

Adaptive invasive species distribution models: a framework for modeling incipient invasions

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Abstract The utilization of species distribution model(s) (SDM) for approximating, explaining, and predicting changes in species' geographic locations is increasingly promoted for proactive ecological management. Although frameworks for modeling non-invasive species distributions are relatively well developed, their counterparts for invasive species—which may not be at equilibrium within recipient environments and often exhibit rapid transformations—are lacking. Additionally, adaptive ecological management strategies address the causes and effects of biological invasions and other complex issues in social-ecological systems. We conducted a review of biological invasions, species distribution models, and adaptive practices in ecological management, and developed a framework for adaptive, niche-based, invasive species distribution model (iSDM)

development and utilization. This iterative, 10-step framework promotes consistency and transparency in iSDM development, allows for changes in invasive drivers and filters, integrates mechanistic and correlative modeling techniques, balances the avoidance of type 1 and type 2 errors in predictions, encourages the linking of monitoring and management actions, and facilitates incremental improvements in models and management across space, time, and institutional boundaries. These improvements are useful for advancing coordinated invasive species modeling, management and monitoring from local scales to the regional, continental and global scales at which biological invasions occur and harm native ecosystems and economies, as well as for anticipating and responding to biological invasions under continuing global change.

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Introduction

Biological invasions and their consequences for ecosystems and economies worldwide have become areas of increasingly focused and active research and management since Elton's (1958) fundamental work on invasion ecology (Pimentel et al. 2005; Richardson 2011; Vila et al. 2011). These efforts have led to the recognition of novel ecosystems (Hobbs et al. 2013), directed management funding (Leung et al. 2005), and

influenced environmental and trade policies (Simberloff 2013). The ways in which invasive species will respond to and interact with future stressors (e.g., coupled climatic and landuse change) are uncertain, yet likely to have substantial repercussions for global economies (e.g., changes in agricultural productivity and input costs) and biodiversity (e.g., changes in species diversity and interactions) (Hobbs et al. 2013; Simberloff 2013; Flanagan et al. 2015). These effects could be positive and/or negative, depending on the species, social-ecological systems, responses, and locations under consideration. Given the pervasiveness and complexity of biological invasions, it is crucial that we increase our understanding of present and future invasive species distributions, spreads and effects (Bertelsmeier et al. 2013). The development of models that yield such insights, according to invasive species habitat requirements and spatial distributions, are one path forward.

Species distribution model(s) (SDM) are low-dimensional abstractions of ecological realities that relate the occurrence or abundance of species to environmental data, identify and describe the processes underlying species distributional patterns, and make predictions concerning species distributions in space and time (Elith and Leathwick 2009). For SDMs applied specifically to invasive species, the term invasive species distribution model(s) (iSDM) has emerged (Table 1; Vaclavik and Meentemeyer 2009; Gallien et al. 2012; Brummer et al. 2013). Using iSDMs to estimate sets of environmental conditions under which invasive species may establish and spread will increase management efficacy and efficiency by helping prevent invasions and/or minimize their spread and detrimental effects in vulnerable locations (Peterson 2003). However, in order to develop reliable and broadly-applicable iSDMs, a basic understanding of the underlying processes (e.g., survival, reproduction and dispersal) that drive patterns in invasive species distributions is required (Rodder et al. 2009; Smolik et al. 2010; Bradley et al. 2015). Unfortunately, modelers and managers often lack this information—a shortcoming that is exacerbated by the fact that the behavior and effects of invasive species may vary in space and time with environmental conditions [e.g., optimum temperature (Iacarella et al. 2015)]. Furthermore, in their representation of ecological phenomena (e.g., range shifts), iSDMs and other spatially explicit ecological models often violate basic

SDM assumptions (e.g., species–environment equilibrium) (Elith et al. 2010). Despite the inevitability of these and other limitations [e.g., model failure to account for demographic stochasticity (Tyre et al. 2001), landcover classification errors (Langford et al. 2006), other data quality issues, and inappropriate modeling technique selection (Jimenez-Valverde et al. 2008)], iSDMs represent a relatively quick and feasible means of addressing, forecasting, and contributing to solutions for biological invasions when decisions must be made and management must be undertaken in the face of uncertainty (Cote and Reynolds 2002).

Within iSDMs, environmental niches are commonly used to model invasive species' geographic occupation potentials in novel areas (Soberon 2007; Jimenez-Valverde et al. 2011). Although describing and estimating the fundamental invasive niche may be relatively straightforward, delineating the realized invasive niche is generally more difficult (Table 1; Hutchinson 1978; Pulliam 2000; Soberon 2007; Angert 2009), especially when there are differences in the realized niche between native and novel ranges (i.e., lack of niche conservatism) (Gallien et al. 2010). The fundamental niche is defined solely by abiotic environmental factors known to broadly constrain the distribution of a species, whereas the realized niche aims to also account for complex interactions between local abiotic and biotic elements. Incomplete information on realized niches often precludes clear and consistent discrimination between suitable and unsuitable invasive species habitats, particularly for locally-rare or patchily-distributed species (Gogol-Prokurat 2011). For example, identifying the temperature threshold responsible for constraining a species to certain portions of a continent (i.e., fundamental niche) is likely to be more straightforward than identifying and quantifying interspecific relationships that allow it to persist in one habitat patch, but not another, when both patches fall within its temperature tolerance (i.e., realized niche). Additionally, for invasive species, occupancy of one patch, but not another, may not be due solely to complex abiotic and biotic interactions and constraints, but also to a lack of dispersal, in that the species has not yet had sufficient time to spread to the uninhabited patch (i.e., low niche infilling). Indeed, both niche infilling and niche shifts increase geographic distributions of invasive species, and may thereby contribute to differences between the

Table 1 Important terms and definitions for modeling invasive species distributions

Term	Definition
Invasive species	A nonnative species that is introduced, establishes and spreads in a novel environment (Simberloff 2013)
Invasive species distribution model(s) (iSDM)	Low-dimensional abstractions of ecological realities that relate the occurrence or abundance of invasive species to environmental data (Elith and Leathwick 2009)
Fundamental niche	Range of conditions under which survival and reproduction of a species may occur (Hutchinson 1978; Pulliam 2000)
Realized niche	The subset of the fundamental niche actually occupied by a given species (Hutchinson 1978; Pulliam 2000)
Niche infilling	The dispersal of a species to uninhabited, yet suitable, areas within its fundamental niche (Webber et al. 2012; Bradley et al. 2015)
Niche shift	Species occurrence in previously-uninhabited areas, as a result of changing environmental conditions (Petitpierre et al. 2012; Webber et al. 2012)
Mechanistic iSDMs	Process-based approaches to explaining and predicting invasive species distributions (Franklin 2010; Gallien et al. 2010)
Correlative iSDMs	Statistical approaches to explaining and predicting invasive species distributions (Jimenez-Valverde et al. 2011)
Spatial scale	The spatial bounds of a phenomenon that is characterized both by grain (i.e., resolution) and extent (i.e., total area) (Wiens 1989)
Spatial autocorrelation	An increased degree of similarity in the values of observations that are closer in geographic space (Legendre 1993)

realized niche in native and novel ranges (Petitpierre et al. 2012; Webber et al. 2012; Bradley et al. 2015).

Key uncertainties regarding the effects of global change, drivers of biological invasions, violations of model assumptions, data quality, modeling technique adoption, and niche characteristics promote proactive and adaptive approaches to invasive species modeling, monitoring and management. In the well-recognized practice of adaptive management (Holling 1978), controlled management actions are simultaneously viewed as means for accomplishing management objectives and experiments for generating data to reduce uncertainties and inform future decisions and policies (Allen et al. 2011). Similarly, adaptive approaches to sampling use information obtained during monitoring to select additional sampling locations (Thompson and Seber 1996). Adaptive inference balances type 1 (i.e., false positive) and type 2 (i.e., false negative) errors by initially focusing on minimizing type 2 error, so patterns may be recognized, and then successively reducing type 1 error, so predictive accuracy may be improved (Holling and Allen 2002). Finally, in adaptive modeling, initial predictive models of species distributions—which may be trained with limited data—are used to inform management and monitoring activities, which in turn yield additional

data for improving models at subsequent modeling iterations (Conroy and Moore 2002; Guisan et al. 2006; D’Evelyn et al. 2008; Conroy et al. 2011). Each approach, when implemented individually, reduces key uncertainties, but does not necessarily accommodate the benefits of other adaptive approaches.

By integrating adaptive management, sampling, inference, and modeling into a single framework for niche-based explanation and prediction of invasive species distributions, we will enhance our ability to explicitly define and reduce uncertainties, which will in turn promote more holistic and effective invasive species modeling, management and monitoring that avoids common shortcomings, such as: failed maximization of financial resources (Stewart-Koster et al. 2015); delayed action in the face of uncertainty (Conroy et al. 2011); lack of coordinated effort across space, time, and institutional boundaries (Crown et al. 2008); and scale mismatches (Cumming et al. 2013) between invasion effects and management responses. Although uncertainty cannot be eliminated immediately or entirely, it can be reduced incrementally, over time, with directed modeling, monitoring, and management that explicitly incorporates learning. Such improvements are needed, given the high levels of uncertainty that often characterize invasions in novel systems, as

well as the propensity of invasive species to exhibit radical changes over short timeframes (Lockwood et al. 2007), especially under global change-induced shifting of social-ecological baselines.

An adaptive framework for niche-based invasive species distribution modeling

In this review, we incorporate adaptive principles from ecological management into a framework for modeling, monitoring and managing invasive species (Fig. 1). Our framework consists of the following 10 stages: (1) invasion characterization; (2) objectives statement; (3) assumption and uncertainty articulation; (4) scale recognition and assignment; (5) predictor variable selection; (6) modeling technique adoption; (7) autocorrelation supervision; (8) prediction, validation and mapping; (9) management and monitoring; and (10) refinement (Fig. 2). A justification and description of each stage, in addition to suggestions for its application, follow.

Invasion characterization (step 1)

Within each iteration of the adaptive iSDM framework, the invasive species of interest, its stage within the invasion process [e.g., transport, establishment,

spread or impact (Williamson 1996; Lockwood et al. 2007)], and the ecosystem being invaded should be clearly specified, because the facilitators and inhibitors of biological invasions differ among taxa, invasion stages, and geographic locations (Hobbs and Humphries 1995; Theoharides and Dukes 2007; Allen et al. 2013). It follows then, that these specifications may subsequently influence predictor variable selection (i.e., step 5), as well as the utility of model predictions for informing management (i.e., step 9). For instance, factors promoting species transport from native to novel ranges (e.g., human travel and trade) may be entirely different than those facilitating their spread in new environments (e.g., competitor absence) (Lockwood et al. 2007; Allen et al. 2013; Bradley et al. 2015). Alternatively, a single factor, such as landscape structure (i.e., spatial patterns in habitat and resource patch arrangement) might affect a species differently at each invasion stage (Higgins et al. 1996; With 2002). Given these and other idiosyncrasies, it may at times be advisable to subdivide individual stages of the invasion process. In the case of the spread stage, model predictions for populations closer to environmental equilibrium (i.e., advanced in the spread stage) are likely to be more robust and accurate than for those with rapidly-expanding ranges (i.e., early in the spread stage) (Theoharides and Dukes 2007; Vaclavik and

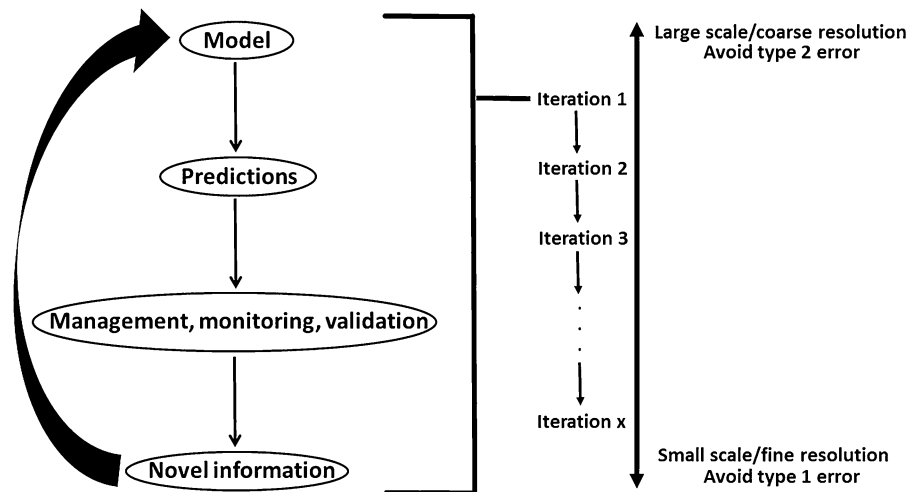


Fig. 1 Generalized example of the adaptive invasive species distribution modeling framework, with an emphasis on the practice of adaptive inference within it. During initial modeling iterations, when information related to the distribution of the invasive species is limited, predictions are made at larger spatial scales and coarse resolutions, with a primary focus on avoiding type 2 error (i.e., false negatives/absences). In subsequent

iterations, as knowledge increases through management, monitoring and model validation at alternative scales and finer resolutions, the focus shifts to increasing predictive accuracy through avoidance of type 1 error (i.e., false positives/presences). Ideally, decreases in uncertainty and increases in precision accompany each iteration

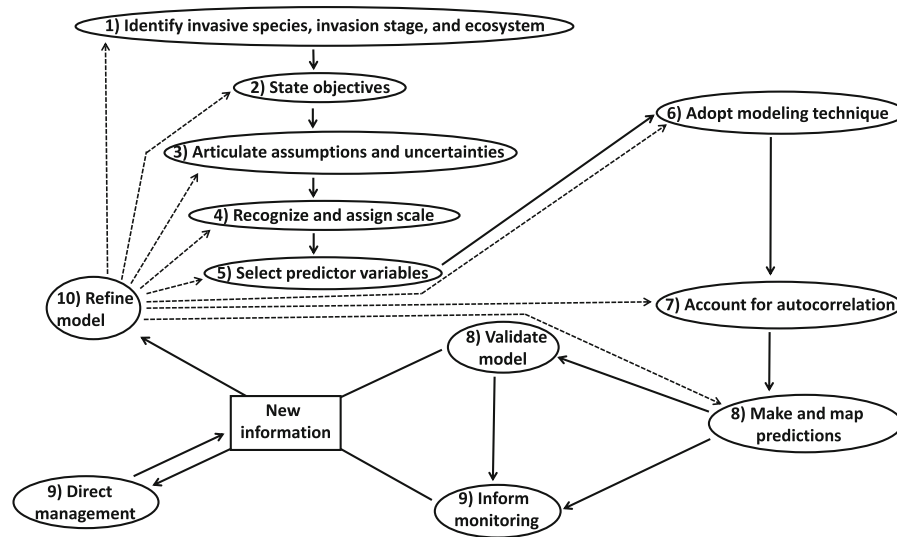


Fig. 2 A detailed explanation of the framework for adaptive invasive species distribution modeling, where newly-acquired information related to invasive species distributions is used for subsequent model improvements. *Solid arrows* show the sequential progression through the first nine steps of the iSDM construction process, whereas *dashed arrows* show alternative options for the application of novel information to model improvement in the 10th and final step. The “articulate

assumptions and uncertainties” step of the framework (i.e., step 3) may also be applied to the “adopt modeling technique” (i.e., step 6) and “make and map predictions” (i.e., step 8) steps. Although presented here individually, some model stages (e.g., monitoring and management) are likely to be accomplished simultaneously in practice, and are therefore assigned identical step numbers

Meentemeyer 2012). During the transport and establishment stages, iSDMs can be used to identify likely colonization sites in novel ranges (Muirhead et al. 2006; Crowl et al. 2008; Vander Zanden and Olden 2008), which can assist preventative action and improve detection likelihood (Mehta et al. 2007). In addition to differentiating between suitable and unsuitable habitats, iSDMs developed for the establishment stage should incorporate the effects of propagule pressure (i.e., number of invasive individuals introduced and number of introduction events) (Leung et al. 2006; Muirhead et al. 2006). For invasive species that have already established or circumvented preventative control efforts at suitable colonization sites, the focus of iSDM predictions may shift to the identification of suitable habitats where the species is most likely to spread and have detrimental effects in the future (Vander Zanden and Olden 2008; Smolik et al. 2010; Sarre et al. 2012).

Objectives statement (step 2)

As in the practice of adaptive management, a clear objective(s) statement is crucial for guiding each

iteration of the adaptive iSDM framework. Although overarching objectives are likely to continually focus on providing information relevant to invasive species management over the entirety of their invaded geographic extents, finer-scale objectives may shift between framework iterations as a result of changes in study scale or location, invasive population status (e.g., invasion stage or political designation as noxious), and/or other social-ecological system components (Tyre and Michaels 2011). For example, at early stages of the invasion process, finer-scale management objectives are likely to focus on preventing the establishment of invasive populations or the spread of those that have recently established, whereas at later invasion stages, focus shifts toward stemming the spread of invasive populations, minimizing negative effects, and eradicating them from invaded areas, which may constitute large geographic extents (Vander Zanden and Olden 2008; Smolik et al. 2010). Management objectives may also be adjusted in light of new information, an example of which is decreasing the risk of spread and adverse effects from specific invasive species under projected future climatic conditions (Bradley et al. 2009; Bradley and Wilcove

2009). Revising and restating objectives at each iSDM framework iteration promotes flexibility in combatting dynamic, location- and situation-specific invasions while working toward the achievement of overarching, larger-scale goals. Furthermore, it increases learning and adaptability for combatting future invasions.

Assumption and uncertainty articulation (step 3)

Spatially explicit ecological models, including iSDMs, are built on the following assumptions: (1) species are at equilibrium with their environments; (2) relevant environmental gradients have been adequately sampled; (3) all limiting factors have been identified; (4) limiting factors and biotic interactions remain constant across space and time; and (5) inter-regional genetic variation within species is negligible (Huston 2002; Latimer et al. 2006; Schroder 2008). These assumptions often conflict with ecological realities (e.g., rapidly-expanding invasive species ranges), and along with other factors (e.g., poor data quality, sampling bias, and model misspecification), increase uncertainty in models and management (Barry and Elith 2006; Elith et al. 2010; Beale and Lennon 2012; Swanson et al. 2013). For instance, long-term predictions related to the domination of aquatic systems by invasive zebra mussels (*Dreissena polymorpha*), which apparently have not yet achieved environmental equilibrium in certain invaded areas, may be proved inaccurate as other ecosystem components adjust and recover (Strayer et al. 2011). Other species with assumed stable geographic ranges may be capable of future expansions as local conditions change (Hill et al. 2012) or niche infilling unfolds (Webber et al. 2012; Bradley et al. 2015). In general, the closer an invasive species is to environmental equilibrium, the more accurate and robust models developed for it are likely to be (Vaclavik and Meentemeyer 2012; Brummer et al. 2013), although effects may differ between spatial scales (Bradley et al. 2015). Mechanistic, process-based approaches to iSDM development, which emphasize physiological limitations and other fundamental constraints on organism distribution and abundance, can be useful under disequilibria (Pearson and Dawson 2003); however, care must be taken to ensure other model assumptions are satisfied. Gallien et al. (2012) have proposed a hierarchical method for utilizing—even embracing—the predictions of assumption-violating

invasive species models, which involves weighting pseudo-absence records in regional realized niche models with the outputs of global niche (i.e., sum of all realized niches) models. More specifically, pseudo-absences in regional models are assigned higher weights if their respective locations are predicted to have lower probabilities of invasive species occurrence in global models.

Uncertainty in distributional predictions may also result from a host of other issues, such as limited information, vagueness or ambiguity in descriptions, measurement or sampling error, inappropriate modeling technique adoption, inaccurate covariate estimation, and changing correlation structures between variables across space (Eiswerth and van Kooten 2002; Horan et al. 2002; Pearson et al. 2006; Dormann et al. 2008; Jimenez-Valverde et al. 2009; Buisson et al. 2010; Beale and Lennon 2012). Elith et al. (2002), Hartley et al. (2006), and Rocchini et al. (2011) recommend that uncertainties related to species distributions be quantified with confidence intervals and communicated visually with maps of ignorance (i.e., uncertainty), which may assist iSDM improvement and management decisions spatially. Given this potential for quantifying and mapping uncertainties, in addition to the fact that individual modeling techniques carry their own sets of assumptions, the articulation of assumptions and uncertainties may be revisited during the “modeling technique adoption” (i.e., step 6) and “prediction, validation and mapping” (i.e., step 8) steps of our proposed iSDM framework.

Computer simulations [i.e., computational models that mimic behavior or patterns in a system of interest (Grant et al. 1997)] provide another avenue for addressing uncertainties in iSDMs, as they allow for replication of natural patterns (Schroder and Seppelt 2006), comparison of model predictions with known virtual population structures (McCune 2006; Elith and Graham 2009), and generation and evaluation of model parameter probability distributions (Link and Sauer 2002). When extrapolating predictions to novel areas (i.e., step 8), simulations can be used to consider dynamic, non-equilibrium conditions often ignored in static distribution models (Guisan and Zimmermann 2000; Miller et al. 2004). Obvious requirements associated with the development of realistic simulations are extensive ecological, environmental, and technical knowledge (Austin 2002). Examples of the application of simulations to invasive species include:

testing alternative sampling methods (Brummer et al. 2013); predicting persistence and spread following disturbance (Smolik et al. 2010; Brown et al. 2013; Shackelford et al. 2013); identifying source populations (Stevenson et al. 2012); testing for Allee effects (Leung et al. 2004); evaluating the roles of propagule and colonization pressure (Lockwood et al. 2009); and evaluating the efficacy of ecosystem-scale management (Marvier et al. 2004).

Scale recognition and assignment (step 4)

The scale(s) of actual or potential invasion events and their consequences should be given careful consideration at each iSDM framework iteration. The scale of data collection can influence relative predictor variable importance, as well as model utility for explaining the driving processes behind invasions (Higgins et al. 1996; Ibanez et al. 2009; Gogol-Prokurat 2011; Fernandez et al. 2012; Bradley et al. 2015). For example, models trained with invasion data spanning large geographic extents (e.g., continents) or steep environmental gradients (e.g., mountains) are likely to place greater emphasis on climatic predictors than models trained with data from smaller or more homogeneous areas (Austin 2002). Similarly, spatial scales of habitat selection (e.g., home ranges) and temporal scales of reproduction (e.g., years) are likely best for evaluating population-level processes (Tyre et al. 2001). Additionally, individual stages of the invasion process may take place at different scales. For example, transport of propagules between native and novel ranges may occur at as great of a spatial scale as global, whereas establishment occurs at local scales, and spread begins at local scales, but may expand to regional or continental scales (Crowl et al. 2008). Because of these potential differences, obtaining data from a range of scales in native and novel ranges can increase understanding of invasions and their consequences and improve predictive accuracy (Vaughan and Ormerod 2003; Ficetola et al. 2007; Ibanez et al. 2009; Gallien et al. 2012).

The most appropriate scale for analysis may differ according to invasive species characteristics, ecosystem properties, and study objectives. Scale determination can be especially difficult when pattern-driving processes operate and/or are detectable at different scales than the patterns themselves (Levin 1992; Schroder 2008; Angeler et al. 2012). Even if presence

or abundance is constant at one scale, it may be changing at others (Johnson and Krohn 2002). Ecological theories concerning invasive interactions in native and novel environments can aid scale-determination decisions, as can sensitivity analyses that compare emergent patterns among scales (Thomas et al. 2002). Effectively differentiating among distributional patterns (e.g., uniform, random, aggregated, or regular) requires the study area to have a greater geographic extent than the population being evaluated, and that the grain of the data be smaller than individual habitat patch areas (O'Neill et al. 1996; Trani 2002). Additional scale-dependent processes that merit consideration in iSDMs include invasive spread rates (Dwyer et al. 1998; Crowl et al. 2008) and spatial variation in predictor variables (Huston 2002). For instance, invasive spread at the local scale can occur naturally, whereas large-scale spread generally depends on human assistance (Neubert and Parker 2004; Bradley et al. 2015). To reduce erroneous scale assignments, Thuiller et al. (2004) recommend modeling large portions of species ranges, even if the actual area of interest is relatively small.

Early iterations of the adaptive iSDM framework may be most appropriately focused at large spatial scales. Here, the primary focus is not on creating a precisely-correct model, but rather on the detection of broad, relevant patterns, such as the top-down constraint of climate on the distribution of an invasive species. In subsequent iterations, as revised, refined, and ideally more accurate model predictions are produced with new information (i.e., step 10) gained during the “prediction, validation and mapping” (i.e., step 8), and “management and monitoring” (i.e., step 9) steps of the iSDM framework, study scale may become increasingly focused. This is analogous to adaptive inference in ecology (Holling and Allen 2002) and also incorporates the hybrid modeling methodology of Gallien et al. (2010, 2012), which involves using broad-scale, liberal models that avoid false absences to delineate the potential range of an invasive species, and then utilizing more detailed mechanistic models to simulate smaller-scale population dynamics within the potential range.

Predictor variable selection (step 5)

Selecting ecologically-relevant predictors is critical when modeling objectives (i.e., step 2) include the

explanation of invasion-driving processes (Guisan and Zimmermann 2000; Schroder and Seppelt 2006). Predictor variable selection is indeed one of the most crucial steps of the adaptive iSDM framework. If simply making predictions without explaining underlying processes is acceptable, predictors that are correlated with the true driving variables, but do not directly influence the response (i.e., indirect predictors), may be used. However, indirect predictors [e.g., elevation and depth (Elith and Leathwick 2009)] tend to decrease model performance, especially during extrapolation (i.e., step 8) (Levin 1992; Austin 2007; Rodder et al. 2009). The majority of iSDM exercises have applied data and known predictor variable relationships from native ranges to predictions in novel ranges; however, the incorporation of data from novel ranges is increasing and being recognized as useful, if not vital (Broennimann and Guisan 2008; Beaumont et al. 2009; Ibanez et al. 2009; Jimenez-Valverde et al. 2011). This realization stems from the fact that ecological differences and/or modeling errors may cause species–environment relationships and niche predictions to differ between native and novel ranges (Fitzpatrick et al. 2007; Peterson and Nakazawa 2008) and among spatial scales (Ficetola et al. 2007).

Numerous biotic, abiotic, resource, and non-resource variables may be important for predicting the distributions of well-established invasive species, whereas geographic location and disturbance frequency and intensity may be most useful for making predictions about recently-introduced invasives (Marvier et al. 2004; Guisan and Thuiller 2005; Brummer et al. 2013). Similarly, environmental influences on sessile species or mobile species with small home ranges may be easier to quantify than those on mobile species with large home ranges (Guisan et al. 2007; Elith and Leathwick 2009), just as predictions for narrowly-distributed specialists may be more accurate than those for wide-ranging generalists (Hernandez et al. 2006; McPherson and Jetz 2007; Tsoar et al. 2007)—among which are some of the most successful invaders (Marvier et al. 2004). Sampling large portions of environmental gradients inhabited by invasive species—when logistically and financially feasible—can assist with elucidation of invasive species–predictor variable relationships (Austin 2002; Brummer et al. 2013), reduce uncertainties in variation of predictor variables across space (i.e., step

3), and avoid inappropriate scale assignment (i.e., step 4).

When ecologically relevant predictors are used at appropriate scales, variability in model performance is generally greater among species than modeling techniques (i.e., step 6) (Guisan et al. 2007), although not always (Pearson et al. 2006). In practice, certain predictors may lend themselves better to modeling than others, and only a limited set of them, which may or may not explain the processes underlying observed phenomena, may be readily accessible (Van Horne 2002; Rodder et al. 2009). Several common, albeit broadly defined, iSDM predictors are propagule pressure, disturbance, downscaled climate data, invasive species residence time, and invasive species range area (Lockwood et al. 2007, 2009; Wilson et al. 2007; Wittman et al. 2014). The application of many statistical techniques requires that strong correlations among predictors be avoided (Zuur et al. 2007), although this is not true of machine learning and multivariate models (Breiman 2001a, b; Abdi and Williams 2010).

Modeling technique adoption (step 6)

The appropriate modeling technique for approximating any actual or potential invasive species distribution is likely to depend on various aspects of the invasion process and the invaded ecosystem under study, which are contemplated in the first five steps of the iSDM framework. Careful consideration must be given to modeling technique adoption, because one of the most important factors affecting the usefulness of iSDM techniques is their appropriate application (Araujo and Peterson 2012). Utilization of the simplest technique that accomplishes objectives is often recommended, because predictive ability does not always increase with more complex—and generally less interpretable—methods (Conroy and Moore 2002; O'Connor 2002), although machine-learning techniques may present exceptions (Breiman 2001b; James et al. 2013). More complex techniques may be appropriate for later iSDM framework iterations, where they can be built upon and used to supplement results produced previously with simpler techniques.

Niche-based models for invasive species utilize occurrence (i.e., presence/absence and presence-only) and abundance records, in coordination with habitat association information, expert knowledge, and

geographic and environmental data from native and novel ranges (i.e., predictor variables), to differentiate between suitable and unsuitable invasive species habitats (Jimenez-Valverde et al. 2011). Alternative classification systems for the multitude of existing niche-based techniques have been suggested, although a spectrum between purely mechanistic (i.e., process-based) and correlative (i.e., statistical) is generally recognized (Table 1; Kearney 2006; Beale and Lennon 2012). Thuiller et al. (2008), Brook et al. (2009) and Gallien et al. (2010) promote the hybridization of traditional mechanistic and correlative techniques, which differ in their requirements for field data and expert knowledge. Kearney and Porter (2004, 2009) similarly note strengths and weaknesses of both correlative and mechanistic approaches—describing them as complementary instead of alternative. For example, a correlative habitat suitability model and a mechanistic metapopulation model may be combined to estimate the spread of an invasive species among landscape patches that satisfy its basic habitat requirements (Stewart-Koster et al. 2015). The initial choice of developing a correlative or mechanistic iSDM may depend on how much process-based understanding is necessary for accomplishing the objectives stated in step 2 of the framework (Gallien et al. 2010). Below, we briefly review a suite of mechanistic and correlative niche-based techniques for modeling invasive species distributions. We also differentiate between presence/absence and presence-only approaches. For more comprehensive reviews and in-depth technique comparisons, see Guisan and Zimmermann (2000), Guisan and Thuiller (2005), Elith et al. (2006), Jeschke and Strayer (2008), and Kearney and Porter (2009).

Mechanistic techniques

Mechanistic modeling techniques rely more heavily on expert knowledge and ecological theory than do correlative techniques (Franklin 2010; Gallien et al. 2010). As such, mechanistic models are commonly used to explain and predict demographic phenomena in invasive species populations, examples of which are predation (MacNeil et al. 2013), competition (Morales et al. 2013), reproduction and growth (Kearney and Porter 2009), spread (Wilson et al. 2007), Allee effects (Mistro et al. 2012), and movement among suitable habitat patches (Uden et al. 2014). One disadvantage of mechanistic models is the time and effort required to develop them;

however, this may be a worthwhile tradeoff in circumstances that require in-depth understanding of the mechanisms of survival and spread, such as under novel climatic conditions (Kearney 2006; Kearney and Porter 2009).

Correlative techniques

Correlative modeling techniques aim to explain and predict realized invasive species niches via the statistical estimation of predictor–response variable relationships (i.e., parameter estimates) (Jimenez-Valverde et al. 2011). Although correlation does not necessarily indicate causation, correlations can support or refute hypotheses related to pattern-driving processes (Austin 2002; Kearney and Porter 2009). Traditional statistical methods rely heavily on null hypothesis testing and the detection of significant differences between means, whereas more recently-developed, information-theoretic approaches place multiple, plausible, a priori models (i.e., hypotheses) at risk with one another and rank them according to their usefulness for explaining variability in the response (Burnham and Anderson 2014; Murtaugh 2014).

Basic correlative techniques that can be used to explain and predict invasive species distributions include generalized linear model(s) (GLM) and generalized additive model(s) (GAM), which incorporate non-normal error distributions and non-linear terms (Elith et al. 2006). Indeed, some statistically-significant linear relationships may in actuality be nonlinear and even better approximated with polynomial terms or non-parametric regression (McCune 2006; Elith and Leathwick 2009). In their basic forms, these techniques do not incorporate spatial structure; therefore, the addition of spatial predictors may improve performance (Latimer et al. 2006; Miller et al. 2007; Kearney and Porter 2009) and account for spatial autocorrelation (Table 1; step 7).

In hierarchical models, the incorporation of random effects terms (i.e., quantifications of variance around the model intercept and/or coefficient estimates for the entire population of a predictor) transforms GLMs and GAMs into generalized linear mixed model(s) (GLMM) and generalized additive mixed model(s) (GAMM), respectively (Zuur et al. 2009). Like spatial predictors, random effects can help account for spatial autocorrelation. Hierarchically-structured

datasets may also be analyzed with Bayesian techniques, which reduce uncertainty by incorporating priors (i.e., knowledge of parameter distributions, spread rates, nonlinearities, and other complexities) into models (Link and Sauer 2002; Hooten and Wikle 2008). This incorporation of prior knowledge could be especially applicable within the proposed adaptive iSDM framework, given its focus on applying learning to model improvement. In addition to Bayesian and mixed effects techniques, decision analysis (MacGuire 2004) and stochastic dynamic programming (Eiswerth and van Kooten 2002; Leung et al. 2002) may be useful for addressing uncertainties in iSDM development. Finally, principal component analysis (PCA) encapsulates various multivariate statistical techniques that may be used to evaluate, rank, and graphically represent relationships among invasive species occurrence and abundance records and multiple predictor variables, which may or may not be inter-correlated (Abdi and Williams 2010). The axes used to describe these relationships can then be used to make distributional predictions.

Envelope-based techniques delineate niche boundaries in multi-dimensional environmental space, where each dimension represents a predictor (Pulliam 2000; Peterson 2006). Like envelope models, distance-based techniques (e.g., DOMAIN) operate in environmental space, but instead of estimating niche boundaries, quantify environmental distances (i.e., similarities) between the locations of known invasive occurrences and other locations (Barry and Elith 2006; de Siqueira et al. 2009). Bioclimatic niche models (e.g., BIOCLIM) use climate data [e.g., WordClim (Hijmans et al. 2005)] to delineate present and future fundamental niches of invasive species (Beaumont et al. 2009; Jeschke and Strayer 2008; Booth et al. 2014). A common criticism of bioclimatic niche models is that they fail to consider the effects of non-climatic variables on invasive distributions (i.e., define realized niches). One means of addressing this issue is using bioclimatic niche models for larger-scale (e.g., continental) predictions, with additional relevant predictors (e.g., landuse change and biotic interactions) being supplemented at smaller scales (Pearson and Dawson 2003; Jeschke and Strayer 2008), which is equivalent to the hybrid modeling approach suggested by Gallien et al. (2010, 2012).

Artificial neural network(s) (ANN), decision trees [e.g., Random Forests (Breiman 2001a)], evolutionary

and genetic algorithms [e.g., genetic algorithm for rule-set prediction (GARP) (Stockwell and Peters 1999)], and other machine-learning methods or machine-learning–statistical hybrids [e.g., boosted regression trees (Friedman et al. 2000; Elith et al. 2008)] can be used to model and predict complex, non-linear relationships between invasive species and their environments (Elith et al. 2006; Olden et al. 2008). Instead of assuming a particular data model between predictors and the response, machine-learning models use algorithms to learn from, and describe relationships in, the data at hand, which often increases predictive accuracy but decreases interpretability (Breiman 2001b). Maximum entropy models (MaxEnt) begin with the assumption of uniformity (i.e., maximum entropy) in invasive distributions, apply weighted constraints to the distribution that are based on response–predictor relationships, iteratively adjust constraint weights until the optimal distribution (i.e., maximum distributional entropy given constraints) is reached, and generate spatially explicit predictions based upon it (Phillips et al. 2006; Elith et al. 2011). Because of the computational skills required to apply machine-learning techniques, in addition to their general lack of interpretability, they are used less often than expected (Elith et al. 2008; Olden et al. 2008).

The large number of correlative techniques available for modeling invasive species distributions creates a need for procedures that rank alternative techniques or obtain some level of consensus among their outputs. Ensemble modeling is an approach that reduces inherent uncertainties in model technique selection by varying initial model conditions, fitting various models to the data, and assessing the variability in their predictions, so that some degree of consensus among the results of alternative techniques can be reached (Araujo and New 2007; Roura-Pascual et al. 2009; Buisson et al. 2010; Elith et al. 2010).

Presence/absence and presence-only techniques

Models built with presence/absence data are hypothesized to be better than presence-only techniques for estimating realized niches, while presence-only techniques better estimate fundamental niches (Jimenez-Valverde et al. 2008; Sutherst and Bourne 2009). Although a wealth of valuable information exists in presence-only data (Graham et al. 2004; Soberon and Peterson 2005), its use for iSDM construction can

present challenges, one of which is spatial bias toward locations or environments that are easy to sample and/or highly suitable for invaders (Austin 2002; Phillips et al. 2009; Jimenez-Valverde et al. 2010). Nevertheless, various modeling techniques support presence-only data (Tsoar et al. 2007; Phillips et al. 2009), and some of them (e.g., MaxEnt and GARP) may be cautiously applied to extremely small datasets (Hernandez et al. 2006; de Siqueira et al. 2009; Marcer et al. 2012). The ability to model invasive species distributions with such minimal data could be useful for informing management and monitoring (i.e., step 9) when invasives are just beginning to spread. For presence-only invasion data in the form of ordinal classifications (e.g., minimal, moderate or maximum degrees of infestation), fuzzy set theory can assist with quantification (Eiswerth and van Kooten 2002).

In presence/absence analyses, the characteristics of absence records influences niche delineation. For example, truly uninhabitable locations in an invasive species' range contribute more useful information for niche determination than absences resulting from other phenomena (e.g., failed dispersal) (Lobo et al. 2010; Jimenez-Valverde et al. 2011)—which may be explained with mechanistic modeling techniques (e.g., metapopulation models). Presence records, even when analyzed collectively, may not represent the full range of conditions in which an invasive species can persist, as is the case with the red-imported fire ant (*Solenopsis invicta*), which continues to expand its fundamental niche in invaded ecosystems (Morrison et al. 2004). Alternatively, invasive species presence records may represent less than ideal conditions (i.e., areas where the species has invaded but is not likely to persist). For these reasons, presence/absence data from locations at or near thresholds of invasive species persistence are especially useful for delineating niche boundaries. In any case, it must be ensured that the reliability of observations is not compromised by georeferencing (Jimenez-Valverde et al. 2010) or detection (Chambert et al. 2015) errors.

Autocorrelation supervision (step 7)

Invasive distributions are not driven solely by environmental dependencies or biotic interactions; they may also be autocorrelated at different spatial and temporal scales. Autocorrelation means that proximate entities tend to be more similar than distant ones,

and that species occupancy at one location or time may be influenced not only by conditions there, but also by those at surrounding locations or times (Table 1; Legendre 1993). Although it is an inherent property of ecological systems and is commonly observed in nature (e.g., environmental patchiness and gradients), autocorrelation violates the independence assumption of many statistical techniques and can distort model predictions by over- or under-emphasizing predictor effects (Diniz-Filho et al. 2003; McPherson and Jetz 2007). Considering the causes and effects of autocorrelation is especially relevant to iSDM development, because spatial patterns in invasive distributions are often strongly influenced by dispersal and colonization (Vaclavik et al. 2012).

Autocorrelation management improves the predictive performance of distributional models (De Marco et al. 2008; Vaclavik et al. 2012). Managing autocorrelation entails either incorporating predictors that quantify spatial and temporal influences on responses (Keitt et al. 2002; Maggini et al. 2006), adopting modeling techniques (i.e., step 6) that account for autocorrelation effects, or ensuring that the minimum distance between observations is greater than the minimum distance at which the effects of autocorrelation are observed (Guisan and Zimmermann 2000). For example, the processes of dispersal and colonization can be incorporated into iSDMs via interacting particle system models (Smolik et al. 2010), which focus on the effects of spatial dependencies in the spread of invasions and other phenomena. Similarly, the adoption of mixed effects models can capture spatial dependencies through the estimation of random effects terms in hierarchically-organized datasets (Hartley et al. 2006). Methods for assessing autocorrelation in datasets include calculating semivariance and the Moran's I coefficient at multiple, between-observation distances or times, plotting those values in semivariograms and correlograms, respectively, and examining changes in them over space or time (Cablak et al. 2002).

Prediction, validation, and mapping (step 8)

Predictions of invasive species distributions—including vector pathways, colonization sites, and spread—may be produced for study areas and/or extrapolated to new areas that did not contribute data to model training (Miller et al. 2004). In either case, predictions

may be used in coordination with geographic data in geographic information systems (GIS) to generate continuous predictive maps (Kearney 2006; Jimenez-Valverde and Lobo 2007; Freeman and Moisen 2008). Ecological differences, modeling errors, and/or mismatches in environmental change or scale assignment may contribute to dissimilar predictive accuracies between training and extrapolation sites (Englund and Cooper 2003; Williams et al. 2007; Fitzpatrick and Hargrove 2009), with the geographic extents of extrapolated distributions often being underrepresented under novel conditions (Jimenez-Valverde et al. 2011).

Model validation involves using independent observations (i.e., data not used for model training) to assess the overall performance and application potential of a model (Stauffer et al. 2002). When sufficient data is available, observations may be randomly or spatially subset into training and testing datasets, whereas bootstrapping, jack-knifing, and cross-validation procedures may be utilized with smaller datasets (Guisan and Zimmermann 2000; Hortal et al. 2007). Spatially subset—instead of randomly subset—k-fold cross-validation procedures may be especially useful for validating iSDMs (Hartley et al. 2006; Fitzpatrick et al. 2007; Jimenez-Valverde et al. 2011), as they allow for comparisons of predictive ability among locations. Other common iSDM validation tools include receiving operator characteristic (ROC) plots, area under the curve (AUC) statistics, and Kappa statistics (Cohen 1960; Manel et al. 2001; Latimer et al. 2006), which, despite their popularity, should be used cautiously (Peterson et al. 2008; Lobo et al. 2010; Gogol-Prokurat 2011; Beale and Lennon 2012). Errors of omission and commission, weighted confusion matrices (Boone and Krohn 2002; Peterson et al. 2008), and expert opinion (Ferrier et al. 2002) may also be used for validation. For iSDMs, errors of omission are likely to be more detrimental than errors of commission (Ward 2007; Jimenez-Valverde et al. 2011), because failing to predict invasive occurrences decreases preparedness in combating them, and commission errors may simply represent locations where an invasive has not yet reached, but eventually will (Guisan and Thuiller 2005). Jimenez-Valverde et al. (2011) recommend placing greater emphasis on successfully predicting presences rather than absences, as the most useful iSDMs tend to exhibit high predictive success with low omission error rates (Ward 2007).

This is a primary focus during early iterations of the adaptive iSDM framework.

Management and monitoring (step 9)

Invasive distribution predictions can be used to direct management actions aimed at preventing, eliminating, or minimizing biological invasions and their effects (Sakai et al. 2001). The exact utilization of predictions depends on decisions made during prior framework steps, such as “invasion characterization” (i.e., step 1) and “objectives statement” (i.e., step 2). Because invasive populations may be established and widespread in areas where models satisfying the species–environment equilibrium assumption are trained, iSDM contributions to management in these areas could include quantifying and mapping risks posed to species and communities of conservation concern (Tulloch et al. 2015). This can be accomplished by applying iSDM predictions to spatial risk assessments, in which the distributions of invasive species are overlaid and compared with those of species of concern, in order to identify areas of co-occurrence (Miller et al. 2011; Allen et al. 2015). In non-surveyed areas, risk assessments may be supplemented by prioritizing locations for preventative action, according to estimates of where invasions have not yet occurred, but are likely to occur in the future (Hobbs and Humphries 1995; Sakai et al. 2001), or where detrimental effects are expected to be greatest (Iacarella et al. 2015). Realistic predictions of future invasion events must take into account the effects of climate change on invasive species. The accuracy of these predictions can be improved by considering invasive species distributions at multiple, instead of single, time horizons (Bertelsmeier et al. 2013).

Using iSDM predictions to direct invasive species monitoring can increase knowledge about invasions and their consequences, especially when information is minimal or absent (Raxworthy et al. 2003; Bourg et al. 2005; Jarvis et al. 2005; Guisan et al. 2006; de Siqueira et al. 2009; Brummer et al. 2013), as can be expected during the transport, establishment, and early spread stages of invasions. Some invasive species may be considered rare or absent until they pass growth or spread thresholds; however, early detection increases the likelihood of their successful elimination, helps mitigate their detrimental effects, and conserves financial resources (Crooks 2005; Mehta et al. 2007;

D'Evelyn et al. 2008). In general, increasing sampling intensity in an area increases the likelihood of encountering rare invasive species, but it also increases monitoring costs; therefore, prioritizing sites for monitoring, according to species detectability (Venette et al. 2002; Mehta et al. 2007), estimates of optimal invasive species habitat conditions (Iacarella et al. 2015) and prevention expenditures (Leung et al. 2005), and even simple iSDM predictions could substantially reduce the geographic extent and cost of monitoring. Furthermore, the long-term focus associated with monitoring within an adaptive iSDM framework may help reduce temporal biases in sampling and information acquisition (Lobo et al. 2007) through the standardization of monitoring procedures and survey sites. Crowl et al. (2008) call for the development of continental-scale monitoring networks for detecting changes in invasive species distributions, identifying the drivers and consequences associated with these changes, and incorporating small-scale experiments into larger-scale monitoring efforts. Because iSDMs trained with presence/absence data from areas with relatively low abundances of the species of interest tend to overestimate distributions and effects, monitoring may also focus on acquiring data on invasive abundances (Bradley 2013) for use in future framework iterations. Brummer et al. (2013) found that reliable models for well-established invasive species can be fit with transect survey presence/absence data from as little as 0.13 % of landscapes. Thus, the sharing and centralization of even small amounts of information from different landscapes at risk from the same invasive species—through mediums like the Global Invasive Species Information Network (GISIN) (2015) or Global Biodiversity Information Facility (GBIF) (2015)—could increase the robustness of iSDMs for informing management at local and regional scales and contribute to subsequent model improvement (Ricciardi et al. 2000; Simpson 2004).

Model refinement (step 10)

The completion of an iteration of the adaptive iSDM framework requires that novel information from the “prediction, validation and mapping” (i.e., step 8) or “management and monitoring” (i.e., step 9) steps of that iteration be applied to iSDM improvement at any or all of the first eight steps of the framework during

subsequent iterations (Fig. 2). Therefore, although represented as a distinct step at the end of each framework iteration, this step is actually carried out in one or more steps of the following iteration. The time between framework iterations may affect the usefulness of novel information for directing management and improving iSDMs. For example, long lags between the generation of predictions in step 8 and the implementation of management or monitoring in step 9 may allow time for substantial changes in invasive populations, such as transitions between invasion stages or further spread, to occur in invaded ecosystems, thereby decreasing the value of the information obtained (Conroy et al. 2011).

Novel information need not precipitate a major shift in modeling techniques or predictions, although more drastic adjustments may occur during earlier iterations. For instance, accounts of management actions undertaken may constitute new information, as they have the potential to substantially influence invasive distributions (e.g., manual removal causes absence from suitable habitat). Ultimately, the nature of refinements will depend on decisions and factors addressed in previous framework steps, including study objectives (i.e., step 2), adopted modeling techniques (i.e., step 6), and resources devoted to monitoring (i.e., step 9), as well as collaboration among managers in space and time.

Discussion

We have presented an adaptive framework for constructing niche-based iSDMs that: promotes consistency and transparency in model development (Elith and Graham 2009); allows for changes in invasive drivers and filters in space and time (Theoharides and Dukes 2007); integrates mechanistic and correlative modeling techniques (Gallien et al. 2010, 2012); balances the avoidance of type 1 and type 2 errors in predictions (Holling and Allen 2002); encourages the standardization of monitoring, as well as the direct linkage of monitoring and management (Crowl et al. 2008); and facilitates incremental improvements in model predictions by addressing critical uncertainties (Conroy et al. 2011). Such a framework is needed, given the current state of rapid environmental change and the high levels of uncertainty that characterize biological invasions (Flanagan

et al. 2015). The implementation of this framework will increase the legitimacy and utility of iSDMs over time. For example, initial fundamental niche approximations for invasive species—which are often based on statistical correlations between invasive species occurrences and their surroundings—may be supplemented with mechanistic representations of demographic processes (e.g., spread) that are important for describing their realized (i.e., actual) niches during subsequent iterations. It is the capacity for continual improvement in iSDM predictions—even in spite of the violation of basic modeling assumptions (Gallien et al. 2012)—that makes adaptive modeling approaches valuable.

One of the greatest challenges to successfully modeling invasive species stems from the fact that many spatial modeling techniques require that species be at equilibrium with their environments. Not only is the achievement of environmental equilibrium difficult to detect and likely to be further complicated by ongoing global change, confirming that an invasive species has reached equilibrium means that the opportunities for preventing that invasion have already passed, and that the prospects of successful control and elimination are likely to be logistically and/or financially daunting—even infeasible. Additional challenges result from reactive, rather than proactive, approaches to invasive species modeling, monitoring and management, as well as insufficient cooperation and communication on the occurrence and risk of biological invasions across space, time and institutional boundaries. This lack of preparation and coordination effectively restricts invasive species management to scales smaller than those at which invasions typically occur and affect ecosystems and economies, a limitation that is especially concerning in light of the prospects for continued invasions and niche infilling worldwide (Webber et al. 2012; Bradley et al. 2015). We posit that incremental innovations and advances in these regards can be made via the utilization of adaptive iSDMs.

Ideally, the adaptive iSDM framework of continually evaluating and improving model predictions with new information will help detect and explain changes in invasive species populations, increase the relevance of models by promoting their continued application to future modeling projects, and lead to the improvement of invasive species management and monitoring across the entirety—or at least large proportions—of invaded ranges. This is likely to

involve the prioritization of sites for management and monitoring, according to spatially explicit predictions of invasive effects (Allen et al. 2015; Iacarella et al. 2015; Tulloch et al. 2015) and financial considerations (Leung et al. 2005). In essence, the framework provides a means for not only improving small-scale invasive species modeling, management and monitoring, but for collectively using ever-improving predictions to combat invasions at the large spatial and temporal scales at which they may occur. To meet these challenges, the framework can be implemented at a number of institutional levels. For instance, many countries have invasive species councils at national, state or provincial levels, which, working in conjunction with management agencies, are a logical home for implementing and directing adaptive iSDMs. We encourage future studies to apply, scrutinize and refine our proposed iSDM framework, as well as modify it to explain and predict native species' distributions under present and putative future environmental conditions.

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