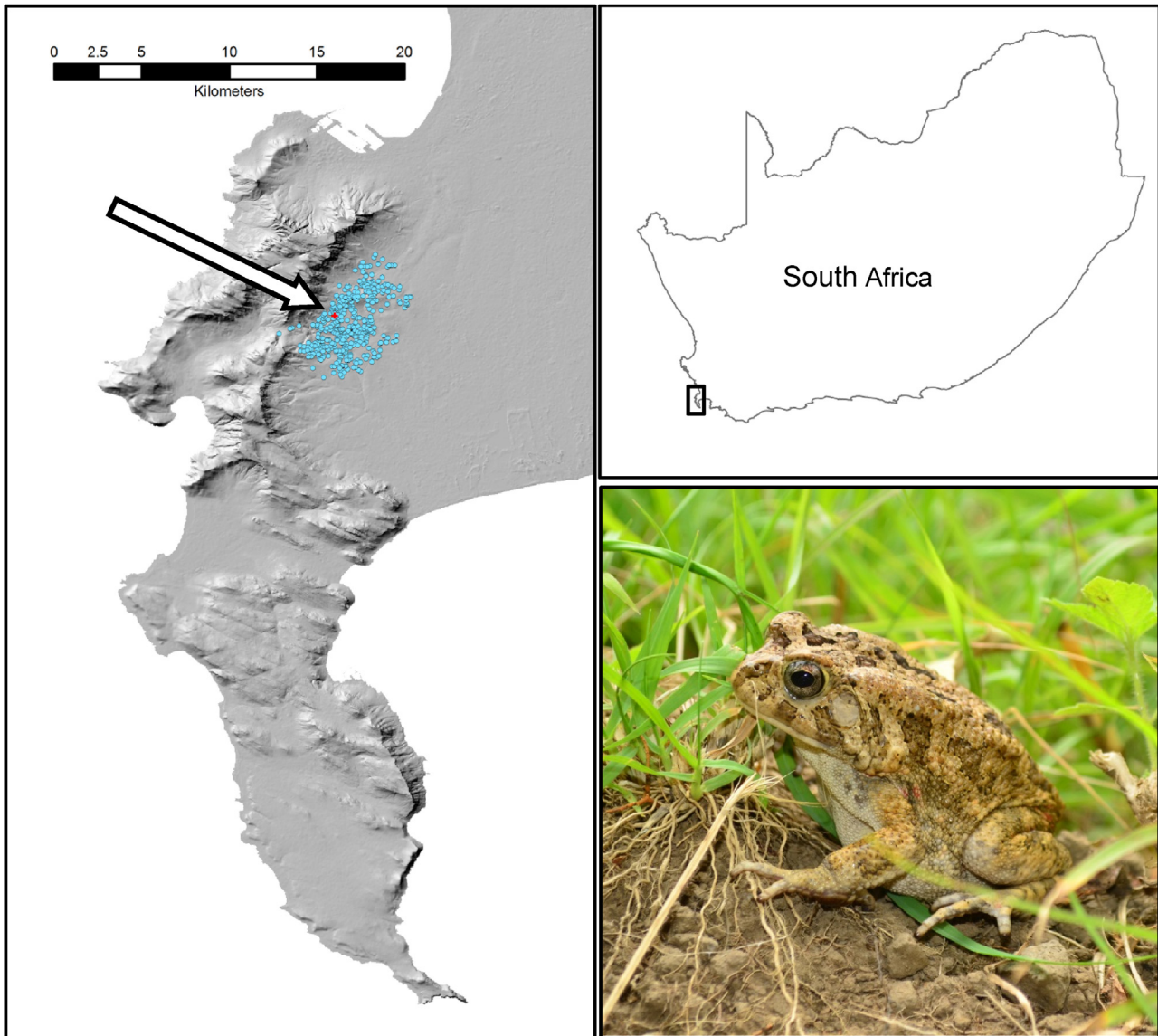
emergent properties of a population by modelling interactions within (e.g. competition) and among (e.g. cannibalism) discrete age classes (Gamelon et al., 2016). Age structured models also allow application of differential dispersal dynamics to each age class by reconstructing how virtual organisms disperse 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.



**Fig. 1.** Spatial layer (provided by Stellenbosch University, Digital Elevation Model –SUDEM- 2016 Edition) showing the ponds located in Constantia and surroundings ( $34^{\circ}01'S$ ,  $18^{\circ}25'E$ ) through aerial imaging (in blue) and the pond where the guttural toad (see photo) where first observed in the season 2000/2001 (in red, see white arrow).

## 2.2. Model description

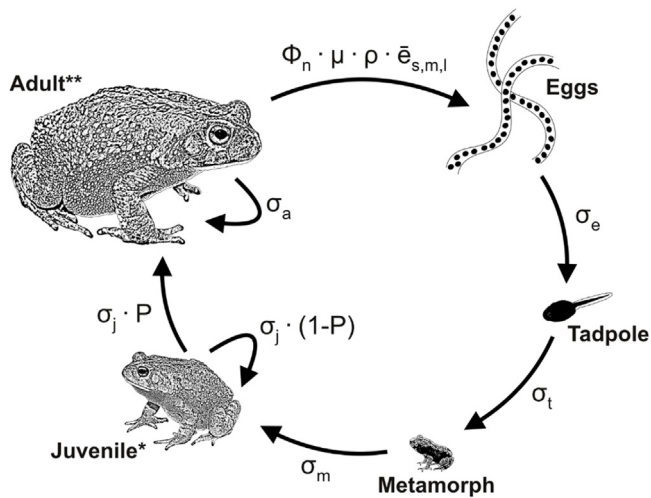
We follow the ODD (Overview, Design concepts, Details) protocol of Grimm et al. (2006) to describe the age structured model. Although the protocol was initially conceptualized to describe individual based models, it can help to delineate any bottom-up simulation and complex model by systematically isolating model components and facilitating their description (Grimm et al., 2006, 2010). Since the landscape resistance model is nested within the age structured model, its description is reported in the sub-model section below (see Section 2.2.7.3). The age structured model is implemented in Mathematica version 10.1 (Wolfram Research Inc., 2015).

### 2.2.1. Purpose

The purpose of the model is to simulate guttural toad population dynamics in the pond network of the invaded area that emerge from species specific life-history traits, density-dependent survival and dispersal behaviour.

### 2.2.2. Entities, state variables and scales

The model is an age structured model of integrodifference equations where each pond utilized by adults to breed represents a population with a detailed life-cycle. The modelled entities are the ponds. Each pond works as a source or sink according to life-history stage specific demography and dispersal behaviour of its individuals. Each pond is characterized by three state variables: number of individuals present for each life-history stage (egg, tadpole, metamorph, juvenile, adult), pond location (x- and y- coordinates) and pond size. Discrete life-history stages of the guttural toad in Cape Town are defined in Section 2.2.3 and depicted in Fig. 2. The number of individuals in a pond is affected by within-pond demographic dynamics and inter-pond dispersal dynamics. Inter-pond connectivity is described below in the Section 2.2.7.3 as a function of Euclidean distance and least-cost path distance calculated through a landscape resistance approach. At the first model step, the number of individuals present in all ponds is zero (i.e. empty ponds) with the exception of the pond in which the guttural toad was first detected (Fig. 1 and Section 2.2.5).



**Fig. 2.** Life-cycle of the guttural toad in Cape Town. Egg deposition starts in late spring (October–November) and the total eggs number per female is determined by the clutch size ( $\phi_n$ ), the number of clutch per year ( $\mu$ ), the sex-ratio ( $\rho$ ) and the probability to lay eggs in a pond according to the pond size ( $\bar{e}_{s,m,l}$ ). Tadpoles hatch from eggs after one week with the probability  $\sigma_e$  and survive to metamorphosis after 4–5 weeks with the probability  $\sigma_t$ .  $\sigma_t$  is a function of the initial density of tadpoles in the pond as described by Eq. (1). Metamorphs over-winter and emerge the next spring as juveniles with the probability  $\sigma_m$ .  $\sigma_m$  is a function of the initial density of metamorphs in the pond edge area described by Eq. (4). After one year, juveniles survive with a probability  $\sigma_j$  and mature with a probability  $P$ . The annual adult survival is  $\sigma_a^*$  and  $**$  represent respectively dispersal of juveniles (no philopatry) as described by the Eq. (7) and of adults (no site fidelity) as described by Eq. (8).

To record the geographic coordinates of all potential breeding sites (ponds) within the invaded range in 2015 plus a 1.5 km wide buffer (Fig. 1), we used aerial images provided by the City of Cape Town (<http://maps.capetown.gov.za/isisiv/>). The effectiveness of the aerial imaging survey to locate toad breeding sites was confirmed by the fact that through this method we located approximately ninety-five percent of ponds already recorded during the extirpation process. We also classified ponds according to size in order to incorporate tadpole and metamorph density-dependence survival into the model. Small (2.5 m<sup>2</sup>), medium (25 m<sup>2</sup>) and large (250 m<sup>2</sup>) ponds represent fountains, garden ponds and small artificial lakes respectively.

### 2.2.3. Process overview and scheduling

In the model, one-time step corresponds to one year. Within each time step, different life phases of an individual are processed according to the guttural toad life-cycle depicted in Fig. 2; the cycle has been defined following the amphibian movement ecology frameworks proposed by Sinsch (2014) and Pittman et al. (2014) and adapted to the invasive population of Cape Town through field observations (see Section 2.2.7.1 for details about each life-history stage). Each individual proceeds sequentially through egg, larval and metamorph stages until the juvenile stage in one step according to demographic dynamics (see Section 2.2.7.1). The same individual turns into an adult in one more step according to its maturing probability. The model runs for thirty steps in total. Only individuals at juvenile and adult stage can disperse across the pond network according to dispersal dynamics (see Section 2.2.7.2) and only adults can breed.

### 2.2.4. Design concept

**2.2.4.1. Emergence of system level phenomena.** Total number of adults in the population and their spatial distribution emerge for each year from individuals that survive, disperse and breed across the pond network.

**2.2.4.2. Sensing.** Individuals that disperse do not selectively target ponds with a low density of conspecifics. However they preferentially move toward nearer ponds according to the dispersal kernel. Moreover pond nearness takes into account functional connectivity calculated through landscape resistance modelling (see Section 2.2.7.3). Toads are assumed to know differential costs of locomotion across elements they encounter in the landscape and adaptively target ponds according to the least-cost path configuration. Individuals are also assumed to know their age in order for them to apply different age-specific dispersal behaviour.

**2.2.4.3. Interaction.** Individuals competitively interact as tadpoles and metamorphs in a pond according to the number of conspecifics at the same stage and pond size. Between-stage interactions (e.g. adult cannibalism on metamorphs) are not incorporated in our model.

**2.2.4.4. Stochasticity.** Stochasticity is not incorporated in our model. All life-history traits are set to constant values. The dispersal kernel derives from a probability distribution estimated through a mark-recapture study (Smith and Green, 2006). Landscape features and their costs on locomotion are modelled deterministically. Environmental stochasticity has not been incorporated in our model as the pond dynamics, i.e. temperature and biomass fluctuations are largely unknown and the climate is approximately homogenous across the arena given its small spatial scale.

**2.2.4.5. Observation.** The model outputs the number of individuals per each pond separately for each life-history stage. So we obtain for each year the total number of adults over time and the spatial distribution of the invaded population calculated in ArcGIS as the minimum convex polygon MCP in km<sup>2</sup> described by the ponds with at least one adult. The total number of adults and their spatial distribution are the auxiliary variables (i.e. “variables containing information that is deduced from low-level entities”, see Grimm et al., 2006).

### 2.2.5. Initialization

In the case of the invasive population of guttural toad in Cape Town, about ten males were heard for the first time in 2000 (De Villiers, 2006) around a large pond at a known site in Constantia. However field observations on this species in Cape Town and Durban showed also that within a chorus some males do not call and this is known to be density dependent (Leary et al., 2008). Thus the model was initialized with 40 adults (i.e. propagule size) on that specific pond in the season 2000/2001 (2001 hereafter), considering the sex ratio to be 1:1. All the other ponds were assumed to be empty at the first step in order to simulate a colonization scenario.

### 2.2.6. Input data

The list of ponds, the size of each pond (2.5 m<sup>2</sup>, 25 m<sup>2</sup>, 250 m<sup>2</sup> for small, medium and large ponds respectively, Section 2.2.2) and the Euclidean and least-cost path distance (see Section 2.2.7.3) are read from external files.

### 2.2.7. Submodels

**2.2.7.1. Demographic dynamics.** We set egg production per female using the clutch size ( $\phi_n$ ) adjusted by the annual clutch number ( $\mu$ ), the adult sex ratio ( $\rho$ ) and the probability of laying eggs in a pond estimated in the field ( $\bar{e}_{s,m,l}$ ). Here and hereafter the subscript “s,m,l” indicates that the parameter uses different values (reported in Table 1) according to the size of the pond (i.e. small, medium and large respectively). In eggs, the probability of hatching successfully is  $\sigma_e$  whereas the tadpole survival ( $\sigma_t$ ) is a function of the larval

**Table 1**  
Model parameters. Shaded cells represent guttural toad species-specific information collected through laboratory and field surveys on the Cape Town population or a literature review on the species. Parameters without asterisk represent information collected from the literature on similar bufonid species.

Parameter	Baseline Values	Source
*Clutch size ( $\phi_n$ )	13000	See <a href="#">Appendix A.4</a>
*Annual clutch number ( $\mu$ )	2	See <a href="#">Appendix A.4</a>
Adult sex ratio ( $\rho$ )	0.5	Assumption
*Probability to lay eggs in small, medium and large ponds respectively ( $\bar{e}_{s,m,l}$ )	0.06 0.4 0.22	See <a href="#">Appendix A.4</a>
Egg survival ( $\sigma_e$ )	0.7	<a href="#">Blaustein et al. (1994)</a> ; <a href="#">Biek et al. (2002)</a>
Maximum larval survival ( $\sigma_{tmax}$ )	0.8	<a href="#">Vonesh and De la Cruz (2002)</a>
Density-dependent coeff. (d)	0.007	<a href="#">Vonesh and De la Cruz (2002)</a>
Annual proportion of competing tadpoles from the same female (c)	0.5	Assumption
*Pond area of small, medium and large ponds respectively ( $A_{s,m,l}$ )	2.5 m <sup>2</sup> 25 m <sup>2</sup> 250 m <sup>2</sup>	Estimated in the invaded area of Cape Town through aerial images
Density-dependent exponent ( $\gamma$ )	1	<a href="#">Vonesh and De la Cruz (2002)</a> ; see <a href="#">Appendix A.1</a>
*Pond-edge area within a radius of 5 m ( $E_{s,m,l}$ )	106.4 m <sup>2</sup> 166 m <sup>2</sup> 357.7 m <sup>2</sup>	Calculated using the pond area $A_{s,m,l}$ , see <a href="#">Appendix A.2</a>
Juvenile survival ( $\sigma_j$ )	0.2	<a href="#">Lampo and De Leo (1998)</a> ; <a href="#">Vonesh and De la Cruz (2002)</a> ; <a href="#">Biek et al. (2002)</a>
Maturing probability (P)	0.25	<a href="#">Vonesh and De la Cruz (2002)</a>
Adult survival ( $\sigma_a$ )	0.6	<a href="#">Vonesh and De la Cruz (2002)</a> ; <a href="#">Biek et al. (2002)</a>
Juvenile probability to show philopatry (phi)	0.66	Assumption
Adult probability to show site fidelity (fid)	0.8	Assumption

density of the pond. The tadpole density of the pond is a function of pond area ( $A_{s,m,l}$ ) and the total initial number of tadpoles ( $T_i$ ):

$$\sigma_t = \frac{\sigma_{tmax}}{\left(1 + d \left(\frac{T_i c}{A_{s,m,l}}\right)^\gamma\right)} \quad (1)$$

where  $\sigma_{tmax}$  is the highest larval survival without density-dependence, d is the density-dependent coefficient (m<sup>2</sup>/number of tadpoles), c is to indicate that for a given female that breeds in a pond there is no competition between the tadpoles of the first clutch and the tadpoles of the second clutch and  $\gamma$  is the density-dependence exponent with:

$$T_i = \phi_n \sigma_e \mu \rho \bar{e}_{s,m,l} \quad (2)$$

The rationale for Eq. (1) is reported in [Appendix A.1](#) Being the total initial number of metamorphs ( $M_i$ )

$$M_i = \phi_n \sigma_e \mu \rho \bar{e}_{s,m,l} \sigma_t \quad (3)$$

the survival of metamorphs ( $\sigma_m$ ) is expressed as the ratio between the final density of metamorphs and their initial density where:

$$\sigma_m = 1 - \left( \frac{\left( \left( \phi_n \sigma_e \mu \rho \bar{e}_{s,m,l} \sigma_t / E_{s,m,l} \right)^2 / 2.76 \right)^{0.623}}{\phi_n \sigma_e \mu \rho \bar{e}_{s,m,l} \sigma_t / E_{s,m,l}} \right) \quad (4)$$

with  $E_{s,m,l}$  representing the pond edge area and  $\sigma_m$  that has to be  $\geq 0$ .

The rationale for Eq. (4) is reported in [Appendix A.2](#)

The number of metamorphs that survive and emerge as juveniles the following spring ( $J_i$ ) is expressed by:

$$J_i = \phi_n \sigma_e \mu \rho \bar{e}_{s,m,l} \sigma_t \sigma_m \quad (5)$$

The survival of juveniles after one year is  $\sigma_j$  whereas the probability to mature is P. So the initial adult number ( $N_i$ ) is:

$$N_i = \phi_n \sigma_e \mu \rho \bar{e}_{s,m,l} \sigma_t \sigma_m \sigma_j P \quad (6)$$

with each adult having a probability of survival to the following year expressed by  $\sigma_a$ .

**2.2.7.2. Dispersal dynamics.** We implemented the life-cycle of the guttural toad in the pond network of Cape Town ([Fig. 1](#)). The movement from a starting pond to a destination pond is always due

to the dispersal of juveniles and adults; eggs, tadpoles and metamorphs are constrained to stay within or around the natal pond. As a consequence of these different dispersal strategies, the number of metamorphs in a pond i at time t (met [i,t]) is determined by the number of eggs in the pond (egg[i,t]), and the survival of eggs ( $\sigma_e$ ) and tadpoles ( $\sigma_t$ ) whereas the number of juveniles (juv [i,t]) is expressed by

$$\text{juv}[i, t] = \sum_{j=1}^{415} m_j [i, j] (\text{met}[j, t] \sigma_m + \text{juv}[j, t-1] \sigma_j (1 - P)) \quad (7)$$

and the number of adults is expressed by

$$\text{adu}[i, t] = \sum_{j=1}^{415} (m_j [i, j] \sigma_j P * \text{juv}[j, t-1] + m [i, j] \sigma_a \text{adu}[j, t-1]) \quad (8)$$

where  $m_j [i, j]$  and  $m [i, j]$  represent the juvenile and the adult movement matrix, respectively. However, not all juveniles and adults disperse toward a new pond; indeed some individuals of a population can show philopatry and site fidelity ([Pittman et al., 2014](#); [Sinsch, 2014](#)). Philopatric juveniles assume a stationary behaviour around the natal breeding site (see “philopatry” in [Sinsch, 2014](#)) whereas non-philopatric ones disperse around the natal pond in order to look for a future alternative breeding site. Thus the juvenile movement matrix ( $m_j [i, j]$ ) is

$$m_j [i, j] = (1 - \text{phi}) \text{kernel}[c_{ij} / \text{norm}] \quad (9)$$

where phi is the probability for juveniles to remain in the same pond (i.e. to perform philopatry) whereas the kernel expresses the probability for juveniles to move from pond i to pond j as a function of: 1) the dispersal kernel defined by the data reported in [Smith and Green \(2006\)](#) and 2) the distance between the two ponds defined by the distance matrix c (see below). The work of [Smith and Green \(2006\)](#) has been chosen because the authors estimated through mark-recapture methods yearly dispersal in the native North American toad *Anaxyrus fowleri* at Long Point, Ontario Canada. Long Point is a sand spit characterized by dune formation and peri-urban landscape. Although *A. fowleri* is not closely related to the guttural toad, this American species is comparable for size, ecology and breeding strategy with our target species ([du Preez et al., 2004](#)). Additionally

no dataset regarding dispersal in toads exists on the African continent and globally no other better dataset is available for peri-urban areas.

In our model, most of the adults select the same breeding site after one year (see “site fidelity” in Sinsch, 2014) whereas the remnants target a novel site. Thus the adult movement matrix ( $m[i,j]$ ) is

$$m[i,j] = (1 - \text{fid}) \text{kernel}[c_{ij}/\text{norm}] \quad (10)$$

where  $\text{fid}$  is the probability for adults to select the same pond one year after breeding (i.e. to perform site fidelity).

Following Smith and Green (2006), we use the same dispersal kernel and the same distance matrix for both adults and juveniles. The kernel is described by an inverse power law as reported below:

$$\text{kernel}[c_{ij}] = 4.1651[c_{ij}]^{-0.884} \quad (11)$$

The kernel outputs the probability to move from pond  $i$  to pond  $j$  according to the distance matrix  $c$  and is normalized by a factor  $\text{norm}$  ( $=3.8003$  in the landscape network).

**2.2.7.3. Landscape resistance model.** A landscape resistance approach is deployed to calculate the functional connectivity between ponds expressed as least-cost paths. A least-cost path is the route that minimize the costs to disperse for an individual between two target patches (i.e. the ponds in our model). The geographic coordinates of the ponds identified through aerial images were converted into shape-files and utilized to obtain two distance matrices through: 1) the Euclidean Distance Tool in the ArcGIS Spatial Analyst Toolbox, which expresses the ordinary distance between two ponds (Euclidean matrix later in the text); 2) the ModelBuilder function in ArcGIS which expresses the least-cost path distance between two ponds (LCP Matrix hereafter). The tool created runs sequentially in four steps: i) the Weighted Overlay tool, in order to overlay the components of a referenced raster using a common scale and to weight each according to its importance; ii) the Cost Distance tool, in order to calculate the least cumulative cost distance for each cell to the nearest source over a cost surface; iii) the Cost Path tool, in order to calculate the least-cost path from one pond to another; iv) the Raster to Polyline tool, in order to convert the path raster to a polyline in meters. To automate the least-cost path calculation for all the ponds, we used a script in Python for ArcGIS (Appendix B.1 in Supplementary material). The referenced raster has to incorporate the spatial elements of the landscape that cause different costs of locomotion. From a toad’s perspective the landscape is mostly characterized by private grassy gardens (where the ponds are located), each surrounded by walls and connected by streets (see Appendix A.3). As a consequence of this simplified structure, we built a raster with 5 m resolution characterized by three features (i.e. grass, wall and street) through overlaying a cadastre spatial layer file on a roads spatial layer of Cape Town. Then we simulated different cost scenarios by assigning different costs to each feature through the Weighted Overlay tool; we successively scored the alternative paths for five pairs of ponds in light of our experience on the species’ locomotion. The most successful configuration of costs (Appendix B, Fig. B1 in Supplementary material) was utilized in the LCP matrix construction for all the pairs of ponds.

**2.2.7.4. Parameterization.** Most demographic and dispersal parameters of the model were obtained by a literature review. When species-specific parameters were not available, we used parameters collected on similar bufonid species (Table 1). However clutch size, annual clutch number and probability to lay eggs in small, medium and large ponds were specifically estimated for the guttural toad population of Cape Town (Appendix A.4).

All demographic and behavioural parameters are set at their baseline value reported in Table 1 (but see sensitivity analysis below) with the exception of the parameter  $h$ . Given the initial pond, the dispersal kernel and the distance matrix, every pond has a specific probability to receive adult toads, with ponds closer to the initial pond having a higher probability of being colonized; thus the number of individuals that colonize a pond is higher at the core of the invasion and lower at the front. The parameter  $h$  regulates which ponds can be used for reproduction (i.e. egg laying) according to the number of toads; in other words, this parameter acts as a threshold where adults can successfully breed in a pond only when their number is equal to or larger than  $h$ . It also implies that this parameter regulates how fast the invasion spread occurs within the pond network where high values of  $h$  result in slow spread and low values of  $h$  result in rapid spread. We cannot know with certainty the demography of the invasive population at the time the extirpation program started; thus we assume for simplicity that the total number of adults removed during the first eradication season in 2011 ( $\approx 700$ ) is representative of the adult population at that time, and we use this number to parameterize  $h$ . Although this assumption is optimistic, it does not necessarily imply that this removal would have allowed extirpating the population in one year; most of the conspecifics from other life-history stages (e.g. juveniles and metamorphs) were not removed during extirpation (Vimercati et al., in prep.) and this could have caused adult recruitment in the successive years.

During the parameterization process, we ran the model with values of  $h$  ranging between 0 and 1 (increment = 0.005) and compared through  $t$ -tests the model outputs for adults (i.e. number of adults predicted by the model per pond) with the eradication data collected in 2011 (i.e. number of adults detected in each pond in 2011), using both Euclidean and LCP matrices. All outputs obtained using the Euclidean matrix were significantly different ( $p < 0.05$ ) from the eradication data. On the contrary, using the LCP matrix we found that the output obtained with  $h = 0.07$  matched best the eradication data ( $t = 0.0795$ ,  $p = 0.937$ ). Thus, we parameterized the model with the LCP matrix using this value of  $h$  and removed the Euclidean distance from further analyses.

### 2.3. Simulation experiments

Firstly we simulate the population dynamics using the parameterized model. Secondly, in order to provide insights into which survival and dispersal parameters have the highest impact on invasive population dynamics, we perform sensitivity analysis by testing each parameter in steps of 0.1 from 0.1 to 1 and keeping all the other parameters at their baseline values (see Table 1). The parameters to be tested were: egg survival; maximum larval survival; juvenile survival; adult survival; maturing probability; site fidelity; philopatry. We chose these parameters because they: i) have been already tested in previous studies (for example see Lampo and De Leo, 1998); ii) are source of uncertainty in the guttural toad; iii) vary a great deal in amphibians (see literature review in Table 1). We also test model sensitivity to propagule size initializing the model with different sizes according to the geometric sequence “5, 10, 20, 40, 80, 160”. This sequence has been chosen in order to test realistic propagule pressures. Lastly we run the parameterized model using the Euclidean matrix instead of the LCP matrix for the baseline propagule size in order to quantify the effect of landscape resistance modelling. Then we ran the parameterized model again for all sensitivity scenarios. The total number of adults over time matches a logistic curve in 63 out of 70 scenarios (and when it does not, the population collapses). Therefore, the Self-Starting Nls Logistic Model in R software (package *stats* version 3.4.0, R Development Core Team, 2014) has been used to estimate “Asym” (i.e. the upper asymptote), “xdim” (the  $x$  value at the

inflection point of the curve) and “scal” (a numeric scale parameter describing the growth rate) for each scenario. Sensitivity analysis is commonly deployed in population modelling to estimate adult demography at equilibrium (i.e. the upper asymptote); however we also aim to investigate to what extent each parameter affects timing and modes of this invasion. The  $x$  value at the inflection point of the logistic curve (i.e. “ $x_{dim}$ ”) indicates when the adult population demography reaches 50% of its maximum value at equilibrium and is a proxy of the lag phase. Conversely the numeric scale parameter (i.e. “scal”) indicates how fast the population grows after the lag phase.

### 3. Results

#### 3.1. Invasion dynamics

The model predicted for the adult population of guttural toads in Cape Town a logistic demographic dynamic (Fig. 3) showing sequentially: i) a lag (2001–2010); ii) an explosion (2011–2013); and iii) a dominance phase (2014–2030). The lag phase is defined by the years at which the adult population is  $\leq 5\%$  of the difference between the upper and the lower asymptote whereas the dominance phase is defined by the years at which the corresponding demographic values are above the 95% of the difference between the upper and the lower asymptote.

The spatial dynamics of the invasive population show a similar trend with: i) a lag phase, during which toads do not spread across the pond network (2001–2005, Fig. 4a); ii) a spread phase, during which toads invade new ponds every year (2006–2012, Fig. 4b–f); and iii) a dominance phase, during which all the ponds are invaded (2013–2030, Fig. 4g–i). It suggests that the guttural toads in Cape Town started to spread across the pond network five years before their demographic explosion. We also identified a linear relationship between the log of the total number of adults and the log of the invaded area (Appendix B, Fig. B2 in Supplementary material).

The lag phases we detected are mainly due to the interaction between the dispersal kernel and density dependent survival. The kernel sourced from Smith and Green (2006) is characterized by a leptokurtic probability distribution that determines the incorporation of rare long distance dispersal events. Thus, just after the introduction, the majority of individuals do not disperse across the pond network and the few which do disperse are not able to breed. This is confirmed by the fact that the spatial spread of the population is delayed until 2006 and starts five years before the demographic explosion (2011). It also suggests that during those years (2006–2011) the density of the invaders is lower than the initial density. Additionally, at the beginning of the invasion many adults bred in the same pond as a consequence of the reduced initial dispersal, with density-dependent survival of tadpoles and metamorphs that led to low recruitment and negative growth rate in the first five years.

The spread/explosion phase shows an accelerating and sigmoidal trend, and is determined by the same mechanisms expressed previously at a different scale of space and time. When the density at the leading edge reaches the threshold allowing reproduction, the population grows faster and faster (Fig. 3) because the low density at the periphery determines high survival of tadpoles and eggs (Fig. 4c–e). This is confirmed by the linear relationship we detected between the number of toads and the area they invaded; since both these auxiliary variables are expressed on a log scale (Appendix B, Fig. B2 in Supplementary material), the spatial spread of the invaded area grows exponentially with the number of adults. Although we plotted the relationship between total number of toads and invaded area in an XY graph for simplicity, neither of these variables should be considered independent, as during the spread they tend to reinforce one to another.

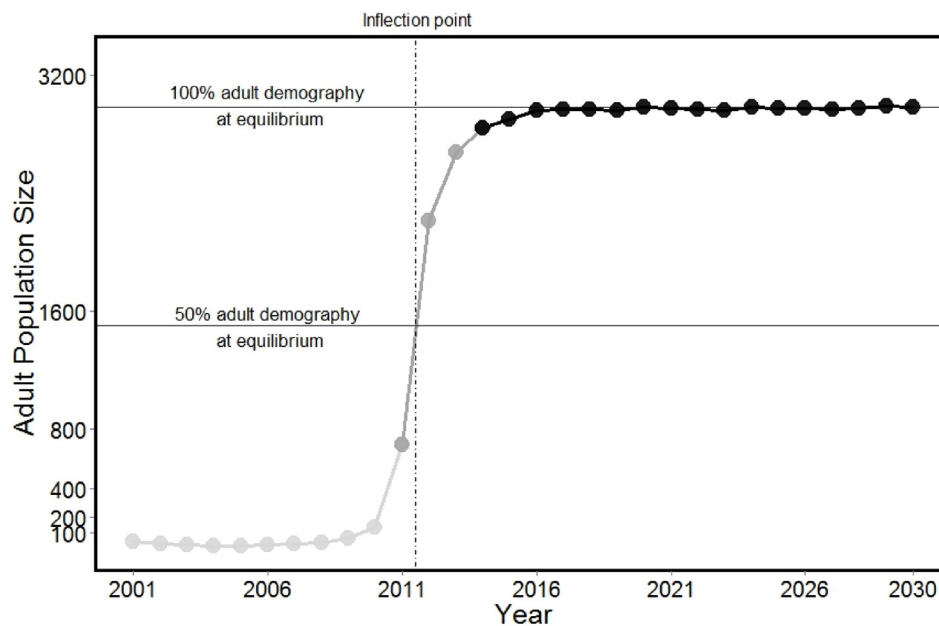
Although a survey on the invasion of the guttural toads across years does not exist for the period before the eradication (pre 2011), some scattered information collected about the invaded area helps to qualitatively compare the outputs of our model against field observations. A lag phase was indeed detected after the first species detection in Cape Town (season 2000–2001), with toads heard calling in less than 2 km<sup>2</sup> in the following years (De Villiers, 2006; Measey et al., 2017); however our model predicted a smaller invaded area during this phase. Lack of a systematic approach to survey the ponds during the eradication and limitation to physically access some properties will not allow quantitatively comparing model predictions to eradication data (e.g. comparing uninvaded ponds predicted by the model with the actual uninvaded ponds). However assuming the invasion front estimated by the eradicators as reliable, our model forecasted for 2011 an invaded area larger than the area estimated through eradication in the same year and more compatible with that estimated in the season 2014–2015 (9.72 km<sup>2</sup>, 3.51 km<sup>2</sup> and 7.56 km<sup>2</sup> respectively). Lastly, the model predicted the invasion of the entire arena (about 27.11 km<sup>2</sup>) by 2012 (Fig. 4f), whereas guttural toads are still known to invade new portions of the arena every year (Measey et al., 2017). To summarize, our model showed a longer lag phase and a shorter exponential phase than those observed in the field.

#### 3.2. Sensitivity analysis

In the model, adult demography at equilibrium increased exponentially with juvenile and adult survival, and linearly with maturing probability (Appendix B, Fig. B3c–e in Supplementary material). Juvenile survival had the highest effect; for example, a survival four times higher than the baseline value in juveniles led to a number of adults approximately ten times higher (Appendix B, Fig. B3c in Supplementary material). Conversely, modelled adult demography was robust to variation in pre-metamorphic demographic traits (e.g. egg survival, Appendix B, Fig. B3a in Supplementary material) and behavioural traits (e.g. site fidelity, Appendix B, Fig. B3f in Supplementary material). Variations in propagule size and different approaches to model pond–pond distance did not affect the total number of adults at equilibrium. (Appendix B, Fig. B3h in Supplementary material). Similarly, population growth was sensitive to juvenile and adult survival but robust to all other demographic and behavioural traits (Appendix B, Fig. B4 in Supplementary material). Conversely timing of invasion, expressed as inflection point, was sensitive to propagule size (Appendix B, Fig. B5h in Supplementary material), with smaller sizes that led to inflection points occurring in later years (i.e. longer lag phase) and bigger sizes that led to points occurring in earlier years (i.e. shorter lag phase). For instance, had the introduction at the initial pond been a propagule size four times bigger (160 individuals instead of 40), it would have resulted in a lag phase seven years shorter. The Euclidean distance matrix led to an earlier inflection point than that obtained using landscape resistance modelling (Appendix B, Fig. B5h in Supplementary material). Lower values of site fidelity and higher values of maturing probability advance the inflection point whereas all the other traits do not show a coherent pattern (Appendix B, Fig. B.5 in Supplementary material). Lastly we observed that extremely high values of site fidelity and philopatry and extremely low values of post-metamorphic survival led the population to collapse before invading the arena (Appendix B, Fig. B3 in Supplementary material).

### 4. Discussion

For the guttural toad invasion of Cape Town our model forecasts demographic and spatial dynamics that are characterized by lag



**Fig. 3.** The modelled demographic population dynamic of the guttural toad follows a logistic curve described by three different stages (lag, explosion and dominance; in pale grey, dark grey and black respectively). The inflection point represents the point with the highest growth rate (i.e. where the curve reaches 50% adult demography at equilibrium) whereas the 100% adult demography at equilibrium is defined by the upper asymptote.

phases and accelerating spread. The spatial spread starts five years earlier than the demographic explosion, suggesting low density of invasive individuals at the beginning of the invasion. Such dynamics noticeably match real field observations and confirmed what was previously detected in other invasive populations (Crooks, 2005; Aikio et al., 2010; Essl et al., 2012). However, sensitivity analysis also suggests that it would be preferable to quantify parameters such as propagule size or post-metamorphic survival in the field. Small oscillations of these parameters may have important consequences on our capacity to effectively reconstruct and predict amphibian invasions.

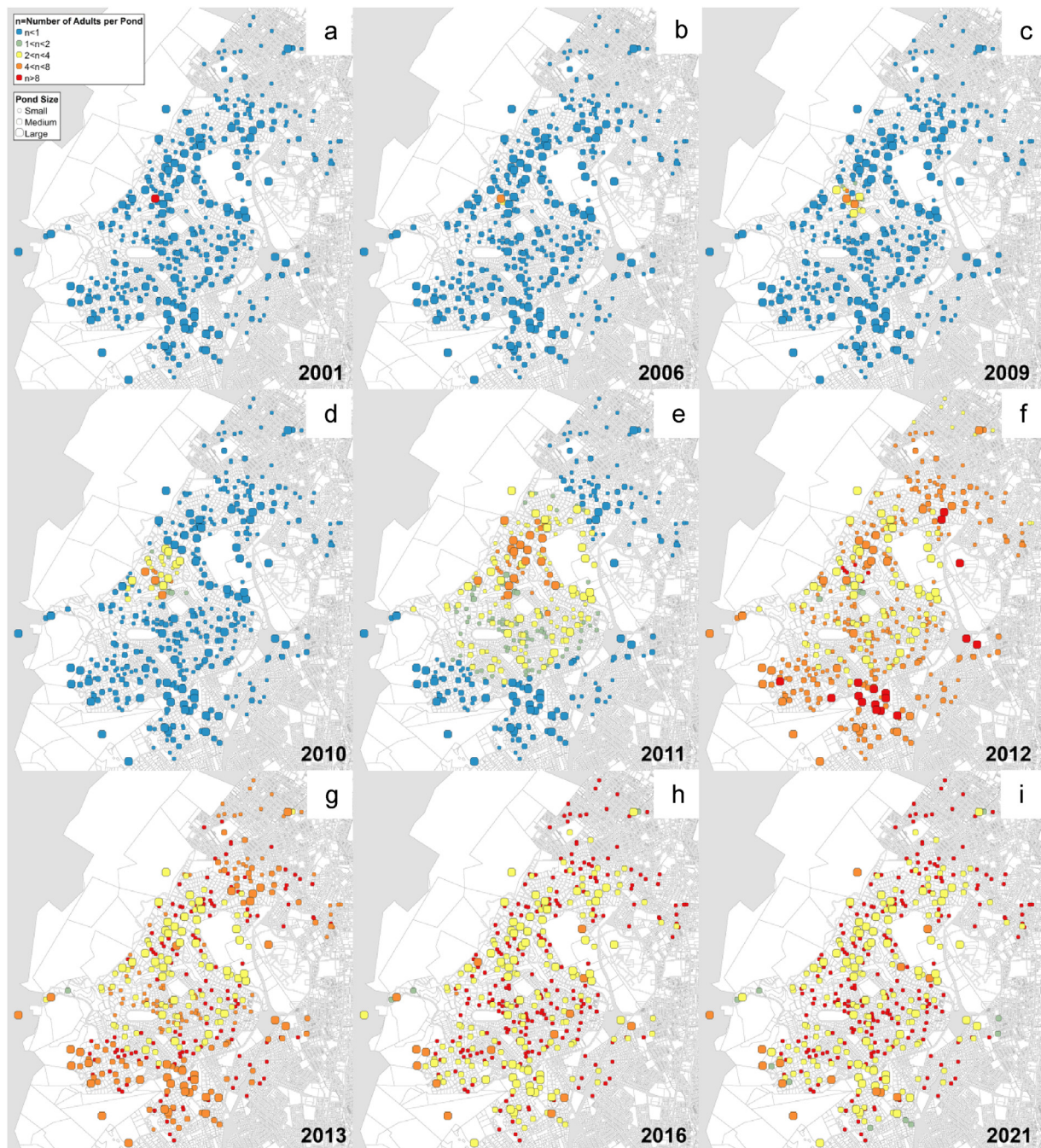
Lag times have been frequently detected at the onset of a biological invasion across different taxa (Crooks, 2005; Aagaard and Lockwood, 2014; van Sittert and Measey, 2016) with multiple mechanisms hypothesized to play a role such as Allee effects (Courchamp et al., 1999; Stephens and Sutherland, 1999), spatial heterogeneity (Schreiber and Lloyd-Smith, 2009) and population growth trajectories (Pyšek and Hulme, 2005). For example, exponential growth trajectories are intrinsically expected to generate lags because at the onset of any invasion the number of individuals and/or invaded areas is necessarily low (Crooks, 2005). However in our model the lag phase deviated from an exponential growth and showed a prolonged trend suggesting the occurrence of more complex processes. Mounting evidence shows this deviation in ecological models (Aikio et al., 2010) where factors such as evolution or competition were hypothesized to prolong lags (Crooks, 2005). Intriguingly the relaxation of competitive interactions caused by lower density at the periphery should cause an abrupt end of the lag phase (Crooks, 2005; Marco et al., 2010), similar to what we observed in our model when invasive toads breed at the invasion front. Notably a prolonged lag and the low density of individuals during the first years of the spatial spread could have delayed the first detection of the population (season 2000/2001) and/or management reactions (season 2010/2011) until the successive phase (Epanchin-Niell et al., 2012). The explosion phase leads to a full invasion of the pond network in only three years; it suggests that a prompt removal of toads during the first phase of the invasion would have been necessary to minimize labour costs and maximize management success. Future versions of the model should explic-

itly test this hypothesis and investigate efficacy and efficiency of a management program only started during the explosive phase.

The sensitivity analysis also showed that bigger propagule sizes determine shorter lag times. Authors have suggested propagule size as a predictor of establishment and invasion success (Hayes and Barry, 2008) and although in our model a small propagule size (five individuals) led to invasion after a very long lag phase (Appendix B, Fig. B5 in Supplementary material), it did not account for demographic and environmental stochasticity. Stochastic effects can potentially eliminate a small established population before the onset of the spread phase; therefore, a shorter lag phase due to a higher propagule pressure could *per se* reduce the occurrence of these effects and lead to a higher probability of invasion. From a management perspective it implies that removing a subset of individuals during a lag phase might not only postpone the invasive spread but also lead to a crash of the established population (Crooks, 2005).

In our model the lag is followed by accelerating spread; this is in accordance to what was predicted by Kot et al. (1996), Neubert and Caswell (2000) and Neubert and Parker (2004) in case of models based on integrodifference equations and characterized by fat-tailed (leptokurtic) kernels. Accelerating spread was confirmed in several other biological invasions across taxa and regions (Hastings et al., 2005; Arim et al., 2006) and it might indicate a recursive pattern in species characterized by long dispersal events (Mundt et al., 2009; Kelly et al., 2014). The choice to incorporate long-distance dispersal events seems appropriate because *Sclerophrys gutturalis* has been anecdotally observed (GV pers. obs.) to show long-distance dispersal events in Cape Town (>1 km) as in many species of toads (Smith and Green, 2005); performance trials on *S. gutturalis* also showed that adult individuals may have locomotive endurance up to 1 km/per night (Vimercati et al., in prep.). However authors suggest that minimal variations in the shape of dispersal kernel could generate different invasion speeds among and within species (Kot et al., 1996; Caswell et al., 2003). The very recent invasion of the species in Cape Town and the necessity to euthanize all individuals detected by the eradicators did not allow performing a mark-recapture study to estimate the dispersal kernel of invasive guttural toads across years. It required us to use the data collected





**Fig. 4.** Maps showing the spatial dynamics of the guttural toad in Cape Town across years as forecasted by the age structure models. Colours represent different number of individuals in each pond (blue, less than one individual; green, between one and two individuals; yellow, between two and four individuals; orange, between four and eight individuals; red, more than eight individuals).

by [Smith and Green \(2006\)](#) for a different species of toad; this may well be a source of uncertainty in our model and we encourage more studies to depict dispersal kernels both at interspecific and intraspecific level in anurans.

Interestingly we observed that the population growth rate was particularly sensitive to variation in post-metamorphic survival ([Appendix B](#), Fig. B4 in Supplementary material), suggesting that high survival at life-history stages with no density dependence may cause faster spreads. Since invasive individuals may have survival significantly higher than native individuals (e.g. due to enemy release, [DeWalt et al., 2004](#); [Lakeman-Fraser and Ewers, 2013](#)), it would be wise to estimate this life-history trait during invasion; small differences in its estimation may have large effects on mod-

elling invasion dynamics of pond-breeding anurans ([Lampo and De Leo, 1998](#)). It also implies that perturbations occurring later in the life-cycle have bigger consequences on amphibian populations, as other theoretical studies on amphibians have suggested ([Vonesh and de la Cruz, 2002](#); [Govindarajulu et al., 2005](#); [Di Minin and Griffiths, 2011](#); [Beaty and Salice, 2013](#)). This is also in accordance to the high sensitivity of adult demography to variation in the post-metamorphic demographic traits we observed ([Appendix B](#), Fig. B3 in Supplementary material). Density of invasive individuals is known to be positively correlated to their impact on ecosystems and native populations ([Yokomizo et al., 2009](#)); thus it would be wise to explore whether a successful management aiming to reduce the guttural toad impact can be reached by removing exclusively

adults and juveniles, as suggested in other amphibian invasions (Beaty and Salice, 2013). We call, however, for more theoretical and field investigations on this aspect because complex non-linear dynamics have been observed in other models (Govindarajulu et al., 2005) and costs and benefits of removal can significantly change across different life-history stages (Buhle et al., 2005; Pichancourt et al., 2012).

Although these invasion dynamics are qualitatively in accordance with field observations, this model is not free of limitations. Firstly, we set that the dispersal behaviour is mainly due to the interaction between the dispersal kernel and LCP distance. Our LCP calculation incorporates an element of realism (i.e. two ponds are distant from each other not only because of their geographic position but also because of their connectivity linked to toad dispersal preferences); however quality of breeding sites, density dependent dispersal, habitat predictability and climate matching between native and invaded area may all interfere with toad dispersal behaviour (Ficetola and De Bernardi, 2004; Smith and Green, 2005; Cayuela et al., 2016). Also, the use of demographic parameters estimated in other toads, given the scarcity of literature on the guttural toad, is a source of uncertainty, although our review suggests the parameters used are within bufonid interspecific variation (Table 1). Future versions of the model should incorporate more life-history traits directly estimated for the target species; for instance time of maturity could be defined through skeletochronological assessment where juvenile and adult survival should be explored through mark-recapture methods.

Lastly, limitations are associated with the field data we used to parameterize the models. For example, we cannot exclude with certainty that when the guttural toad was first detected in 2000, some toads had already colonized a few more ponds. In that case our parameterization would overestimate the species' capacity to spread across the pond network, resulting in a faster spread across the arena. Similarly, the spatial eradication data collected in 2011 could be inaccurate because it was observed that the eradicators only systematically targeted the invasion front just after 2013 (SD pers. obs.). Therefore, the spatial extent of the invaded area in 2011 and 2012 could also have been underestimated.

Despite these limitations, our approach appears particularly promising to further explore demographic and spatial dynamics of pond-breeding invasive anurans from a management perspective (Vimercati et al. in prep). Since in our model we can regulate survival of virtual individuals at different life-stages for any target pond, it would be possible to simulate different management strategies that remove individuals from the population and then forecast their effects on population dynamics. Such strategies can be simulated not only across space (e.g. removal of individuals from some specific ponds) and time (e.g. removal of individuals in some specific years) but also across the whole life-cycle. The age structured approach allows for example simulating removal of: i) eggs and tadpoles at the invasion front using chemical traps (Crossland and Shine, 2011); ii) adults and juveniles by hand or mechanical traps (Schwarzkopf and Alford, 2007) during the exponential phase; iii) toads at any life-stage but only in a subset of target ponds. Since these strategies may have different time and labour costs, their impacts on population dynamics may be compared and the most effective strategy selected through cost-benefit approach.

To conclude, we suggest that the model described here may help not only to reconstruct invasion dynamics of pond-breeding anurans by the integration of the invader and characteristics of the invaded landscape; it can be further deployed to gain insights on management decision making (Caplat et al., 2012; Addison et al., 2013).

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## Appendix A.

### Appendix A.1.

Eq. (1) derives from the model proposed by Hassell (1975) to incorporate the effect of intraspecific competition on tadpole survival and follows the parameter estimation reported in Vonesh and De la Cruz (2002). The density-dependence coefficient  $d$  acts as a scaling parameter, whereas the density-dependence exponent  $\gamma$  regulates the relationship between the number of metamorphs (here  $M_i$ ) and the initial number of tadpoles ( $T_i$ ). Although this relationship can be linear ( $\gamma = 0$ ), weakly density dependent ( $0 < \gamma < 1$ ), compensatory ( $\gamma = 1$ ) or overcompensatory ( $\gamma > 1$ ), we decided to set it as compensatory following the literature reviewed by Vonesh and De la Cruz (2002) for the family Bufonidae. We used surface area to estimate density-dependent survival following Vonesh and De la Cruz (2002) and Tejedo and Reques (2014), as tadpoles of *S. gutturalis* are browsers of superficial algae (JM pers. obs.). We eliminated competition between the tadpoles of the first clutch and those of the second clutch by incorporating the annual proportion of competing tadpoles from the same female ( $c$ ) into Eq. (1).

### Appendix A.2.

Eq. (4) derives from the manipulative study conducted by Harper and Semlitsch (2007) in *Anaxyrus americanus*. The authors used enclosures of 2 m<sup>2</sup> to manipulate metamorph density and detected density-dependent survival after one year. We observed in the field that most metamorphs can be detected within 1 m from the pond edge and that all of them were found within 5 m. This spatial distribution around the pond edge may be due to dehydration sensitivity of toads at this life-history stage as largely hypothesized in the literature (see pre-departure phase in Pittman et al., 2014) and confirmed by field studies (Child et al., 2008a, 2008b). Since in Cape Town metamorphosis takes place during the dry, hot summer, we suggest that the dehydration stress of metamorphs should be high, strongly limiting their dispersal from the natal pond. Thus we calculated the pond edge area within a radius of 5 m ( $E_{s,m,1}$ ) and used it to estimate the initial density of metamorphs (during the pre-departure phase). It should be noted that Eq. (4) describes a theta-logistic growth model in which the first year survival of metamorphs is strongly over-compensatory, i.e. with lower survival at very low and very high density and higher survival at intermediate density. The constants 2.76 and 0.623 used in Eq. (4) are defined in Harper and Semlitsch (2007) by the theta logistic growth model as best descriptor of the relationship between the initial density and density after one year.

### Appendix A.3.

We observed that all ponds of the arena are located in private properties; moreover field surveys showed guttural toads tend to use paved streets for moving from one property to another as

detected in radiotracking studies on the western leopard toad in Cape Town (JM pers. obs.) and in other bufonids (Brown et al., 2006), conversely avoiding habitats with dense vegetation. Toad locomotion on paved surfaces is also more effective (faster speed) than on vegetated and grassy habitat (GV pers. obs.) as already detected in invasive cane toads (Brown et al., 2006). Conversely toads were strongly limited in their movement by the walls that surround each property, using gates preferentially to move from the street to get inside a property. Lastly, green corridors and water channels are not preferentially used by toads to disperse, contrary to what has been observed in other species of invasive frogs (Peterson et al., 2013).

#### Appendix A.4.

In the laboratory, dissection of 15 females captured and euthanized during the extirpation followed by removal of their ovaries allowed estimation of clutch size (i.e. number of eggs per clutch per female) through subsampling. Additionally, field surveys showed that in Cape Town the breeding season occurs between October and February (instead of between August and March as in the South Africa native range, du Preez et al., 2004), thus restricting annual number of clutches to two instead of three. Lastly, probability to lay eggs was calculated separately for each pond size category (small, medium, large) as the probability to detect eggs and tadpoles in a pond where the presence of females was already confirmed around the same pond during the extirpation process. For example the high probability to lay eggs in a medium pond (0.4) means that eggs and tadpoles were detected in four out of ten medium ponds where at least a female was detected.

#### Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2017.03.017>.

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