Using public surveys to rapidly profile biological invasions in hard-to-monitor areas

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Abstract

Understanding the impact and dynamics of invasive alien species (IAS) is essential for tailoring appropriate management plans. This information can be difficult to obtain in the short term, and intrinsic difficulties of monitoring hard-to-reach areas may hamper prompt estimation of IAS distributions. Using the case of the invasive Asian common toad (*Duttaphrynus melanostictus*) in Madagascar, we show how public surveys coupled with a multi-analytical approach can promptly provide accurate information on invasion dynamics and impacts. On the basis of key-informant responses, we built polynomial regressions to investigate the spatiotemporal invasion patterns, false-positive occupancy models to estimate species occupancy, and mixed-effect models to evaluate the public perception and attitudes. We found that the invasion followed a linear expansion of approx. 2 km year^{-1}, with human-mediated dispersal facilitating the spread of the species. Toad occupancy decreased towards the invasion front and increased in the southern portion of its range. Negative perception decreased in urban areas, where people were less concerned by toad impacts on ecosystems, and in recently invaded localities, suggesting density- or time-dependent effects. We also identified 12 potential impacts, with "loss of domestic apiaries", "poisoning of poultry" and "decline of snakes" standing out for prevalence and potential severity. Our results bring important insights into the invasion dynamics and the human-toad interactions in Madagascar, highigting the versatility of public surveys to obtain essential information for invasion science and management, which can be especially useful in hard-to-monitor regions of the world with a low in-country capacity to counter invasive species.

Key words

invasion dynamics, impacts, public perception, *Duttaphrynus melanostictus*, invasive species, Madagascar, occupancy modelling, false positive

Introduction

Invasive alien species (IAS) are major drivers of global and local environmental change, affecting both biodiversity (Bellard, Cassey, & Blackburn, 2016) and human well-being and livelihoods (Shackleton, Larson, et al., 2019; Shackleton, Shackleton, & Kull, 2019). The effects of invasions on ecosystems have long been studied in great detail, while the socioeconomic impacts are recently gaining resonance (Pejchar & Mooney, 2009). IAS may either provide benefits or make local communities more vulnerable to environmental or societal changes, directly altering livelihood systems or facilitating other drivers of disturbance. For instance, the invasive floating aquatic plants in the Wular lake in India increase the prevalence of nuisance animals and diseases (Keller, Masoodi, & Shackleton, 2018). Information on the socioeconomic dimensions of IAS is thus a prerequisite for setting up management plans (Shackleton, Adriaens, et al., 2019). IAS effects can vary spatially and temporally depending on invasion dynamics, which are in turn regulated by both intrinsic (population and spreading dynamics of the species; Shackleton et al. 2017; Bradley et al. 2019) and extrinsic factors (connectivity, habitat suitability; Van Moorter et

al. 2021). Taking into account this variability can help optimize resource allocation for invasion management, and mitigate negative societal impacts (Hulme, 2006).

Invasion dynamics and impacts represent the minimum suite of information required to characterise a biological invasion, as they provide the basis for quantifying several derived variables and indicators of invasion trends, allowing comparison with other known IAS and the implementation of adequate management measures (Latombe et al., 2017). Unfortunately, this information is often partially available, difficult to obtain in the short term, or may be prone to errors and biases (Fitzpatrick et al., 2009; Crystal-Ornelas & Lockwood, 2020). For instance, spatiotemporal patterns of biological invasions are usually traced using distributional records from herbaria, museums, or grey literature, which can be biased by imperfect detection of species or insufficient monitoring efforts over time and space (Pyšek et al., 2008). Monitoring biases can be particularly exacerbated in countries with limited capacity to act against invasions, which typically lack structured, costly monitoring plans (Pyšek et al. 2008; Nuñez & Pauchard 2010). Furthermore, limited access to remote areas can make the monitoring process difficult, hampering the determination of species occupancy (MacKenzie et al. 2002). Public surveys may be a valid alternative to more traditional methods, as they facilitate the rapid collection of a large amount of data at broad spatio-temporal scales and, at the same time, can play a role in improving public engagement (e.g., Cerri et al., 2020). The advantages of this approach lie in its manifold applications. Traditionally, public surveys are used to gather information about people's perceptions, attitudes, and beliefs towards IAS, and their determining factors, which can help to identify potential socio-economic impacts (Crowley, Hinchliffe, & McDonald, 2017; Ribeiro et al., 2021). Public surveys have been successfully used to estimate the occupancy of IAS, and investigate the determinant factors for their occurrence, provided that the target species can be easily recognized by the public and the probability of its misidentification is taken into account (e.g., Mohanty et al. 2018; Mohanty & Measey 2019). Public surveys are also a promising way to reconstruct relatively recent invasion histories, although a recurrent problem is the recall error phenomenon (i.e., the decrease of respondents' accuracy with time since the event; Beckett et al., 2001), which limits precise estimate of IAS establishment time in a locality (Mohanty & Measey, 2019).

The recent discovery of an invasive population of Asian common toads (*Duttaphrynus melanostictus*) in the eastern coast of Madagascar — one of the world's most diverse and most threatened biodiversity hotspots (Conservation International, 2021) — raised concerns about potential ecological and socioeconomic impacts (Andreone et al., 2014; Kolby et al., 2014). The invasive population is reportedly expanding its range at an accelerating pace (Licata et al., 2019), but it is still not clear whether natural or anthropogenic processes (i.e., human-mediated dispersal; Hui & Richardson, 2017) are responsible for the observed acceleration, therefore reconstructing the invasion history is important to elucidate the processes underling the spreading dynamics of toads. The Asian common toad is strongly associated with anthropogenic habitats (van Dijk et al., 2004), and is easily recognizable by locals due to its morphological distinctiveness from native Malagasy amphibians. The area affected by the toad invasion is among the most populated of

Madagascar (United Nations 2019), but its topography and poor road infrastructure render extensive monitoring efforts challenging. This area is thus ideal to test the usefulness of public surveys for rapid monitoring actions and to obtain information on invasion dynamics and potential impacts to be integrated into management strategies, in hard-to-monitor areas.

In this study, we contribute to the application of public surveys in invasion science, emphasizing the use of this method for rapidly profiling biological invasions. First, we reconstruct the invasion history and identify the factors shaping the invasion pattern, taking into account recall error in respondents, and assessing the hypothesis of human-mediated dispersal of the invasive species. Second, we evaluate the identification reliability of local inhabitants, by estimating the probability of false-positive detection, and identifying determinant environmental factors for the occurrence of the species. Lastly, we evaluate public attitudes towards the Asian common toad, testing variation in responses based on sociodemographic determinants and residence time, and revealing potential socio-economic impacts on the human population.

Materials and Methods

The invasive Asian common toad in Madagascar

Duttaphrynus melanostictus is a species complex of medium-sized toads, widely distributed in South and Southeast Asia (Wogan et al., 2016), which are often associated with anthropogenic habitats (van Dijk et al., 2004). The Asian common toad invaded several islands of Wallacea (Reilly et al. 2017) and was recently reported in Madagascar, where it was likely introduced via unintentional transport in commercial containers between 2007 and 2011 (Moore, Solofo Niaina Fidy, & Edmonds, 2015; Licata et al., 2020). The invasion likely started from a single point of introduction (i.e., where containers were first opened), which was identified just south of Toamasina (see Fig. 1; Moore, Solofo Niaina Fidy, & Edmonds, 2015). In 2017, the invasive toad was reported in an area of 549 km^2 and was reported expanding in all landward directions colonizing all available habitats, with higher abundances in and around human settlements —especially in presence of garbage dumps (Licata et al., 2019).

Study design

We sampled 79 localities from November 2018 to May 2019 (Appendix S1). Localities were opportunistically selected to cover the whole urban and suburban areas of Toamasina (Toamasina I district) and the surrounding countryside (Toamasina II district), and were at least 400 m apart from each other (Fig. 1a). We categorized localities into two community types. Urban communities were located within the Toamasina I district, and included contiguous suburban peripheral localities (Fig. 1b, c), while rural communities included small to large settlements (>50 households) interspersed in seminatural and agricultural landscapes in the Toamasina II district (Fig. 1d, e).We conducted two different types of surveys: i) visual encounter surveys (VESs) to

determine toad occurrence and ii) key informant surveys to reconstruct the spatiotemporal dynamics of the invasion and obtain data about the public perception of the IAS.

The probability of detecting invasive toads in public spaces, when they are present, is very high (site-level detection probability ranges between 62% and 99% depending on local abundances; Licata et al., 2019). Two experienced observers conducted VESs starting after dusk (after 6 pm, when toads are active), searching for toads on the streets, green spaces, around settlements, and near water sources, within 200 m of the locations where key informant surveys were conducted. VESs ended as soon as the invasive species was detected, or lasted a minimum of 30 minutes and were repeated a second evening to confirm the non-detection of the species (Mohanty & Measey, 2019). Overall, we performed field observations in 51 localities (64.5% of the total). Due to security issues, we could not carry out nocturnal VESs at 28 localities (35.45% of the total). As the Asian common toad is strongly synanthropic (van Dijk et al., 2004), we assumed all residents (excluding visitors and new arrivals) have a similar probability of detecting toads, and therefore selected them as key informants. In-person interviews of local inhabitants followed the structure of the questionnaire used by Mohanty & Measey (2019), which includes a combination of structured and semi-structured questions. Interviews were conducted in the local language (Malagasy Betsimisaraka dialect; Appendix S1) and lasted approximately 5 minutes per respondent. We visited households, courtyards, and local grocery stores to conduct the public surveys, selecting them within a 200-m radius from the site where the first interview was conducted. After collecting basic sociodemographic data (i.e., age and gender of respondents), the questionnaire started by gathering information about invasive toad occurrence ("Have you seen this animal in this particular locality?"), with the support of a picture of the toad. Respondents were asked to report on toad occurrence within 100 m of the site of the interview. If we received an affirmative response, we elicited information about the time of first observation of the toad in the locality ("When did you first see the toad in this locality?"). Secondarily, we investigated whether respondents perceived a positive or negative impact of the invasive toad ("Do you incur any benefit / loss due to the toad's presence in this village?"; asked as two separate questions and eliciting yes / no answers), and details about the specific negative or positive effects incurred. Lastly, we asked "Do you kill the toad?" (eliciting yes / no answers), to assess the public attitude towards localised management of this species. The participation in the survey was anonymous and voluntary, and personal data collected were limited to the participants' gender and age, and did not contain any personal sensitive data (e.g., home address, telephone number, or health conditions), therefore ethical approval was not required by the Ethical Committee of the Malagasy Ministry of Environment and Forests.

Statistical analysis

Spatiotemporal dynamics of the invasion

We used people's responses about the time of first observation to estimate the time of the establishment of the invasive toad in each locality, excluding localities with fewer than three key

informants (n = 3). For each locality, we calculated the median time of establishment, along with the median absolute deviance (MAD), which is a robust estimator of relative dispersion that is less influenced by outliers (Arachchige, Prendergast, & Staudte, 2020). We used simple linear, second-, and third-order polynomial regressions to investigate the relationship between the median time of establishment and distance from the introduction site (i.e., the centroid of the invasive range estimated in 2014; Moore, Solofo Niaina Fidy, & Edmonds, 2015). We used weighted least squares to incorporate observational variation into the regression analysis. Weights were given using the reciprocal MAD values, approximating zero values to 0.5 (i.e., less than one year) to avoid undefined reciprocal values. In addition to the distance from the introduction point and its polynomial terms, as independent variables we also considered: i) community type (urban vs. rural), to test whether urban habitats facilitate toad colonization and increase the invasion speed, and ii) the distance from Route Nationale 2 (hereafter RN2), the main road connecting Toamasina to the capital Antananarivo, to assess its potential role as a dispersal corridor. Invasive populations may show heterogeneous spread rates across the invaded range (Hui & Richardson, 2017), therefore we also included iii) the direction of the locality from the introduction site to test for differential spread dynamics in opposing directions. The direction was calculated with respect to the coastline, which is offset from the north by 14.6° (Fig. 1a). We, therefore, drew a line through the introduction point which was offset from the north by 14.6°, and used the cosine of the angle between the locality and this line to obtain the direction of the locality (i.e., "1" was equal to 14.6° and "-1" to 194.6°). We ln-transformed the distance from the RN2, to reduce skewness. Furthermore, we scaled all continuous variables (i.e., mean = 0; SD = 1) for easier comparison of their effects. Collinearity between explanatory variables was low [Variance Inflation Factors (VIF) were always < 2], thus we included all of them in the models. We built models (function *lm* of the package *stats*; R Core Team, 2021) using all possible combinations of independent variables (without interactions) and ranked them based on the Akaike's Information Criterion corrected for small sample sizes (AIC$_c$), using the *dredge* function of the *MuMIn* package (Barton, 2020). All models which had a simpler nested model with lower AIC$_c$ were removed from the list of candidate models (i.e., nesting rule; Richards, Whittingham, & Stephens, 2011). Finally, we assessed the spatial autocorrelation of the residuals of the best AIC model through Moran's *I* (Legendre, 1993), using the package *EcoGenetics* (Roser et al., 2017).

Assessing the time of establishment across the invasive range

Several field survey campaigns have been conducted to assess the occurrence of this species in the province of Toamasina since the invasive toad population was first documented (Kolby et al., 2014). We collated all the distributional records resulting from these field surveys (Appendix S2), also including one locality (named Analalava) opportunistically surveyed in April 2020 after receiving reports of toad presence. We considered the date in which each distributional record was reported as the minimum time of establishment of the toad in the locality, and compared it with the expected time of establishment, based on the distance from the introduction point of the

locality, as predicted by the best AIC_c model of the spatiotemporal dynamics of the invasion (see the previous section).

To individuate possible areas of early establishment of toads as compared to model prediction, we retained all localities with the date of observation below a threshold value obtained by subtracting the average MAD value from the predicted time of establishment.

Occupancy analysis

We estimated site occupancy using multimethod false-positive occupancy models (Miller et al., 2011). This class of models incorporates detection data obtained from several survey methods characterized by various degrees of certainty, explicitly taking into account the possibility of false-positives, which are intrinsic to some types of dataset (e.g., public surveys, citizen science programs, acoustic surveys) (Pillay et al., 2014; Chambert, Miller, & Nichols, 2015). This approach allows the use of public survey data as a source of information for species occurrence, considerably reducing the sampling effort as compared to more labour-intensive, time-consuming ecological studies (Miller et al., 2011, 2013; Pillay et al., 2014, 2022). Records from key informants were assumed to be uncertain observations (i.e., both false positives and false negatives are possible), while for our own field observations false negatives were possible but not false positives. We assigned a value of "2" to certain detections (field VESs data), "1" to uncertain detections (public surveys), and "0" to non-detections. We evaluated the effect of four site-specific covariates in occupancy models: the distance and direction from the introduction point, the community type, and the distance from the RN2. Linear distance from RN2 was ln-transformed and all continuous variables were scaled to allow comparison of estimated effect size. VIFs of all variables were < 2 in this analysis. We built false-positive occupancy models including all potential combinations of site-specific covariates (without interactions) and ranked them on the basis of their AIC_c values (Burnham & Anderson, 2002). The final candidate set of models was obtained by using the nesting rule (Richards, Whittingham, & Stephens, 2011). Detection probability was held constant among sites, and Moran's I was calculated on the residuals of the best occupancy models to assess spatial autocorrelation (Legendre, 1993). Since preliminary analyses showed that false-positive detection probability among respondents was negligible (i.e., approx. 1%; see Results), we considered a single respondent's detection/non-detection as the observed occupancy state for the spatial autocorrelation analysis. We estimated occupancy rates (ψ), false-positive detection probability ($p10$), true-positive detection probability ($p11$) and associated 95% confidence intervals. False-positive occupancy models were run using the *occuFP* function in the R package *unmarked* (Fiske & Chandler, 2011), while spatial autocorrelation analysis were performed using the package *EcoGenetics* (Roser et al., 2017).

Public perception

We used generalized linear mixed models (GLMMs) with binomial error distribution to test the variation in responses as a function of distance from the introduction point and with respect to sociodemographic determinants (i.e., community type, gender, and age of respondents). The distance from the introduction point showed a nearly perfect correlation with the estimated time of establishment obtained from people's responses (Pearson's $r = 0.89$; $p < 0.001$), and was used as a proxy of the cohabitation time with the IAS. We tested the effect of the selected variables on the primary perceived impact (i.e., response to the questions "Do you incur any benefit / loss due to the toad's presence in this village?"). Preliminary results showed that positive responses were very few (n=14), as a consequence, we treated people's responses as binomial dependent variables ("negative", "non-negative"). Since the questionnaire included semi-structured questions, we obtained specific responses about the perceived impact of toads, which were assigned to four main impact categories ("Nuisance", "Health threat", "Economic threat" and "Ecosystem threat"; see Results). As impact categories were not-exclusive (i.e., each respondent could report multiple impact categories), we considered each of them as a distinct binomial dependent variable (dummy variables). We ln-transformed and scaled all continuous variables, to reduce skewness and allow comparison between each variable's estimated effect sizes. In all models, we considered "locality" as a random effect to account for variation between sampled localities. Also, in this analysis low VIF values (VIF < 2) confirmed lack of multicollinearity issues. We built models including all potential combinations of independent variables, not considering their interaction, ranking them on the basis of their AIC values (Burnham & Anderson, 2002), and using the nesting rule to filter out overly complex models (Richards, Whittingham, & Stephens, 2011). To assess the spatial autocorrelation of the residuals of our model, we performed Moran's I test (Legendre, 1993). We used the package *lme4* (function *glmer;* Bates et al., 2015) to implement GLMMs, *lmerTest* (Kuznetsova, Brockhoff, & Christensen, 2017) to obtain test statistics, *MuMIn* to build the full set of models (Barton, 2020), *EcoGenetics* (Roser et al., 2017) for analysis of spatial autocorrelation and *ggeffects* (Lüdecke, 2018) to plot model predictions. All analyses were performed in the R environment (vers. 4.1.1; R Core Team 2021).

Results

Spatiotemporal dynamics of the invasion and identification of outlier localities

Overall, 691 respondents from 43 localities (mean respondents per locality = 15.9; SD = 8.2) provided information about the time of the establishment of the invasive toad. The majority of respondents were from urban communities (57.7%), which were located between 0.98 and 14.57 km from the introduction point. The locality where toads were recorded earliest was 2.8 km from the proposed introduction point (Moore, Solofo Niaina Fidy, & Edmonds, 2015), where the median value of responses regarding the year of arrival was mid-2009, while the most recent one (median response for the approximate year of arrival = 2019) was located at 14.57 km from the introduction point. The average MAD value was 1.5 years (SD = 1.08; range = 0–4.45), but long-invaded

localities showed significantly higher MAD values (Pearson's r = -0.809, df = 41, p < 0.0001). The model that best described the relationship between the time of establishment and distance from the introduction point, which had no competing models, showed a linear pattern and a very good fit (coefficient estimate, B = 0.496; SE = 0.036; p < 0.0001, R^2 = 0.819), and did not include any other variable (Appendix S3). Residuals of the best model were not spatially autocorrelated (Moran's I = 0.22; p > 0.1). The annual spread rate predicted by the model was 2.014 km year^{-1} (95% CI 1.76–2.36).

Distributional records obtained from literature revealed that toads established in at least 21 localities much earlier than expected by our model, based on the distance from the introduction point (Appendix S4). In these localities, the known time of establishment was below the threshold value (i.e., expected time of establishment – average MAD value) (Fig. 2). For 16 of these localities, the difference between the predicted and the observed time of establishment was greater than two years (Fig. 2; Appendix S4). The most extreme case is represented by the locality Analalava, located 56 km north of Toamasina, where the toad was recorded in April 2020, 19 years before its expected establishment on the basis of its distance from the introduction point (Fig. 2; Appendix S4).

Detection probabilities and factors determining the occurrence of the Asian common toad

Overall, 1,175 respondents from 79 localities (mean = 14.9; SD = 8.4) provided information on toad occurrence. Field surveys allowed us to detect the Asian common toad in 44 localities located up to 15.5 km from the introduction point, while the toad was not detected in seven surveyed localities (located between 13.4 and 17.2 km from the introduction point).

The estimated true positive detection probability by respondents (p11) was 0.93 (95% CI 0.91–0.94) while their false positive detection probability (p10) was very low (0.01; 95% CI 0.004–0.03). The best model showed a significant negative relationship between toad occupancy and two independent variables: distance from the introduction point and direction, with occupancy rates declining far from the introduction point (B = -5.30; SE = 1.58; p < 0.001) and higher in the southern portion of our study area (B = -0.91; SE = 0.46; p = 0.047) (Appendix S5). A second competing model included the distance from the introduction point —with similar coefficient estimates— and the distance from RN2, which, however, was marginally non-significant (B = -0.80; SE = 0.41; p = 0.052). The residuals of the best models did not show spatial autocorrelation (Moran's I = 0.38; p > 0.1).

Factors determining the public perception of the Asian common toad

Overall, 692 respondents from 49 localities (mean = 14.1; SD = 8.9) answered the attitude survey questions. The average age of respondents was 38.6 years (SD = 14.1 years); 56.5% were women and 57.1% resided in urban communities. Localities were between 0.98 and 14.57 km from the introduction point (mean = 8.3; SD = 3.4).

59.5% of respondents reported negative impacts related to the presence of toads, while 38.4% did not report any benefit or loss. The remaining 14 respondents (2%) reported both types of effect (n = 10) or positive effects only (n = 4). The perceived negative impact of the invasive toad decreased significantly as the distance from the introduction point increased (binomial GLMMs, B = -0.95; SE = 0.20; $p < 0.001$), and was significantly higher in rural communities (B = -1.46; SE = 0.41; $p < 0.001$; Fig. 3a; Appendix S6).

Responses revealed 12 potential sources of impact by the toad, which we assigned to four main categories: "Nuisance", "Health threat", "Economic threat" and "Ecosystem threat" (Table 1). Variation of responses about negative impacts was associated with both sociodemographic determinants and distance from the introduction point. Nuisance was the most reported impact. The best model explaining variation in this perceived impact category had no competing models and indicated that toads were considered less of a nuisance in urban communities (B = -1.45; SE = 0.65; $p = 0.027$), and in areas further from the introduction point (B = -0.98; SE = 0.27; $p < 0.001$; Fig. 3b; Appendix S6). Toads were also often considered a health threat (e.g., causing skin irritations, polluting water bodies; Table 1), but no predictors explained variation in this perceived threat (p always > 0.05), with candidate models showing a similar fit to the null model (Appendix S6). The economic threats most frequently mentioned included "loss of apiaries" and "poisoning of poultry", or other livestock/pets (Table 1). The best model for this impact category included gender and age as predictors, which, however, were not significant (p always > 0.05; Appendix S6). None of the competing models included different or significant predictors. The reported impacts on ecosystems included "competition with Indian bullfrog (*Hoplobatrachus tigerinus*)" (which is non-native and invasive in Madagascar but commonly consumed by local communities; Mohanty et al. 2021) and general concern for environmental degradation, often related to the "decline of snakes", which was sometimes considered as the only positive effect (n = 14). The best model —with no competing models—, indicated that the perception of invasive toads as an ecosystem threat was reported more frequently by men (B = 0.79; SE = 0.37; $p = 0.032$) and in rural communities (B = -1.53; SE = 0.62; $p = 0.014$) (Fig. 3c; Appendix S6).

Of the 701 respondents interviewed, 482 (68.8%) reported killing the toad. The best model for this response category indicated that the probability of community members reporting killing toads was higher in men (B = 0.51; SE = 0.18; $p = 0.004$), and increased in localities further from the introduction point (B = 0.23; SE = 0.11; $p = 0.043$; Fig. 3d; Appendix S6). A second competing model (ΔAIC = 1.96) only included gender, with similar coefficient estimates (B = 0.50; SE = 0.18; $p = 0.005$). We did not detect spatial autocorrelation in the residuals of any of the models (Moran's I always < 0.1; $p > 0.1$).

Discussion

Biological invasions need to be rapidly profiled in hard-to-monitor, megadiverse regions, to address impacts on ecosystems and human populations. Public surveys can help to rapidly generate essential information to inform possible management interventions, while at the same

time improving public awareness. Our combination of multiple analytical approaches allowed us to i) determine that the invasion is following a nearly-linear range expansion of approximately 2 km year^{-1}, and identify outlier localities where toads arrived substantially earlier than predicted, possibly through human-mediated dispersal; ii) ascertain the reliability of occurrence data obtained from public surveys, identifying differential occupancy patterns across the invasive range, with toad occupancy rates increasing in the southern portion of the range and iii) unveil perception of the invasive species in urban and rural human communities along the invasion gradient identifying 12 perceived impacts that cause the greatest societal concerns.

Our work extends prior research (Mohanty et al., 2018; Mohanty & Measey, 2019) on the application of public surveys in invasion science by: i) incorporating uncertainty of people's responses (recall error) in the reconstruction of invasion history; ii) identifying long-distance dispersal events using deviation from the spread pattern; iii) improving our understanding of invasion trajectories by testing potential drivers; iv) assessing determinants of public perception.

Improving the application of public surveys to investigate invasion dynamics

IAS spread is highly context-dependent, with strongly heterogeneous range expansion patterns (Hui & Richardson, 2017). Invasive populations often show an exponential range expansion followed by a sigmoidal phase, which reflects population growth dynamics (Hui & Richardson, 2017). The Asian common toad in Madagascar showed a linear range expansion of approx. 2 km year^{-1} (Fig. 2), which is a pattern often observed in species with limited dispersal (Hui & Richardson, 2017). Although toads exhibit the longest dispersal distances amongst anurans, these may substantially differ between and within species (Cayuela et al., 2020). Limited dispersal potentially explains why *D. melanostictus* is currently invading Madagascar at a much slower rate than the cane toad during the early stages of the Australian invasion (approx. 2 vs. 10–15 km year^{-1}; Urban et al., 2008), however, multiple non-exclusive processes may be responsible for the observed rate of spread (Appendix S7).

Our findings contrast with initial evidence of an accelerating range expansion of the species (Licata et al., 2019), suggesting that other factors are contributing to speeding up the invasion. Using deviation from model expectations we detected several outlier localities where the establishment of the species likely did not follow the normal leading-edge dispersal but could be attributed to long-distance or human-mediated dispersal (Appendix S8). The observation of an extralimital, disconnected population 56 km north of Toamasina (i.e., Analalava; Fig. 2) confirms that human-mediated dispersal is facilitating the invasion. Although there is no direct evidence of the dispersal pathway responsible for the introduction in this locality, apart from anecdotal reports of toad arrival with the transport of manure (BM, pers. comm.), accidental human-mediated dispersal is likely to occur in Madagascar, due to lack of biosecurity measures for domestic trading (Licata et al., 2019; Randriamoria, 2019). Nevertheless, among the outlier localities that we have identified, those closest to the introduction point might suffer from prediction biases caused by

recall error (i.e., higher MAD values; see Results), or an offset position of the point of introduction, for which some uncertainties still exist (Moore, Solofo Niaina Fidy, & Edmonds, 2015).

Public survey data have proven reliable in the reconstruction of early-stage invasions, but their application for older invasions was cautioned against due to recall error (Mohanty & Measey, 2019). Recall error can be taken into account by introducing measures of statistical dispersion, by considering the level of confidence in respondents' accuracy with specific questions, or by explicitly modelling respondent characteristics that can determine recall error (Beckett et al., 2001), thus extending the applicability of this method to older invasions (Mohanty & Measey, 2019).

False-positive occupancy models

The involvement of the general public is crucial for management actions targeting IAS (Green, Underwood, & Akins, 2017), but misidentification of target species can hamper the precise assessment of impacts, or cause misestimation of species distributions (Costa et al., 2015; Faúndez, Carvajal, & Villablanca, 2020). False-positive detection rate, although not equivalent, is related to the misidentification rate (Clement et al., 2014), and could provide the first proxy to assess the public's suitability to contribute to IAS management.

Occupancy estimates decreased along the invasion gradient and were higher in southern localities, where invasion could have been facilitated by man-made waterways (Appendix S4). However, our results only refer to human settlements, which are particularly suitable for the species (Licata et al., 2019), and do not necessarily provide information on natural habitats. Furthermore, our estimates do not consider possible changes in the occurrence status in recently invaded localities, and a dynamic occupancy modelling approach will be needed to evaluate the occupancy dynamics over time.

Occupancy modelling based on public survey data is a well-established method that has found important applications in invasion science (e.g., Mohanty et al. 2018; Mohanty & Measey 2019). Recent developments in the occupancy modelling framework (i.e., multispecies occupancy models; Pillay et al., 2022), could improve the use of public survey data for occupancy predictions, allowing estimates of the distribution and determining factors of occurrence of multiple species, as often is the case for freshwater IAS (Preston, Henderson, & Johnson, 2012).

Public perception in the impact assessment framework

Negative perception and negative attitude towards invasive species are strongly determined by species characteristics (Knight, 2008). The toads' toxicity, appearance, and association with unhealthy environments such as latrines and garbage dumps may have contributed to the widespread public dislike, however, the reasons adduced were largely community- and gender-dependent, and could vary along the invasion gradient. Negative perception and attitude towards the Asian toad followed distinct spatial trends (Fig. 3a, b, d), which were likely dictated either by

toad abundance or time since establishment (Kulhanek, Ricciardi, & Leung, 2011; Bradley et al., 2019; Mohanty & Measey, 2019). Relating impacts (and their magnitude) to invasion stages or to specific socioenvironmental contexts can be pivotal to informing management strategies, as it allows anticipating the type and direction of impacts at novel sites (Kulhanek, Ricciardi, & Leung, 2011).

As impacts (both real and perceived) may differ substantially across demographic groups, weighing up costs and benefits for the well-being and livelihoods of different public categories may avoid culturally inadequate or socially unjust management actions (Shackleton, Shackleton, & Kull, 2019), ultimately improving management outcomes. Rural communities had a more negative perception of the toad (Fig. 3a, b; Appendix S6), which reflected higher perceived impacts (Fig. 3c) but could also be related to the effect of the toad's presence on the general landscape aesthetics (Shackleton, Richardson, et al., 2019).

Citizens identified multiple impacts on human well-being, livelihoods, and ecosystems (Table 1). On one hand, some perceived impacts (Appendix S9) could be the result of a shared narrative about the toad's toxicity (maybe originating from public awareness campaigns; see Licata et al. 2020), which is a phenomenon often reported or inferred for public perception of invasive species (Beckmann & Shine, 2010; Mohanty & Measey, 2019). On the other hand, the consistency of the numerous reports of toad poisoning in poultry, decline of snakes, and loss of apiaries is worrying and deserves further consideration, also because some of these impacts have already been reported for this species in other invaded regions (e.g., Timor-Leste; Trainor, 2009). Poisoning of poultry could represent a major impact on local livelihoods, due to the economic relevance of poultry in Madagascar (Thomas & Gaspart, 2015), but actual impacts must be ascertained and quantified given the contrasting evidence in the literature (e.g., Beckmann & Shine, 2010; Gadelha et al., 2014; Marshall et al., 2018). Conversely, many Malagasy native predators are predicted to be vulnerable to toad toxins (Marshall et al., 2018), and at least one species of snake suffers severe mortality rates due to toad poisoning (Licata et al., 2022). The reported decline of snakes in rural and suburban areas might therefore indicate that negative impacts on wildlife are already taking place (Table 1). Likewise, the reported loss of apiaries is substantiated by field evidence (Appendix S9) and may cause substantial problems, especially in recently invaded localities where beekeepers may suffer abrupt losses of beehives.

The risks posed by IAS are translated into environmental and socio-economic impact scores (e.g., Blackburn et al. 2014; Bacher et al. 2018), which may be subjected to changes when additional evidence of impacts is provided. A previous assessment suggested a 'moderate' socio-economic impact by *D. melanostictus* (Bacher et al. 2018), but the perceived impacts on apiaries and poultry suggest a 'major' impact on human livelihoods in Madagascar.

The propensity to kill toads was widespread and univocal among community types, with a decrease of toad culling in long-invaded localities likely driven by the awareness of its inefficacy (Fig. 3d), suggesting general public support for this management method. However, this is not always the case, and public acceptance must be evaluated and taken into account to avoid unsuccessful management initiatives (Jarić et al., 2020). Culling by unspecialized people can be

problematic, because misidentification errors are possible, with potential impacts on native species (Somaweera, Somaweera, & Shine, 2010). Complicating matters further, the time taken to understand and build community support can make any subsequent management action costlier and less effective (Caplat & Coutts, 2011). Public surveys can acquit this twofold purpose by taking the pulse of public acceptance, while at the same time disseminating knowledge and raising public awareness, allowing time optimization over the decision-making process.

Limitations of using public surveys

Data quality is a recurrent issue in the use of data obtained from the public (Ellwood, Crimmins, & Miller-Rushing, 2017), which, however, can be mitigated through a suite of statistical tools (Bird et al., 2014). Nevertheless, the reliability of information obtained can strongly depend on the study system. The traits of IAS can strongly affect people's perception and beliefs, with negative effects of charismatic, aesthetically pleasing or recreational species frequently downplayed or overlooked by the general public, as observed for the rainbow trout in South Africa or the American squirrel in Europe (Bertolino & Genovesi, 2003; du Preez & Lee, 2010). Furthermore, some IAS traits may make it difficult to obtain meaningful information from public surveys data. For instance, IAS lacking distinctive traits that make them easily recognizable by the public, or showing strong similarity with native species may suffer an excessively high number of false-positive detections, hindering both monitoring and impact assessment. The distinctiveness and synanthropic nature of the Asian toad probably facilitated its identification by respondents, but greater efforts in selecting key informants may be required in other study systems with habitat specialists, cryptic, or less abundant target species (Mohanty & Measey, 2019; Pillay et al., 2022).

People's perception of IAS may change over time and space depending both on the relevance of the invasion process (i.e., its magnitude and rate of spread) and the overarching socio-cultural factors (Shackleton, Richardson, et al., 2019), which may have implications on the use of public surveys data. For instance, people may not report impacts during the initial phase of an invasion simply because they have not been perceived yet, or their perception of IAS can shift from beneficial or non-threatening towards more negative perceptions, as a result of increasing abundance or residence time of the invasive species (e.g., this study). The timing and spatial distribution of public surveys might therefore affect the invasion profiling, thus requiring minimum *a priori* knowledge of the study system and the invasion stage.

Conclusions

Biological invasions will likely increase worldwide in the future (Seebens et al., 2021), but most countries, especially those with a lower per-capita GDP, remain unprepared to counter IAS spread (Early et al., 2016). New technologies provide a growing panel of tools for species monitoring and detection, which enable advanced forecasting of invasive species spread and distribution (Kamenova et al., 2017), but also have their own limitations. For instance, invasion

dynamics can be traced using agent-based models (e.g., Vimercati et al., 2017), which, however, are computationally expensive and may provide inexact predictions if they do not adequately take into account the context-specific variation and endogenous variability of the study species (Melbourne & Hastings, 2009). Similarly, environmental DNA can facilitate the detection of IAS, but can be costly, may suffer from detection biases, and requires adhering to high-quality standards to provide reliable information (Ficetola, Manenti, & Taberlet, 2019; Klymus et al., 2020). Although increasingly affordable (Lahoz-Monfort & Tingley, 2018), these tools may not always be easily accessible in regions lacking in-country expertise and structured funding to support long-term management programs. Public surveys can be particularly useful in these circumstances, as they do not require specific technical knowledge, are cost-effective, and extremely versatile. The implementation of this method in Madagascar revealed potential in addressing shortcomings in monitoring capacities, while raw public survey data can be translated into actionable science to inform the decision-making process, potentially facilitating early intervention against IAS. For invasive species that are easily recognizable and detectable, public surveys are a powerful tool to address fundamental requirements for invasion science.

This method may be used in the framework of translational ecology (Enquist et al., 2017), as it creates a direct link between decision-makers, ecologists, and stakeholders. Public surveys can help disseminate awareness, build public support and identify shared strategies between local communities and regulatory agencies and, therefore, have the potential to foster integrated management of IAS and improve the probability of successful outcomes.

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Author contributions statement

FL, NPM, and GFF conceived the ideas and designed methodology; FL, FRH and TMR collected the data; FL analysed the data; FL and GFF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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TABLES

Table 1. Proportion of respondents reporting a specific perceived impact of the invasive Asian common toad *Duttaphrynus melanostictus* at 49 localities surveyed in the province of Toamasina (Madagascar) from November 2018 to May 2019.. The total number of respondents in each category may be lower than the numbers reported between parentheses as one respondent could report multiple specific impacts. Between parentheses we report the number of respondents and localities from where the specific impact is reported; n indicates the number of respondents reporting the specific perceived impact for the impact category considered.

Impact category	Specific impact	Respondents	Perceived impact
Nuisance		n = 189	
	Toad presence	99.5% (188; 32)	Nuisance caused by the presence of the toad
	Chorus noise	0.5% (1; 1)	Nuisance caused by the chorus noise
Health threat		n = 132	
	Skin disease	94.7% (125; 29)	Toad's toxicity can induce skin irritation, causing itching
	Poisoning of water	5.3% (7; 4)	Toad tadpoles and adults can poison water sources
Economic threat		n = 77	
	Poisoning of poultry	72.7% (56; 23)	Lethal toad poisoning of poultry
	Loss of apiaries	27.3% (21; 10)	Apiaries loss due to toad predation on bees
	Poisoning of pigs	3.9% (3; 2)	Lethal toad poisoning of pigs
	Poisoning of dogs	2.6% (2; 1)	Lethal toad poisoning of dogs
Ecosystem threat		n = 47	
	Decline of snakes	80.8% (38; 14)	Snakes decline due to toad poisoning
	Competition with Indian bullfrog	10.6% (5; 3)	Indian bull frog declines due to competition with the toad
	Environmental degradation	8.5% (4; 4)	Environment degrades after toad arrival due to toad toxicity

Increase of rodents	4.2% (2; 2)	Increase of rodents after toad arrival

FIGURE LEGENDS

Figure 1. a) Distribution of 79 localities in the province of Toamasina (Madagascar) where in-person interviews on the occurrence and perceived impact of the invasive Asian common toad *Duttaphrynus melanostictus* were conducted (blue squares = urban communities; green circles = rural communities) from November 2018 to May 2019. The map shows the district of Toamasina I (dark grey area), the putative point of introduction of the Asian common toad (orange bull's eye; Moore et al. 2015), and the road Route Nationale 2 (black line); b, c) urban (along Route Nationale 2) and suburban habitats characteristic of the urban communities; d, e) rural/agricultural and seminatural habitats characteristic of the rural communities.

Figure 2. Predicted time of establishment as a function of the distance from the point of introduction of the invasive Asian common toad *Duttaphrynus melanostictus* in the province of Toamasina (Madagascar), as obtained from a weighted linear regression of public surveys data collected in 43 localities between November 2018 and May 2019. The estimated year of establishment is obtained from people's responses about the time of first observation of the invasive toad in the surveyed locality (median of responses) and the error bars represent the MAD values used for the method of the weighted least squares. In red, the localities lying below the chosen threshold values (i.e., predicted time of establishment – average MAD value) and identified as possible extralimital populations of Asian common toad. Shapes indicate distributional records published in different articles (see legend).

Figure 3. Predicted probabilities of response for primary (a), and main categories (b, c) of perceived impacts, and attitude (d) towards the invasive Asian common toad *Duttaphrynus melanostictus* in Toamasina (Madagascar), as obtained from binomial GLMMs of public surveys data collected between November 2018 and May 2019. The graphics only show impact categories for which predictors are significant. a) Predicted probability of negative response in different community types at different distances from the introduction point; b) predicted probability of toad's presence being perceived as a nuisance in different community types at different distances from the introduction point; c) predicted probability of toads being perceived as an ecosystem threat between different genders and community types. d) Predicted probability of respondents reporting killing the invasive Asian common toad, as a function of the gender and the distance from the introduction point.
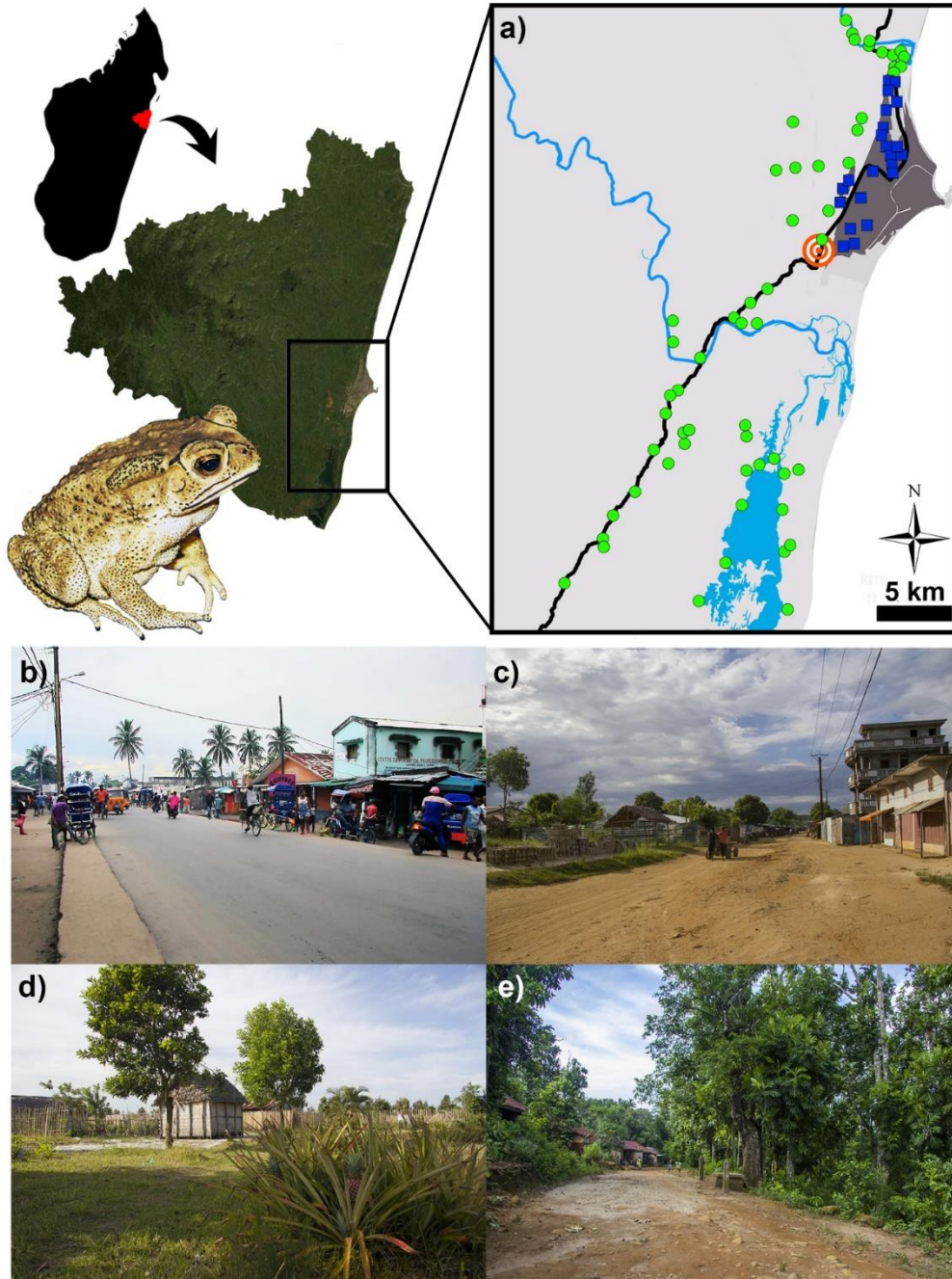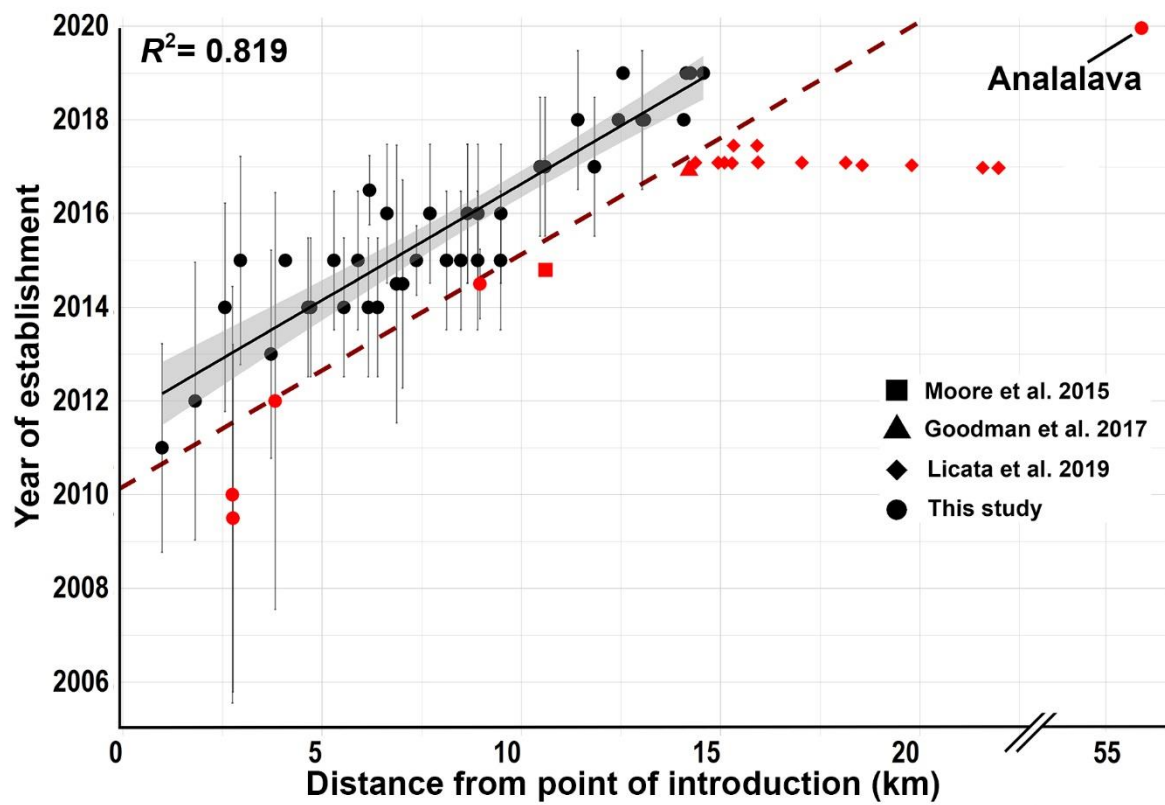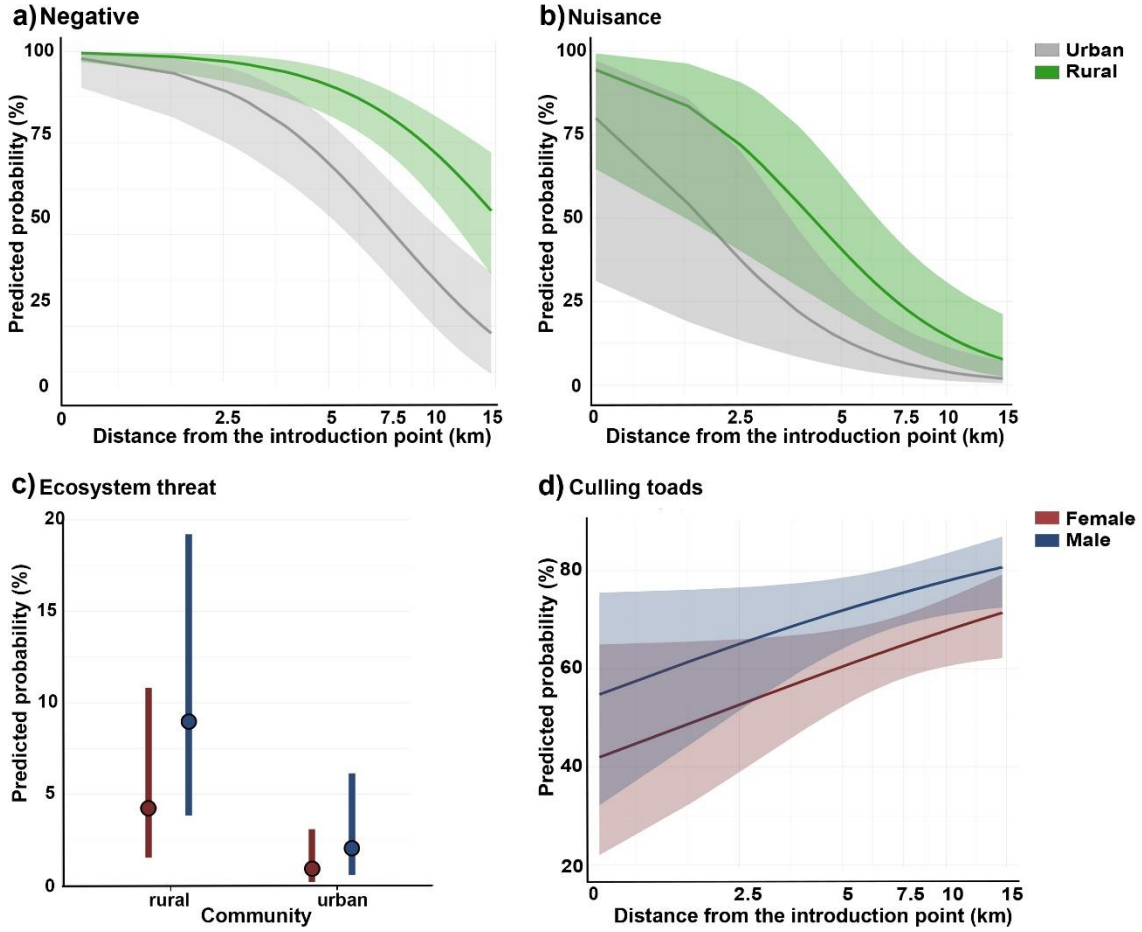
Figure 1

Figure 2

a) Negative

b) Nuisance

c) Ecosystem threat

d) Culling toads

Figure 3